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ASPECTS OF THE ECOLOGY OF BLACK BEETLE (HETERONYCHUS ARATOR (F.), COLEOPTERA : DYNASTINAE)

A thesis

submitted in partial fulfilment

of the requirements for the Degree

of

Doctor of Philosophy

at the

University of Waikato

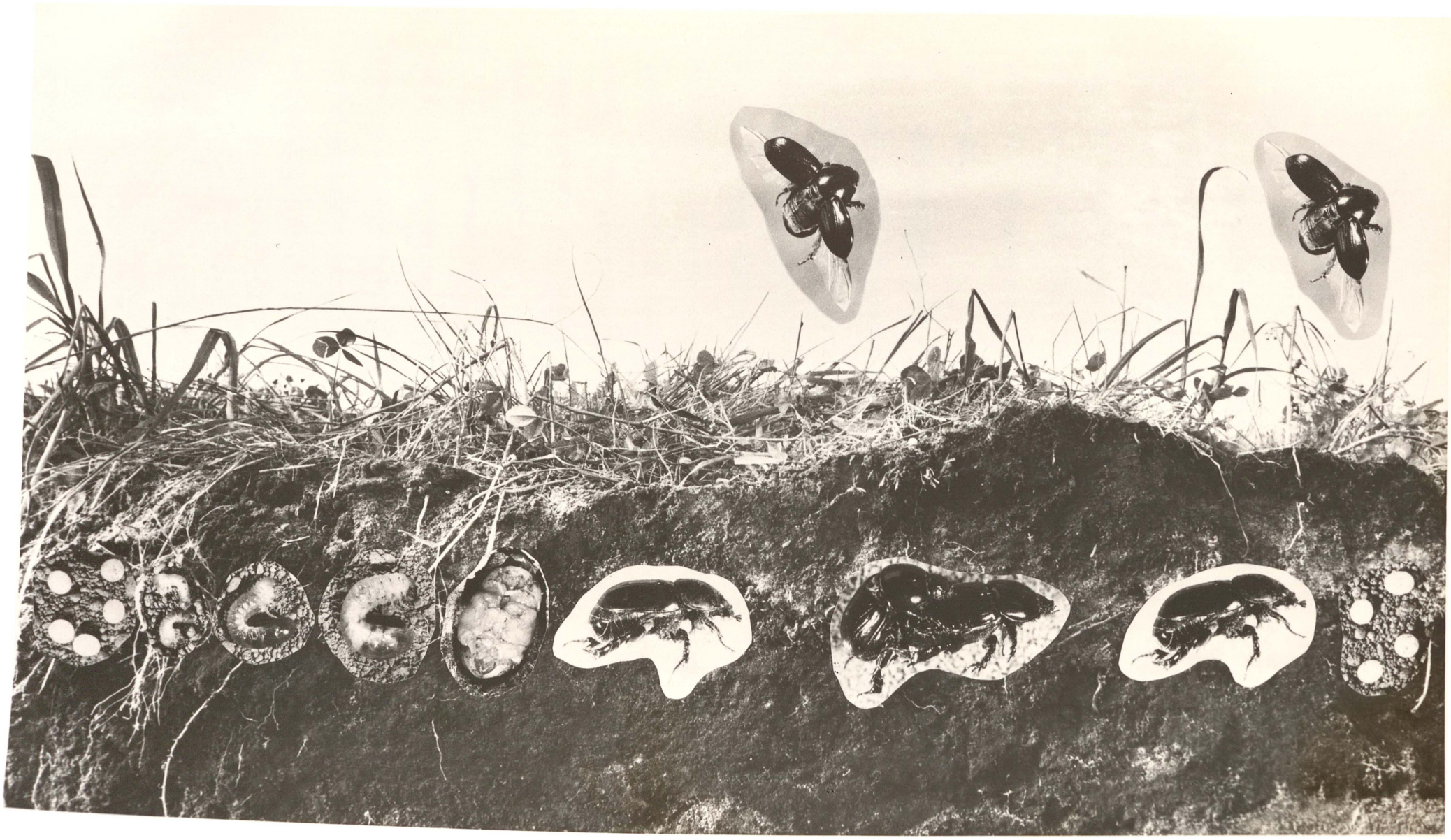
by

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1979

Stages in the life cycle of Heteronychus arator F. over one generation. From left to right; eggs, first instar larvae, second instar larva, third instar larva, pupa, adult, adult autumn flight, mating adults, over-wintering adult, adult spring flight and eggs in spring. (The life stages are not shown to scale.)



ABSTRACT

The study included laboratory and field studies of the ecology of the black beetle (Heteronychus arator F.) pre-adult and adult stages and field studies of population dynamics. The objectives were to understand population change and regulation, particularly in relation to host plant species and explore the possibilities of the prediction of outbreaks in order to rationalise the use of control strategies.

Whereas eggs were relatively tolerant to a range of soil moisture conditions, first instar larvae were very susceptible to extremes in soil moisture. In comparison to temperate scarabs, relatively high temperatures were necessary for optimum egg viability, larval feeding, utilisation, growth and survival. Adult oviposition preference, fecundity and survival, and larval food consumption, growth and survival were all influenced by the pasture plant species eaten. All grass species tested with the exception of phalaris were favourable for population growth while phalaris and the legumes tested were unfavourable.

The dynamic nature of the life cycle, the relatively low population densities and dispersal of adults made estimation of populations with reasonable levels of precision difficult. Life tables were constructed which quantified individual and generation mortalities, and identified the key factors causing population change. These were variation in natality, summer mortality and/or winter-spring disappearance. Significant relationships were found between key mortalities and the level of population development which in turn was related to spring and summer temperatures.

Two very different types of population dynamics were evident. Populations in paspalum pastures which are tolerant to feeding damage were relatively stable. These pastures act as refuge areas during adverse climatic conditions. In contrast, population development was more rapid and large population decreases occurred between autumn and spring in ryegrass based pastures which were less tolerant of damage. Ryegrass based pastures appear to be favourable habitats during spring and summer only, and adult immigration in the spring is necessary for populations to reach high levels. Since spring migration only occurs in warm years, outbreaks in ryegrass based pasture are sporadic.

A population model was constructed which used mean daily air temperatures in September, October and November to simulate population densities over a 23 year period from temperature records. The prediction of high population numbers showed good correlation with years of previous outbreaks. Some density dependence was found to be necessary in the model for paspalum pasture indicating the occurrence of population regulation. It was concluded that except in years of high population numbers, population regulation does not occur in ryegrass based pastures.

Rationalisation of control strategies was discussed in the light of the differences in the two types of population dynamics and the prediction of outbreaks.

This research has revealed the necessity for a well designed population study in order to understand the manner in which mortalities operate and the way they affect numbers. As the first attempt at a quantitative ecological study of black beetle, the results have provided some understanding of black beetle ecology and suggested further areas for investigation.

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GENERAL INTRODUCTION

I THE BLACK BEETLE PROBLEM IN NEW ZEALAND

Exports from pastoral farming provide the major portion of New Zealand's overseas income. Insect pests which affect pasture plants and hence the grazing animal are therefore major agricultural problems. With the notable exceptions of grass grub Costelytra zealandica(White) and porina Wiseana spp., the major pests in New Zealand are of exotic origin.

Black beetle Heteronychus arator F., a voracious root feeder on graminaceous plants, is of African origin. Since the initial identification of black beetle in New Zealand in 1937, the insect has spread rapidly through the northern area of the North Island of New Zealand. Although occurrences of black beetle in epidemic proportions are sporadic (Todd, 1959), in years of high population numbers severe damage is done to pastures and crops. The problem is accentuated by the very catholic feeding habits of black beetle which are evident in the long list of plants susceptible to attack (Atkinson et al., 1956; Todd, 1959; Esson, 1973).

By the 1950's, reports from farmers and advisors of black beetle causing widespread pasture damage prompted a programme of research into control measures for the pest, undertaken by Entomology Division, D.S.I.R. The introduction of the persistent organo-chlorine insecticide, dieldrin, resulting from this research gave satisfactory control of black beetle until the use of the material was prohibited in 1967. Following the loss of this insecticide to the farmer, further rapid spread of black beetle occurred (Esson, 1973) after

several years of climatic conditions favourable for population increase. Severe pasture and crop damage was reported in the North Auckland peninsula, South Auckland, Waihi, the Bay of Plenty and Waikato (White, 1972).

Pasture damage from black beetle larval root feeding was particularly severe in coastal areas where soils were light and sandy, and in peat soils (Todd, 1959; Merry, 1964; White, 1972). Watson and Webber (1975) recorded that germinating maize crops were severely damaged by adult black beetle in spring often necessitating replanting of the crop in Northland and Waikato. Esson (1973) reported that adult damage to kumara tubers in the Ruawai district of Northland had reached very serious levels.

In their review of the black beetle and black field cricket, Teleogryllus commodus Walker, problem in Northland, Reynolds and Langton (1973) considered black beetle was the more serious problem of the two because of its wider habitat acceptance and the difficulty in obtaining economic control. Although it is difficult to separate the effects of black beetle damage occurring in dry years from the direct effects of drought, Reynolds and Langton summarised the effect of black beetle and crickets on individual farms in Northland as follows:

"(1) A reduction in overall carrying capacity of approximately 30% on severely infested farms (15 stock units down to 11 stock units per hectare).

(2) A drop in animal performance and a forced change to selling store stock rather than fat stock.

(3) A loss of paspalum from the pasture resulting in a greater need for summer feed crops.

(4) A resultant need for a pasture renewal programme.

(5) Added costs for controlling weeds.

(6) A greater incidence of facial eczema (Pithomyces chartarum) as a result of harder grazing over the summer.

(7) The loss of the turf mat resulting in a wetter soil, problems in wintering cattle, and loss of soil structure".

Reynolds and Langton concluded that the resultant added costs and lower production amounted to an overall estimated loss of $5 million per annum in Northland. In addition, because of increased workloads and the worry of difficult decision making, Northland farmers suffered greater management related stress. Estimates of the costs of black beetle damage must be "guesstimates" in the absence of detailed damage assessment studies and economic analysis. The magnitude of the black beetle problem in years of severe pasture damage in New Zealand as it affects the pasture economy has been aptly expressed by Reynolds and Langton: "there can be no doubt that black beetle attack can turn an otherwise dry summer period into an effective drought". In addition, black beetle damage through the removal of grasses from pasture, can affect carrying capacity in summer dry years for many years afterwards.

II OBJECTIVES OF THE STUDY

Research within the Ministry of Agriculture and Fisheries on the control of black beetle in pastures commenced in 1973, following representations from the agricultural producer organisations. The study reported in this thesis was undertaken by the author during a period of full time study leave from the Ministry for a D. Phil. degree from 1975 to 1979.

The need for long-term ecological research to allow the basis of insect pest control to proceed from an ad hoc level to a rational level, based on a detailed understanding of pest ecology, has been stressed by many authors (e.g., Varley, 1960; Richards, 1961; Chant, 1964; Milne, 1965; Clark et al., 1967; Pottinger, 1967; Springett, 1970). Kain (1978) in reviewing the insecticidal control of pasture pests in New Zealand noted that the high cost of these controls and the practical limitations imposed by their chemical and biological characteristics had meant that control of pasture pests cannot rest solely with insecticides. These problems have increased interest in the use of pest management systems which combine all possible control tactics. Such an approach however, is dependent on a detailed knowledge of the biology and ecology of the pest species.

Prior to 1973, little was known of the ecology of black beetle, as most research had been directed to providing ad hoc controls. For this reason, the primary objective of the studies reported here was to investigate aspects of black beetle ecology which would aid in an understanding of the population dynamics of the insect and highlight the sensitivity of the pest to controls based on the manipulation of the physical and biotic environment. For this reason aspects such as soil moisture and temperature shown by earlier work in New Zealand on grass grub to be important (e.g. East, 1972; Kain 1975) were examined. An intensive study of all the mortality factors such as has been undertaken for the Australian pasture scarabaeid complex (e.g. Davidson et al., 1972a,b; Hassan and Hilditch, 1976) was not attempted however. Emphasis was placed on an examination of the effects of different pasture species on the

ecology of black beetle larvae and adults with the aim of investigating the possibility of using resistant and/or tolerant pasture species against black beetle.

As part of the objective, the population dynamics of black beetle in pastures of different species composition were investigated to monitor the effect of the pasture on populations over several generations, as moderated by the influence of seasonal conditions. Although the importance of the three major pathways of population change were recognised, namely natality, mortality and dispersal, intensive research on the dispersal of black beetle adults was carried out by another worker, R.N. Watson.

In summary, the aims of the study were to provide ecological information that would explain why different pastures supported varying black beetle densities, and so allow identification of those pastures at risk from black beetle damage. Further, a greater understanding of the factors responsible for determining population change and regulation would allow some rationalisation of the use of *ad hoc* control measures into a more integrated and efficient approach.

The results of the study are presented in three main sections: the ecology of the pre-adult stages, that of the adult stage and finally black beetle population ecology. The first two sections were largely carried out as laboratory and small field plot studies while the population studies involved intensive sampling of black beetle populations in large field plots.

SECTION 1

REVIEW OF THE LITERATURE

CHAPTER 1

LITERATURE REVIEW ON THE BIOLOGY AND ECOLOGY OF BLACK BEETLE

I INTRODUCTION

Prior to 1970 there was little published literature dealing with black beetle ecology. In New Zealand this was primarily a reflection of the preoccupation of researchers such as Todd with the development of short-term control measures and in particular, the great efficacy achieved with the persistent insecticide dieldrin. The relative absence of reported research from South Africa and Australia where black beetle also occurs, is probably the result of the insignificant nature of the insect as a persistent, economically important pest in these countries. Recently studies have been made in New Zealand by Johannesson (1975) of some aspects of adult black beetle ecology, and by Archibald (1976) of the influence of pathogens on black beetle populations.

To provide a background to the further investigation of the ecology of black beetle, all relevant literature has been reviewed and is summarised in this chapter. The systematic position and distribution of black beetle are presented as an introduction, followed by a detailed coverage of the bionomics of the insect under the headings of seasonal history, morphology, adult sexual development, mating, oviposition and fecundity, flight and dispersal, over-wintering, stridulation and habitat preferences.

This reveals deficiencies in the information available on general larval ecology in addition to some aspects of adult ecology,

particularly fecundity and oviposition behaviour and the interaction of pasture plants with these parameters. The influence of pathogens, parasites and predators on black beetle is also reviewed. Finally, as the major aim of the thesis research was to provide information which could be used in the development of controls for the insect, the literature dealing with the pest status and control of black beetle is briefly examined.

II SYSTEMATIC POSITION

The systematic position of black beetle has been the subject of considerable confusion. This has largely arisen from different interpretations of the species *Scarabaeus arator* described by Fabricius in 1775. Landin (1964) compiled a historical review of the identity of *S. arator* Fabr. which he designated the neotype of black beetle.

In 1801, Fabricius listed "*arator*" under the genus *Geotrupes* although it was reintroduced into the genus *Scarabaeus* by Illiger in 1803. Burmeister (1847, cited in Landin, 1964) used authentic Fabrician material to give a detailed description of the genus *Heteronychus*, so validating this name (previously an invalid *nomen nudum* introduced by Dejean, 1833), and ranged *arator* under *Heteronychus* having synonymy with *G. arator* Fabr. 1801. Wollaston (1869, cited in Landin, 1964) listed *H. sanctae helenae* Blanchard as synonymous with *H. arator* Fabr. and Jack (1924, cited in Landin, 1964) in revising the *Heteronychus* genus considered *H. transvaalensis* Peringuey synonymous with *H. arator* Fabr..

Following the outline of Crowson (1955) of the classification of Scarabaeidae and the evidence of Landin (1964), the taxonomic position of black beetle as accepted today is as follows:

Order	Coleoptera Linnaeus
Family	Scarabaeidae Latreille
Sub-family	Dynastinae Arrow
Tribe	Oryctini Le Conte and Horn
Genus	Heteronychus Burmeister
Species	H. arator (Fabricius, 1775; nec Illiger, 1803)
Syn.	S. arator Fabr., 1775
	H. arator Burm., 1847
	H. sanctae helenae Blanch., 1853
	H. transvaalensis Pering., 1901

III DISTRIBUTION

Members of the Dynastinae have predominantly warm climate affiliations. The genus Heteronychus consists of 45 species endemic to the Ethiopian zoo-geographic area, with one endemic Paleartic species (Endrodi, 1974) and seven species endemic in the Asian region (Endrodi, 1969). Endrodi (1974) notes that of these, only H. arator appears to have established outside its natural range of Africa, occurring in Australia, New Guinea, Central and South America as well as in New Zealand.

The first record of the species near South Africa seems to be that of Wollaston (1869, cited in Harrington, 1964) who reported that "the South African H. arator appears to be common at St Helena

where it was taken ... in 1860." Harrington (1964) notes that the account of Peringuey (1901-1903) seems to be the first reference to the species in South Africa, although it was probably well established before that date, and its presence in South Africa before 1860 is implicit in the remark of Wollaston. Jack (1924) recorded the species from Southern Rhodesia, Northern Rhodesia, Belgian Congo, Kenya, Tanganyika and Abyssinia. Todd (1959) gave an unsupported report of its occurrence in Madagascar.

The earliest record of black beetle in Australia is a specimen collected near Newcastle, N.S.W., in 1920 (Wright, 1958), but it is likely that it became established after an unknown introduction several years previously. Gurney (1934) first noted H. arator as a pest in N.S.W., and Wright (1958) reports that since 1920 it has spread over practically the whole length of the N.S.W. coast. Harrington (1964) records that it was first seen in Western Australia, at Albany in 1938 and is now widespread in the Perth area. In 1949 it was found near Adelaide, (Britton, 1951).

Black beetle was first recorded in New Zealand in March 1937, from Waiheke Island in the Hauraki Gulf (Spiller and Turbott 1944). Once again, the means of introduction are unknown. The spread of the insect has been rapid as shown by Watson (1978) with successive surveys reporting establishment both north and south from the Auckland region (Todd, 1959; Esson 1973; Watson, 1978). Although establishment has occurred in Taranaki, the present distribution is still confined to the northern, warmer areas of the North Island, with the southern limits of occurrence corresponding closely to the isotherm of 12.8 ^{o}C mean annual surface temperature

(Watson, 1978). Brown (1964) records the taking of a single adult female at Cass, near Arthurs Pass in 1958, and the collection of four adults (two female) from a garden at Heathcote Valley, Christchurch in 1963 which were identified as H. arator. Although these specimens were placed in the collection of the Entomology Department, Lincoln University College of Agriculture, their present unknown location prevents verification of this identification. In view of the more recent identification of the red-headed pasture cockchafer Adoryphorus couloni from Bank's Peninsula, Thomas (pers. comm.) considers that this insect may have been the wrongly identified H. arator of Brown (1964).

IV BIONOMICS

(1) Seasonal history

The seasonal history of black beetle has been reviewed in detail in South Africa (Taylor, 1951; Harrington, 1953), in Australia (Cumpston, 1940; Wallace, 1946; Wright, 1958) and in New Zealand (Todd, 1959; Esson, 1973). Major differences in the seasonal history between New Zealand and the other two countries appear to be largely an effect of lower soil temperatures in New Zealand. Overwintering adults become active in spring from late September to November and commence egg laying a few weeks later. This is up to a month later than for southern South Africa (Petty, 1976) and N.S.W. (Wright, 1958), although similar to Adelaide (Anon, 1959) and the South African high veld area (Taylor, 1951). The onset of spring flight in New Zealand is also a month later than that in N.S.W. (Nikitin, 1967).

This delay in development is maintained through the summer and is expressed in a corresponding lag in the onset of adult emergence in autumn in New Zealand (Watson, 1978). This is a month behind southern South Africa (Petty, cited in Watson, 1978) and N.S.W. (Nikitin, 1967).

In New Zealand, Todd found eggs in the soil at a study site at Hahei on the east coast of the Coromandel Peninsula from mid-October until early January. The incubation period is about six weeks, early in the season, but probably decreases later when higher soil temperatures are normally experienced. Larvae pass through three instars before pupating. New generation beetles emerge during March, April and May with a small number appearing in February. During warm autumn evenings massed flights of adults occur in heavily infested areas in New Zealand, which Todd considered acted as dispersal flights.

By June, most adults have become dormant, and remain in this condition throughout the winter. Todd considered adults resume feeding in spring. Johannesson (1975) however found that from examination of crop smears, adults fed throughout the year. After oviposition in the spring, Todd notes that there is a gradual decline in numbers of adults. He did not mention spring flight, but Johannesson, Watson (1978), and King (unpublished data) all noted adult flights in September and October, although of lower numbers than in the autumn.

Todd found only one generation per year, although owing to a certain amount of overlapping during the season, it is usual to find larvae present in the population which is predominantly in the adult

stage during the winter period. He described this as a late compound brood which is non-synchronous with the main generation. Todd concluded that as a result of varying climatic conditions and seasonal trends, there are probably some variations in the life cycle of black beetle from one season to another and from place to place. Esson showed that there was considerable variation between sites from Awanui to Whangarei, with late development in peat soils. He concluded however that variations in the rate of development seemed to depend very much more on the physical and microclimatic conditions of a particular site (e.g. aspect), than on geographical location. Watson (1978) noted a delay of 3-4 weeks in population development between the favourable years with warm springs of 1973-1975, and the unfavourable years of 1977-1978, which was related to the delay in the rise of temperature in the spring.

(2) Biology and Morphology

Cumpston (1940) described in detail the morphology of all stages of black beetle, and the general biology was reviewed by Cumpston (1940), Taylor (1951), Harrington (1953), Wright (1958), Todd (1959) and Johannesson (1975).

(a) Morphology

The newly emerged adult is a chestnut colour, but soon changes to a glossy black. The female is about 1.4 cm long, and in most cases, the male is slightly smaller. The sex difference is readily detected by the shape of the fore tarsus: in the female the segments are elongate and narrow, in the male they are relatively short and broad. Cumpston (1940) and Johannesson (1975) also

describe variation in the arrangement of the sclerites between the sexes.

The egg is at first ovoid, white to creamy white in colour and about 2 mm in length, but during incubation swells and becomes almost spherical before hatching. The head capsule of larvae is light brown, the body is creamy-white or greyish-white except for the hind segments which appear black where the contents of the hindgut show through the integument. Fully grown final instar larvae are about 2.5 cm long and are uniformly creamy-white in colour as the gut contents are evacuated prior to pupation (the pre-pupal stage). The pupa is at first pale yellow, but changes to reddish-brown before the adult emerges.

(b) Adult sexual development

Todd (1959) found that female black beetle adults were in an unfertilised state from April until July, but that dissections made in October at the start of oviposition showed all females were fertilised and ovaries developed. Todd's conclusion that mating took place in the spring suggests that the mated condition was a precursor to ovarian development (O.D.). Mercer and King (1976) found that O.D. was seasonally influenced however, becoming progressively more advanced over the winter period. They proposed a five stage O.D. ranking scheme where in Stage 1, the teneral adult stage differentiation within the ovariole was not apparent and in Stage 5, the pre-oviposition stage, ripe oocytes were visible in the ovarioles and/or the calyces and oviducts. Mercer and King found that in the autumn, newly emerged adults were sexually undeveloped,

and although mated individuals were noted in May, full sexual development was not reached until September.

In a concurrent study of black beetle female O.D., Johannesson (1975) also proposed a five level scheme to describe sexual maturation. At Stage 1, the ovarioles were without apparent differentiation of oocytes from the prefollicular tissue as in the Mercer and King ranking, but ranks 2 - 5 in their scheme were compressed to 2 - 4 in that of Johannesson. Ranking 5 of Johannesson related to the stage of development where most of the ovarioles had at least one occyte which was white and shiny due to the presence of the chlorion, but contained no oocytes of an earlier stage of differentiation. Females at this level were described as being in the final stages of egg laying.

The pattern of sexual development found by Johannesson was similar to that described by Mercer and King with females immature on emergence, but with most not reaching the Stage 5 level of the former author until November. The proportion of mated females was also found to increase throughout the year. Johannesson found males contained motile sperm throughout the year.

The condition of the fat body of the female, determined by visual ranking on a 0 - 5 scale, was low in the autumn after adult emergence, reached a maximum in mid-May and then declined from September, coinciding with the formation of mature eggs (Johannesson). Johannesson collected samples of 50 females from pasture in March, July and November. These were air dried over silica gel and the phospholipids, neutral fats, fatty acids and other ether soluble substances of the insect fat body were then extracted by petroleum

ether in a Soxhlet over 24 hours. Johannesson found % fat levels (air dried basis) of 1.76%, 11.15% and 7.89% respectively in females at the three sampling occasions. This result followed the pattern determined by visual ranking and suggested a decrease in fat levels with increasing O.D. over the winter, spring period.

(c) Mating and oviposition

Cumpston (1940), Taylor (1951), Harrington (1953) and Johannesson (1975) all found that copulation takes place beneath the soil. Harrington noted that this had been observed to last as long as 12¼ hours, and Johannesson found that in the laboratory beetles remained linked for 12-16 hours. No form of courtship was observed by Johannesson, and Hutchings (cited in Johannesson, 1975) found no evidence to suggest the presence of a sex pheromone in mating behaviour.

Johannesson found that the spermatophore, when transferred from the male to the bursa copulatrix of the female during mating is never extruded, but simply pushed to the distal end of the bursa. A similar situation was shown to occur in Melolontha melolontha Fabr. by Landa (1960). Chitinous teeth in the bursa copulatrix rupture in the spermatophore and sperm is released for storage in the spermatheca (Johannesson). Multiple matings occurred (Johannesson), and the presence of the disrupted spermatophore in the bursa copulatrix 6-8 months after mating allowed a measure of the degree to which this occurred. Although Johannesson found that females were mated between 1 - 6 times in the laboratory over a 50 day period, only 16% of females collected from the field at the spring flight period had mated twice. Johannesson found sperm in the spermathecae

of all females with spermatophores, and so used the presence of a spermatophore in the bursa copulatrix as an index of the ability of the female to lay fertile eggs. Collection of females however, from a field population in the spring by Johannesson indicated that 17% were sterile as evidenced by poor ovarian development (stage 2) and their having virtually no fat body.

Females of black beetle were shown by Cumpston (1940) and Todd (1959) to always lay eggs singly in the soil, either freely or enclosed loosely in a pellet of soil. Todd noted that eggs were usually found approximately 1.5 cm below ground level, although in some cases they had been found at a greater depth.

(d) Fecundity

Cumpston (1940) noted that largest number of eggs deposited by a single black beetle female under insectary conditions, when feeding on maize seedlings, was 90 eggs, laid irregularly over a period of four months from November till the end of February. Taylor (1951) recorded fecundity in the laboratory as 20-80 eggs per female, while Wright (1958) stated that each female beetle may lay from 30 to 60 eggs, suggesting a large range in black beetle fecundity.

(e) Adult flight and dispersal

The crepuscular dispersal flight abilities of black beetle adults have been reported by many workers. Wallace (1946), Taylor (1951), Wright (1958), Todd (1959), Nikitin (1967), Johannesson (1975), Petty (1976) and Watson (1978) described the occurrence of massed flights of adults in autumn and smaller flights in spring in South Africa, Australia and New Zealand. The autumn flights (late

February - April) consist of post-teneral, reproductively immature and usually unmated beetles, prior to the overwintering inactive period (Johannesson, Watson). Spring flight (late September - December) which is also associated with a period of intense feeding activity is more sporadic in New Zealand, and major flights have not been recorded since King (unpublished data) monitored large flights in the western Waikato coastal area in spring 1973 (Watson 1978).

Both Johannesson and Watson found a correlation between rainfall of more than 4 mm and autumn flight, but there was no apparent relationship between rainfall and subsequent spring flight. Watson found that the occurrence of autumn flight was delayed for two to three days following rainfall associated with the passage of a cold front, but occurred on the evening after heavy afternoon thundershowers. A similar situation was noted for flights of Aphodius tasmaniae, the melolonthid, by Maelzer (1961a) in South Australia, and both workers concluded the difference in behaviour was due to evening temperature. The numbers of adults trapped by Watson increased logarithmically with surface air temperatures above a threshold of 17-18 ^{o}C.

Johannesson and Watson found some 75% or more of the total number of adults trapped in one season were caught on four evenings or less, and Watson noted that autumn flights cease once soil temperatures at 1 cm depth fall below 17 ^{o}C at dusk. Adult emergence from the soil commenced 24-33 minutes after sunset when light intensity was at a range of 2-6 lux (Johannesson).

This pattern of black beetle behaviour has similarities to those of other dynastid insects. Taylor (1964) found that a dynastid pest of yams in Nigeria, Heteroligus meles, has two periods of flight; the post-teneral flight in March and April termed the "feeding migration" and a second period commencing in October termed the "breeding migration". The feeding migration is induced by rainfall, with a threshold of around 0.5 inches.

Taylor (1966) reported that the dynastid pest of sugar cane in Nigeria, Heteronychus licus Klug is a nocturnal flier, with two flight seasons during a generation. The first lasts from April to June and is a post-teneral flight of the new generation adults; the second usually occurs in late October and November and is distinctly a pre-reproductive flight (Taylor), but during both flights, beetles are attracted to light. Major flights are associated with recent rain (usually within the last 24 hours) and low mean temperatures (25^{o} - 29^{o}) either on the day of flight or on the day before. Taylor considered that the practical effect of these flights is to enhance the chances of survival and reproduction of the beetles by adequate and timely dispersal. The first flight, occurring after the mass emergence of adults, tends to disperse the beetles at a time when they might suffer from overcrowding in particular sites within a habitat, and affords chances of obtaining adequate and new sources of food. The second (pre-reproductive) flight ensures further dispersal at a time when the species is on the threshold of a substantial increase in numbers.

Adults of the dynastid Pericoptus truncatus Fabr., unlike H. meles and H. licus, have only one flight period, with most flight

occurring in October in both Islands in New Zealand (Dale, 1963). Massed flight has been reported, but Dale concluded the function appeared to be purely distributive and had no connection with mating.

The flight behaviour of black beetle, as with the other dynastids previously mentioned, does not have the feeding or mating function typical of that described for such Melolonthinae as Costelytra zealandica (hereafter referred to in this thesis as grass grub), (Kelsey, 1951; Fenemore, 1965), Phyllophaga horticola (Milne, 1960), M. melolontha (Schneider, 1962), Amphimallon majalis (Evans, 1965), A. tasmaniae (Maelzer, 1961b).

Johannesson (1975) and Watson (1978) consider that the function of autumn flight in black beetle is to take adults from larval feeding areas to adult overwintering areas, and postulate that the function of spring flight is to return the overwintering adults to the larval feeding areas for oviposition. Watson however, acknowledges that autumn flight may also play a significant role in finding new areas for subsequent larval development.

Johannesson was able to demonstrate that high black beetle adult populations in valley floor pasture in March ($10/m^2$) decreased to low levels ($2.5/m^2$) at the end of April after autumn flight, and were $2.0/m^2$ in August. At nearby ridge-top sites, numbers increased from $3.0/m^2$ in March to $38/m^2$ and $67/m^2$ on two sites in August. She postulated that these changes were the result of autumn dispersal flights from larval development areas to adult over-wintering areas. The reverse population trend in the spring, necessary to further develop her thesis on flight was not observed by Johannesson possibly due to the combined influences of disease and changed climatic conditions.

Watson (1978) points out that due to the marginal climatic conditions for black beetle in New Zealand, in most years full expression of the inherent dispersal behaviour is largely inhibited by conditions adverse to flight. Consequently the potential expression of flight behaviour demonstrated for black beetle and other dynastid species in Africa, is rarely achieved in New Zealand in terms of dispersal of populations from one area to another for reproductive and overwintering purposes. Instead, Watson concludes "that flight acts as a biseasonal, opportunistic mixing and redistribution of the population."

(f) Overwintering

Johnson (1968) noted that in many insects which fly for only a short period of their adult lives, the flight musculature degenerates during flightless periods. Johannesson (1975) however found the flight muscules of overwintering inactive black beetles were identical to those caught during spring and autumn flight, indicating the potential for flight throughout the adult life. King and Mercer (pers. observation) noted significant adult flight in mid-June from pasture on a coastal Waikato farm soon after mid-day on hot, humid days when soil temperatures would have been relatively high.

To investigate if the inactive adult overwintering was a temperature induced diapause state, Johannesson maintained females at 27 ^{o}C-30 ^{o}C in a laboratory with abundant food from March to November. Although ovarian development progressed more rapidly than in the field, it still took six months for the production of gravid females.

As feeding and mating took place right through the winter and the state of the flight musculature indicated flight was possible during this period, Johannesson concluded that the inactive overwintering period of black beetle did not comply with the concept of diapause as an endocrine controlled mechanism for surviving adverse conditions. Males are sexually mature and capable of mating throughout the year, in contrast to females which are immature during the winter, although there does not appear to be a single stage of ovarian maturation at which overwintering occurs (Johannesson).

Accordingly, she concluded that the evidence points to females being in a state of reproductive diapause during the winter period. This statement must be open to speculation however, as some sexual maturation of the female still occurred while overwintering took place.

(g) Stridulation

Johannesson (1975) recorded that both isolated and aggregated beetles, male and female, in laboratory and field conditions were heard to stridulate during both day and night throughout the year. Stridulation is produced by the sudden retraction of the abdomen, so that the posterior edges of the elytra are rasped against the pars stridens. This consists of ten double ridges of sclerotization, borne on the unsclerotized part of the propygidium. In view of the opinion that no pheromone is involved in attraction between the sexes Johannesson considered that stridulation is important in aggregating beetles in favourable areas, thus leading to a greater chance of encounter between sexes and mating.

(h) Habitat preferences

Cumpston (1940) recorded the preferred habitat of black beetle in N.S.W. as low-lying paspalum pasture. Wallace (1946) noted that the chief breeding grounds are grass land pastures with paspalum most affected, although old cultivation land or land under crop which is infested with summer grass or paspalum is also favoured. The sites most attractive to ovipositing females are those where the soil has a high predominance of grass species with fine grass turf on golf and bowling greens most favoured, (Wright, 1958). Legumes, (particularly lucerne), are not favoured by black beetle as breeding grounds (Wallace; Taylor, 1951). Taylor considered the insect appeared to favour soils of a grey sandy loam rich in humus in the high veld area of South Africa, and had never been found on black, peaty soils. This latter finding is in marked contrast to the evidence of Todd (1959), Esson (1973) and King and Mercer (1974) that in New Zealand black beetle occurs in large numbers causing severe damage in peaty soils.

Todd also noted that grass dominant pastures, particularly those containing paspalum, are the chief breeding grounds in New Zealand, and the soil favoured is usually light, sandy and extremely friable. He recorded that large populations had not been found in heavier soil types or on hill country. In more recent years severe damage has been recorded in both these habitats, (King, unpublished data). Although adults do not appear to be adversely affected by wet conditions, Todd (1959) found that during the winter they do tend to favour drier situations. King (unpublished data) noted aggregations of adults in the drain banks on peat land, and

Johannesson (1975) presented evidence for movement from low-lying pasture to ridge-tops in the autumn.

(3) Influence of pathogens, parasites and predators

Although parasites and predators of scarabs are known to cause population mortality, considerably more information exists on the significance of the wide range of pathogens known to occur in scarabaeids. Kain (1975) presented an extensive review of the natural enemies of the Melolonthinae sub-family, and in particular, those of the grass grub. Many of the natural enemies of grass grubs have been also found to play a role in black beetle mortality, although until recently the significance, particularly of pathogens was little understood. In this section, known biotic mortality agents of black beetle and their influence are reviewed.

(a) Pathogens

(i) Bacteria

Dumbleton (1945), Helson (1965) and Fowler (1974) recorded milky disease Bacillus spp., in black beetle in New Zealand. Harrington (1953) observed larvae with the 'symptoms and appearance' of infection with milky disease similar to that described as affecting larvae of Popillia japonica in the U.S.A. by Hawley and White (1935). Beard (1956) in a survey of disease of Australian scarabaeids found black beetle larvae in December with symptoms similar to those of larvae of P. japonica infected with Bacillus popilliae or B. lentimorbus in the U.S.A. He proposed the name B. euloomarahae for the disease which was found to be infective in a wide range of scarabaeid hosts.

Longworth and Archibald (1975) in a survey of pathogens in a black beetle population at Wharepapa, near Helensville, found the facultative bacterial pathogen, Serratia marcescens. Although this pathogen has been the cause of outbreaks of disease in some laboratory cultures of insects, there have been no records of it causing an epizootic in field populations (Bucher, 1963).

(ii) Fungi

Latch (1965) and Longworth and Archibald (1975) recorded the presence of the green muscardine Metarrhizium anisopliae in black beetle larvae. Longworth and Archibald found a further two fungal pathogens, Cordyceps sp. and the white muscardine Beauvaria sp. The pathogenicity of these fungi is well documented (Madelin, 1966). Longworth and Archibald record that in a population of black beetle at Wharepapa, 4% of third-instar larvae were infected with Beauvaria sp.

(iii) Rickettsia

Longworth and Archibald (1975) recorded a rickettsia in the black beetle population at Wharepapa. Rickettsia infected less than 10% of the population between January and May 1974 (Archibald, 1976) and was not considered a significant pathogen.

(iv) Viruses

Thomas (cited in Archibald, 1976) reports an iridescent virus in black beetle in South Africa. Longworth and Archibald (1975) found a small RNA virus at Wharepapa. Between January and May 1974, Archibald recorded a highest level of 8.8% infection of black beetle with the virus. The virus has a divided genome,

belongs to the picornavirus family and is similar to Nodamura virus in size and density (Murphy et al. (1970). Nodamura virus can multiply in and kill mammals (Bailey and Scott, 1973; Newman and Brown, 1973). Archibald noted that the divided genome and the similarities to Nodamura virus therefore make black beetle virus potentially dangerous and unsuitable for microbial control.

(v) Protozoa

Helson (1965) reported a gregarine species as being pathogenic to black beetle in New Zealand. Longworth and Archibald (1975) found a coccidian protozoan, Adelina sp. in black beetle larvae, pupae and adults, at Wharepapa. Adelina develops in the gut and has been shown to infect a wide range of insects. A coccidian infection, subsequently identified as Adelina sericesthis (Weiser and Beard, 1959), was recorded as causing up to 65% of Sericesthis pruinosa (= geminata) larvae in populations at Canberra, A.C.T. to "succumb" (Carne and Chinnick, 1957).

Other insects recorded as being infected with Adelina are a cockroach Crytocarcus punctulatus (Yarwood, 1937), Tribolium spp. (Park and Frank, 1950; Weiser, 1963), Melolontha melolontha (Tuzet, et al. 1956) and Galleria mellonella (Beard, 1970). Classification of Adelina has largely been based on its host and the dimensions of oocysts and sporocysts. However, as Weiser and Beard found that A. sericesthis infects not only S. geminata, but also Aphodius howitti and Beard (1970) showed that an Adelina sp. infecting G. mellonella also infected Tribolium confusum, serious doubt exists over using host specificity as a basis for classification.

Archibald (1976) examined the life cycle of Adelina in black beetle and recognised and named five stages of the cycle according to Yarwood (1937). He found oocyst and sporocyst size seemed to be spread over a particularly wide range and concluded that differentiation of the species on the range of size of the sporocysts as proposed by Hall et al. (1971) would seem impractical. Archibald observed life stages in black beetle with a strong resemblance to those of an Adelina sp. attacking the dermestid Trogoderma parabile (Loschiaro, 1969). The sporozoites were capable of exactly the same movements as were observed by Bhatia (1937) in merozoites of Adelina tribolii.

Archibald found that at Wharepapa between January and May 1974, Adelina sp. was the most common pathogen present in the population, with a maximum of 46.8% of the population present being infected at any one sampling occasion. At Coatsville, 35.8% of the population was found to be infected with Adelina sp. Archibald et al. (1975) while monitoring pathogen incidence at Wharepapa over the same period in 1975, found over 60% of black beetle present were infected with the protozoan. In reporting a concurrent field population decline over this period, they presented data on laboratory mortality in samples from the population and put forward a hypothesis that pathogen mortality played a major role in the observed black beetle decrease. Archibald et al. (1975) and Archibald (1976) however, point out that no definite conclusion can be made on the role of Adelina in population mortality in the absence of data on adult autumn migration.

Adelina is transmitted per os. and resistant infective stage oocysts are released into the environment only when the insect dies (Weiser, 1963). Weiser noted that the ingestion of one insect by another (alive or as a cadaver) could also be a means of transmission, which suggests a possible density-dependent mortality. Although Weiser considered protozoan infections may often be sub-lethal, it is of interest that Gangler and Brooks (1975) have shown that sub-lethal infections by the microsporidian *Nosema heliothidis* in *Heliothis zea* have reduced reproductive potential significantly by reducing fecundity, longevity and mating success.

Adelina has been shown to be dispersed by a range of agencies. Archibald records that infected adults were caught in light traps. Small mammals may also disperse *Adelina* as Archibald discovered hedgehog faeces with broken pieces of black beetle adult integument in which was incorporated oocysts of *Adelina* sp. Anipilogova (1971) and Barnard *et al.* (1974) have also found *Adelina* in the faeces of small mammals. Courtney *et al.* (1975) report that *Adelina* sp. was found in faeces of sandhill cranes *Grus canadensis* and considered the pathogen a 'spurious parasite' of the cranes, ingested with an invertebrate food source.

(b) *Parasites*

Among a number of nematode parasites of black beetle in South Africa, Harrington (1953) recorded that *Neoaplectana* sp. closely resembling *Neoaplectana glaseri* Steiner, was the most numerous. Longworth and Archibald (1975) found a small proportion of adults infected with *Neoaplectana* sp. at Wharepapa. Another

nematode Heterorhabditis bacteriophora Poinar, found in black beetle from the Manakau Heads appears to be highly pathogenic to black beetle larvae and adults (Wouts, pers. comm.). Harrington reported a number of Hymenopterous parasites of the families Tiphiidae and Scoliidae as attacking black beetle larvae in South Africa. Parasitism of over 45% by a Tachinid, Microphthalma capensis (Regnard, cited in Harrington, 1953) was probably not of black beetle but another scarab, Temnorhyndius retusus according to Valentine (1978). M. capensis is considered to have little potential as a natural enemy of black beetle in New Zealand (Valentine, 1978). An investigation carried out by Entomology Division, D.S.I.R., for black beetle parasites in South Africa suggests that it is unlikely that possible parasites would adapt to New Zealand conditions, which in general do not adequately fulfil temperature, feeding and habitat requirements (Valentine, 1978).

(c) Predators

The staphylinid predator Thyreocephalus orthodoxus has been shown to be common in some Northland and Auckland pastures (Cameron and Butcher, 1978), and Butcher (1978) has shown that black beetle larvae are a food source. However, it is unlikely that this predator would cause significant black beetle population mortality (Butcher, pers. comm.). Large numbers of an elaterid Conoderus sp. which has been shown to be a facultative predator of grass grub (Farrell, 1972), have been found in conjunction with populations of black beetle (King, pers. observ.). Their role in population mortality is unknown however.

Representatives of families of insects assumed to be predatory on Scarabaeides, including Asilidae, Staphilinidae and Carabidae were found during sampling in South Africa (Valentine, 1978). He considered none of these with the exception of carabids of the genus Scarites, were numerous enough to be significant. Scarites sp. has recently been introduced to New Zealand and Cameron and Butcher note that food preferences and voracity of this predator suggest that if it establishes in New Zealand, it could make a significant contribution to 'the control' of pest scarabs, (black beetle included).

V PEST STATUS

There are considerable differences in the pest status of black beetle in the countries in which it occurs. As was shown in the general introduction to this thesis, black beetle is a serious, if sporadic pest in pastures and maize crops in the northern parts of the North Island.

In South Africa, H. arator is referred to as the Black Maize Beetle (Taylor, 1951; Harrington, 1953), with the adults causing significant damage to young maize plants by eating into the stem just below the soil surface. Both authors note that young wheat crops, potato tubers and the root systems of various grasses (particularly those on golf and bowling greens) are also susceptible to attack by the adult. Petty (1976) records black maize beetle as a pest of pineapple. Within South Africa, its distribution coincides with regions of relatively higher, more regular rainfall and the range is localised to lighter soils with sufficient organic

matter for successful larval development (Valentine, 1978). Valentine however, considers that as the adult is only occasionally damaging, and as there is no evidence of larvae feeding on plants (Taylor; Harrington), black maize beetle is not regarded as a serious pest.

In the Perth and Adelaide areas, black beetle occurs principally in irrigated lawns, other fine turf areas, and in horticultural situations (Anon, 1959; Jenkins, 1965, P.J. Allan, pers. comm.). Although not considered a significant pest in South Australia, recent reports suggest considerable damage to vegetable crops near Perth (Sproule, pers. comm.).

In coastal N.S.W., Cumpston (1940) recorded black beetle as a major pest, attacking any lawn surfaces such as golf or bowling greens, also maize, sugar cane, and vegetable crops such as cauliflowers and tomatoes. In addition it was noted as attacking banana plantings and rose cuttings. Wallace (1946) considered black beetle a serious pest of dairy farms in coastal N.S.W. where it destroys large areas of crop and damages pasture, with maize and paspalum, the two plants most grown for dairy cattle being the favourite food plants of H. arator. This pest status is mainly confined to the wide river flats (Wright, 1958), and black beetle are seldom found at distances greater than about 60 miles from the coast. Both Wallace and Wright noted the sporadic occurrence, similar to the New Zealand situation, of years of high numbers with black beetle being favoured by dry conditions during spring and summer. When two dry summers follow in succession, numbers reach plague proportions by the second autumn as occurred in 1923, 1929 to 1933, 1936, 1944-1945,

1952 to 1954 and 1957 (Wright). Should the following spring be very wet, populations decline and the pest causes little further trouble.

In a dairying situation in coastal N.S.W., just north of the Victoria-N.S.W. border, Russell (1973) reported that the degradation of pastures caused by severe damage by larval feeding resulted in a 45% decrease in milk production between 1957 and 1967. In 1962 Russell took 600 bales of hay from seven acres of paspalum, but after severe pasture damage, the same area yielded only 400 bales in 1971, containing no paspalum and being basically Yorkshire fog (Russell, 1973). The resowing of severely damaged pasture areas to ryegrass/white clover was a complete failure due to the change in soil texture, brought about by larval feeding, to a powdery texture that would not hold moisture necessary for germination and growth (Russell).

VI CONTROL OF BLACK BEETLE

Trials with insecticides for the control of black beetle appear to have been initiated in the late 1940's in both South Africa and N.S.W., Australia. Taylor (1951) found that benzene hexachloride (lindane) gave good control of black beetle both when the powder was incorporated into the soil, or when maize seed was treated prior to planting, but that black beetle appeared immune to DDT. Lindane was also recommended in N.S.W. (Anon, 1970) either broadcast as a powder with broken maize seed before planting, mixed with fertiliser at planting, or jetted as a solution on to the soil.

In the first trial work carried out in New Zealand, Todd (1959) reported that DDT was ineffective, lindane partially effective and dieldrin and aldrin highly effective, and recommended dieldrin applied at 6 oz active ingredient per acre, mixed with superphosphate, be used as a control measure. This was the standard control until 1961, when because of the hazards of residues in milk or animal tissue, the Agricultural Chemicals (Insecticides) Regulations restricted the use of dieldrin/superphosphate on pasture. Trials carried out between 1962-1964 (Todd, 1964) showed that endrin, "Telodrin", and dieldrin, all formulated as pellets gave excellent control of larvae 60 weeks after treatment. In 1964, the Agricultural Chemicals (Insecticides) Regulations prohibited the application of dieldrin to pasture and field crops except in pelleted form.

In 1967, all forms of dieldrin were banned from use on pastures. The need for an effective new control became apparent and led to the evaluation of other insecticides and formulations, with particular emphasis being given to control of adults using transient materials unlikely to leave residues. In preliminary studies Todd (1964, 1967) found that high adult mortality was obtained with the organophosphorous insecticides, diazinon and trichloronat. Todd (1969) reported that diazinon when formulated as a slow release granule gave excellent control of black beetle adults, but that ten other transient insecticides were not significantly toxic. Lindane was approved for use against the insect on non-dairying land.

Todd (1969) pointed out however, that because of the cost of diazinon, there is little incentive for its use, thus emphasising

the need to continue investigation, with the hope that a more economical method of control will eventually be found.

The widespread and severe pasture damage that occurred in the late 60's and early 70's prompted farmer pressure for improved control, and extensive screening trials were carried out. Esson (1973) found that two organophosphates, fensulfothion and ethoprophos gave good control of larvae when applied to the pasture in early December as granules. However, the disadvantage of the long stock with-holding period after application and the need for rainfall soon after broadcasting, their high cost and unreliability on high organic matter soil types provided little incentive for their use, as was noted by Todd (1969) for diazinon.

King and Mercer (1974) showed that both fensulfothion and ethoprophos gave control of black beetle on peat soils when drilled into the pasture. Attention has been concentrated in recent years on the control of adults in maize crops, where the high treatment costs are more easily justified in protecting the high value maize crop (Watson and Webber, 1975; Watson et al., 1978).

Economic control of black beetle in pasture with insecticides is still at a stage similar to that existing in 1969. Watson and Webber (1976) showed that earlier treatment with granular insecticide applications directed against the adult prior to egg laying gave good control, and that another organophosphate, isazophos appeared promising when compared with fensulfothion. Recently, the use of a 'jet-squirt' method of application where the insecticide is jetted at low pressure as a spaced spray on to the pasture has shown promising results (Blank and Olsen, 1978; Watson and Wren, pers. comm.).

Unless a low cost, non-persistent insecticide, effective against black beetle is developed (and the chances of this appear remote), then insecticidal control can never be expected to reach the level of widespread adoption by farmers that characterised the years when dieldrin was used. Rather, more selective use of existing materials in situations where pasture protection is desirable, such as newly sown pasture, is likely to be the extent of insecticide usage.

CHAPTER 2

LITERATURE REVIEW ON THE MEASUREMENT OF AND FACTORS INVOLVED IN THE GROWTH OF SCARABAEIDAE FEEDING ON PLANTS

I INTRODUCTION

The ecology of phytophagous insect species is understandably influenced to a large extent by the plant-insect interaction. Elucidation of this aspect of black beetle ecology, which comprises a significant proportion of this thesis, must be considered with reference to the response of other insect species, including scarabaeids, reported in the literature.

In this chapter, the relevant literature dealing with techniques for measuring the relative consumption and utilisation of food by insects for growth will be reviewed. This will be followed by an examination of the growth, survival and larval locomotor responses of some scarabaeids to different plant species, consideration of secondary plant substances specific to individual species which influence feeding and growth, and finally, the effect of mixtures of plant species on insect population numbers. The very small amount of published literature on the black beetle-plant interaction is contrasted with current knowledge on grass grub.

II MEASUREMENT OF CONSUMPTION AND UTILISATION OF FOOD

A considerable amount of research on insect food consumption and utilisation has been reported in the literature relating primarily to foliage feeding Lepidoptera and Orthoptera. Much of this is

difficult to relate from one insect group to another, or even between different data from the same insect as the methods used have varied greatly in technique and accuracy. Waldbauer (1968) has reviewed the topic and suggested some standard forms of calculating consumption, growth and utilisation indices.

(1) Gravimetric techniques

Much of the confusion over interpretation of data has resulted from varying methods of determining the actual weight of food consumed. In the gravimetric method used to measure food utilisation, the food eaten is determined by subtracting the weight of uneaten food from the weight of food provided. Waldbauer described this as the consumption index (C.I.) which is defined as:

$$C.I. = \frac{F}{TA}$$

where F = fresh or dry weight of food eaten,

T = duration of feeding period,

A = mean fresh or dry weight of animal during the feeding period.

If fresh weights are used, it is necessary to control for a loss or gain of water by the food, unless loss is minimised in a humid atmosphere. The method of Evans (1939) estimated the "natural loss" of leaves provided as food by maintaining an aliquot of food in the absence of feeding insects over the feeding period. Waldbauer suggests that this method provides an accurate estimate provided two assumptions are operating:

(i) "The % weight loss of the food is independent of the amount of food;

(ii) "Feeding itself does not increase natural loss by constantly providing a freshly cut surface."

Carne (1966) and Waldbauer (1962) found that natural loss of weight will often be negligible if excess food is held to a minimum.

These problems of natural loss can be avoided to a large extent by the use of the dry weights of food. Those foods which cannot be dried before feeding must be estimated from the % dry matter of an aliquot (Waldbauer, 1968), although judicious selection of the aliquot is necessary to prevent variation in the material used for the aliquot and that as the food source. Where leaves are used as food, Waldbauer (1964) and Soo Hoo and Fraenkel (1966) found that greater precision is obtained by cutting leaves into two symmetrical portions along the mid-rib, using one portion as food and the other as the aliquot.

Waldbauer (1968) suggested that the dry weight loss of excised leaves (food) by metabolism is probably negligible and can be minimised by frequent changes of food and the immediate drying of uneaten food. The potential error could be further minimised by estimating the dry weight of eaten food from the mean % dry matter of the aliquot and the % dry matter of the uneaten food (Waldbauer, 1968). He further stated that "the small but inevitable discrepancy between the % dry matter determined from the aliquot and the actual % dry matter of the food causes an error in the estimated dry weight of the food provided. The absolute size of the error in weight of food eaten will increase with the quantity of food introduced, while its relative size will increase with the proportion of uneaten food." Little can apparently be done to further improve this consumption

estimate within the constraints of the gravimetric technique, but realisation of the sources and level of error do not detract from the merits of this technique to provide relative indices between plant species.

The mean weight of the animal is most accurately calculated from the area under its growth curve by integration or direct measurement (Waldbauer, 1968), although a weighted average of daily weights will give an almost identical value if the growth curve is smooth (Waldbauer, 1964). Of other techniques, Lafon (1951) used mg of food eaten per g of insect (final weight), Legay (1957) proposed mg of food eaten per g of initial insect weight per day, and Smith (1959), used weight of food eaten divided by weight gained. All can result in large errors in many instances through their relative insensitivity.

The selection of the period during which consumption is measured can be critical. Of most convenience is an arbitrarily defined period within an instar. However, although less convenient, a physiologically defined period such as from instar to instar is more likely to yield reproducible results as Waldbauer (1968) points out. This approach has been used by Crowell (1941), Hiratsuka (1920), Soo Hoo and Fraenkel (1966), Waldbauer (1964) and others. Rigorous selection at the start of a feeding trial to obtain larvae within the same instar of similar size, appearance and activity can reduce the errors sufficiently to still enable estimates of consumption between plant species. Care must be taken in determining the insect weight changes if a moult occurs during the feeding period.

The influence of insect age on feeding relationships should be allowed for in planning consumption and utilisation experiments.

Ridsdill Smith *et al.* (1975) found that daily C.I. for third instar *Sericesthis nigrolineata* larvae (wet weight basis) varied from 0.13 in January to 0.07 in June. Hurpin (1960) found a change in C.I. in *Melolontha melolontha* third instar larvae from 0.15 at the beginning of the instar to a maximum of 0.24 and a fall to 0.02 at the end of the instar. In the case where larval feeding studies are carried out during an arbitrarily defined period within an instar, the use of shorter and convenient experimental periods will ensure that age induced variation is of minimal importance when comparing efficiencies on different diets.

Obtaining feeding data from groups of insects rather than individuals can lead to inaccurate results due to problems with mortality, cannibalism or the eating of dead individuals, (Waldbauer, 1968). Crowding is also likely to affect the rates of feeding and growth as shown by Fewkes (1960), and so the size of the container the experiment is being conducted in should be considered.

The relative growth rate (G.R.) can be calculated as shown by Waldbauer (1968):

$$G.R. = \frac{G}{TA}$$

where G = fresh or dry weight gain of the animal during the feeding period,

T = duration of feeding period,

A = mean fresh or dry weight of animal during the feeding period.

The efficiency of conversion of ingested food to body substance (E.C.I.) Waldbauer (1968) is calculated as:

$$E.C.I. = \frac{\text{weight gain}}{\text{weight of food ingested}} \times 100 = \frac{G.R.}{C.I.}$$

The E.C.I. is an overall measure of an insect's ability to utilise the food it ingests for growth. Waldbauer noted "that the E.C.I. will vary with both the digestibility of a food and the proportional amounts of the digestible portion of that food which are, on the one hand, converted to body substance, and on the other hand, metabolized for energy to maintain life".

Waldbauer pointed out that the moulting of insects presents a special problem in the determination of the E.C.I., since the insect reaches a maximum weight in each instar and loses weight during the moult. This can be overcome when using an arbitrarily defined period within an instar by commencing the feeding period at the start of an instar and ceasing the trial at a point before weight loss begins. Such a technique is satisfactory when comparing E.C.I.'s on different food sources.

(2) Indigestible marker technique

As an alternative to the gravimetric method of determining consumption and utilization, indirect methods have been developed using markers. Ridsdill Smith (1975) developed a marker technique to assess the rate of passage of food through the gut of S. nigrolineata larvae in the presence and absence of roots. Individual larvae were allowed to feed on a slice of carrot in ice cube tray compartments containing 0.2 mm diameter glass beads dampened with water. After 16 hours in the dark, larvae were transferred to soil with and without growing plants. After 6-9 hours, the larvae were removed and deep frozen to prevent gut activity. Guts were dissected and the

abundance of beads in each section was estimated using a ranking method. Larvae with fewer beads in the foregut and midgut were feeding at a higher rate than those with more beads in these sections since feeding pushed the beads through the gut. This enabled an index of the relative rate of consumption or ingestion to be determined.

Another method which has been used to measure utilisation is the addition of a known concentration of an indigestible marker such as chromic oxide to the diet. The concentration of the marker in the faeces is then determined using a sensitive colorimetric analysis and utilisation can then be determined without quantitative collection of the faeces or measurement of the food eaten. The technique was first used with insects by McGinnis and Kasting (1964a) on Agrotis orthogonia larvae. A comparison of the results determined by chromic oxide and gravimetric methods led McGinnis and Kasting (1964b) to conclude that the gravimetric method overestimated utilisation. Waldbauer (1964) however, used a more refined gravimetric technique and obtained values of about the same size as those of McGinnis and Kasting with the chromic oxide method. McGinnis and Kasting (1964b) concluded that the chromic oxide method is more rapid and practical, and avoids some of the error which may result from the gravimetric method. When working with Heliothis zea and Spodoptera frugiperda, McMillian et al. (1966) suggested that the chromic oxide method may have deterred larval feeding. In addition, the method is probably only usable with foods that can be ground and mixed to assure even distribution of the marker. This is certainly not possible where a feeding study of root feeding insects is simulating natural conditions.

(3) Radioactive tracers

These have also been used to assess food consumption by measuring the passage of radio-isotopes from the food to the animal and their subsequent loss. Crossley (1963) used cesium-137 to estimate the intake of Chrysomela knabi feeding on Salix nigra and obtained estimates of the daily food consumption of third instar larvae similar to the results of direct laboratory measurements. Using sucrose-U-^{14}C Kasting and McGinnis (1965) found that estimates of food consumption by first and fifth instar Agrotis were generally higher than those obtained by either the gravimetric or chromic oxide method. The use of insoluble cellulose-U-^{14}C gave results which agreed closely with those obtained by the chromic oxide method.

The tracer technique has been used extensively in the study of assimilation by aquatic invertebrates. Calow and Fletcher (1972) developed a double labelled technique whereby animals were fed on a diet labelled with an assimilated radio tracer ^{14}C, and a non-assimilated tracer ^{51}Chromium. The assimilation efficiency (A.E.), which is an index of the proportion of an animal's ingesta that is transferred from the gut lumen into its body (Wightman, 1975) can be calculated from the ratio of the two radio tracers in the food and the faeces. Nash (1974) modified Calow and Fletcher's technique by using ^{144}Cerium as a non-absorbed indicator instead of ^{51}Cr in studies of the A.E.'s of freshwater shrimps and snails. This technique was further modified by Prestidge (1976) to determine A.E.'s of two species of dragon flies.

Use was made of the double-labelled radio tracer technique for a terrestrial invertebrate by Wightman (1975). In a study of food consumption and utilisation by a Kenyan scarabaeid Pachnoda [illegible] Gerst., the ^{14}C and ^{51}Cr radio tracers were incorporated into an

artificial diet. Use of the technique for studying food utilisation by a soil inhabiting, root feeding insect larva poses several problems. Roots would have to be labelled, firstly by growing plants in an atmosphere of ^{14}C, or in a Sucrose-U-^{14}C solution to attach the assimilated tracer, and then labelled with a non-absorbed tracer such as ^{51}Cr or ^{144}Ce. To reduce labelling variation, roots would probably need to be lyophilized and incorporated in an agar diet. Such a study would require considerable inputs to develop satisfactory methods and time spent may increase the cost benefit of the admittedly laborious gravimetric method.

III FACTORS INFLUENCING CONSUMPTION AND GROWTH

(1) Effects of plant species

The consumption of food and subsequent growth by root feeding insects, both adults and larvae, has been shown by a number of workers to vary markedly between plant species. In addition, larvae exhibit preferences for aggregation under some species, in some cases regardless of the influence the plant has on growth and survival. Wensler (1971) found that third instar larvae of Sericesthis geminata preferred to aggregate and feed under plants of ryegrass and cocksfoot, compared with phalaris and white clover, but preferred all three grasses to white clover.* Davidson and Roberts (1968a) noted however, that S. geminata larvae caused more damage to white clover than four other scarab species, which is evidence of intensive feeding on the species. Davidson and Roberts (1968a) observed that larvae of Anoplognathus spp. appeared to avoid white clover.

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* All plant species are referred to in this thesis by their common names. A list of Generic, specific and common names for each species is given in Appendix O-1.

In a further study, Davidson and Roberts (1968b) found that white clover had an adverse effect on the live weight gain and rate of development of third instar larvae of both Rhopaea morbillosa and Anoplognathus spp. On the basis of root damage observed, they concluded that this result was not the outcome of reduced feeding activity by the larvae on white clover compared with cocksfoot, tall fescue, ryegrass and phalaris, but gave no other reason. In addition, phalaris was found to have a similar adverse effect on liveweight gain, rate of development and survival of larvae of both scarabaeid species. They concluded that the toxic alkaloids known to occur in phalaris (Gallagher et al.,1964; Moore and Hutchings, 1967; Moore et al.,1966) may be responsible.

The low numbers of June beetles Phyllophaga spp. found in legume pasture compared with grass by many workers was noted by Chamberlain and Callenbach (1943). In a field trial carried out to investigate the effect of blue grass and sweetclover on P. rugosa and P. hirticula, adults were confined on plots of these species by cages, and survival of the offspring was recorded (Chamberlain and Callenbach, 1943). They found that mortality of larvae was much higher in sweet clover with grubs failing to reach the second instar.

Both laboratory and field studies have been made of the growth and survival of grass grub larvae on plant species. Farrell and Sweney (1972,1974b) found that the growth rate of grass grub larvae feeding on plants grown in plastic boxes of soil was significantly lower under lotus, lucerne and lupin than under red clover, white clover or perennial ryegrass. Kain and Atkinson (1970) found that stands of lucerne supported low numbers of grass grub, but as seedling lucerne was attacked, speculated that larvae were not able to feed

satisfactorily on the woody tap root of the older plants. The poor weight gain and survival of grass grub on these legume species relative to white clover was demonstrated by Kain et al. (1975) and Kain and Atkinson (1977).

This is of particular interest in view of the locomotor and aggregation behaviour shown by grass grub larvae. Sutherland and Hillier (1974), Kain et al. (1975) and Kain and Atkinson (1977) showed that larvae were more strongly attracted to the roots of lucerne, lotus, red clover and white clover, than ryegrass and phalaris. In spite of the unfavourable nature of lucerne and lotus for weight gain and survival, larvae would remain at the roots of these species in preference to the grass. In addition to these two legume species, the work of Farrell and Sweney (1974a), Kain et al. (1975) and Kain and Atkinson (1977) has shown that the grass species, phalaris, Yorkshire fog and blue grass result in low weight gain and survival of larvae feeding on them and so can be termed resistant. Field trials of these favourable and unfavourable species showed that larval weight gain in the laboratory appeared to be a good indicator of survival in the field (Kain et al., 1975; Kain and Atkinson, 197[illegible].

The terminology used to describe the nature of the plant-insect response is largely a function of whether the plant or the insect is the major area of interest. In referring to cultivars of single plant species which result in the high weight gain and survival of grass grub larvae feeding on them, Kain et al. (1975) and Kain and Atkinson (1977) refer to these as susceptible species. Larval weight gain and survival is low on species termed resistant. East and King (1977) prefer to use the terms favourable and unfavourable

to describe the effects of different plant species on insect populations. A favourable plant species is one which supports high population densities in the field. An unfavourable plant is one which suppresses insect population density. East and King consider population density is the sum total of a number of different factors including fecundity, survival, dispersal, growth and development, all influenced to some extent by the plant-insect interaction.

Black beetle is also known to be influenced by plant species. Wallace (1946) noted that black beetle 'avoided' legumes where heavy infestations attacked mixed crops of legumes and non-legumes. Clovers alone were found to survive when a mixture of grasses and clovers was sown with barley as a cover crop. He states that "lucerne appears to have an immunity from black beetle attack and that lucerne, cowpeas, clovers, peas and beans can be grown with success under conditions of beetle infestation that would ruin crops of susceptible species".

King et al. (1975), demonstrated low black beetle larval weight gains on lucerne and low numbers in the field under a lucerne stand and concluded this species was resistant. Laboratory studies were carried out on black beetle larvae feeding on the roots of plant species held in a vermiculite medium by King (1977). These showed that third instar larval weight gain and the number of faecal pellets produced were significantly greater on ryegrass roots than on white clover and lotus.

In a laboratory comparison of grass grub and black beetle third instar larval feeding and growth on these three species, King and Kain (1974) found that the converse situation occurred with grass grub.

Grass grub weight gains and faecal pellet counts were significantly greater on white clover than ryegrass, although lotus caused a larval weight loss. The different performance of these two scarabaeid species demonstrates the complexity of the plant-insect interaction.

(2) Secondary plant substances

The plant-insect interaction may be a function of the secondary plant substances that different species possess, and the influence of these on the insect. Painter (1951) in his review of plant resistance to insect feeding grouped this resistance in terms of non-preference, antibiotic properties and tolerance. In his later review of the subject, Beck (1965) pointed out that there may be no clear distinction between non-preference and antibiosis. Non-preference may arise through interruption of the normal feeding pattern at different points, Beck (1965). The insect may be actively repelled by making directed movements away from the plant; or having made contact further feeding activity such as biting, may be suppressed; or having bitten the food, the insect may be deterred from further feeding. The chemicals involved in inhibiting feeding behaviour at these various points are known as repellants, suppressants and deterrents respectively, (Chapman, 1974). Goodhue (1963) did not differentiate between the last two and classifies both types as rejectants.

Some difficulties arise in ascribing poor larval growth on the roots of a plant species to a feeding deterrent. Chapman (1974) noted that experiments which simply demonstrate a failure to eat a plant or its extract do not provide evidence of the presence of inhibitors, since the same result could arise from an absence of suitable phagostimulants.

Studies of the feeding behaviour of grass grub larvae have shown that several nutrient chemicals influence the rate of ingestion by third instar larvae (Sutherland, 1971; Sutherland and Hillier, 1974). A combination of 0.1 M sucrose and 0.01 M ascorbic acid was shown to be a particularly potent phagostimulant mixture by Sutherland and Hillier (1974). The use of these phagostimulants in an agar/cellulose medium was used to investigate grass grub feeding deterrents in legumes. Similar studies of black beetle larval feeding behaviour demonstrated that the presence of 0.1 M maltose in the agar/cellulose medium as a phagostimulant produced a strong feeding response (Sutherland and Hillier, 1976).

Legumes have been shown to contain both strong feeding deterrents and toxins to grass grub and black beetle larvae feeding on the roots of these species. The failure of grass grub larvae to feed actively on a media containing either crude lucerne root extracts or sterol-precipitable saponins isolated from such extracts was shown by Sutherland *et al.* (1975a), Sutherland (1976). They concluded that these compounds could clearly affect larval ingestion, and consequently, weight gain and survival. The addition of a crude extract of root to a medium containing phagostimulants for grass grub larvae reduced ingestion to a negligible level (Sutherland *et al.*, 1975b; Sutherland 1976). One of the feeding deterrents to grass grub larvae present in the roots of 'Maku' lotus was shown to be the isoflavanoid, vestitol by Sutherland (1978). The presence of compounds toxic to grass grub larvae in the roots of lotus and lucerne was shown by Sutherland and Greenfield (1976) and Sutherland (1978), when the injection of doses of root extract directly into the

larval foregut caused significant mortality. Horber (1964) suggested that poor growth and development of the European scarabaeid Melolontha vulgaris F. on lucerne could be ascribed to the saponin content of the root.

Crude root extracts of the legumes red clover, white clover, lupin, 'Maku' lotus and lucerne incorporated into an artificial medium containing 0.1 M maltose as a phagostimulant, significantly reduced feeding by third instar black beetle larvae (Sutherland and Greenfield, 1976, 1978). In addition, the same extracts were shown to be toxic when injected into the foregut of black beetle larvae. Black beetle larval consumption, utilisation, growth and survival on these legume species would be expected to be affected by the presence of the feeding deterrents and toxins. The unfavourable influence of white clover on black beetle larval growth was shown by King and Kain (1974) and King (1977).

(3) Effects of mixtures of species

As mixtures of several species are much more common in the natural field situation than swards of single species, research on the influence of mixtures of species on scarabaeid insects has been undertaken as part of the elucidation of plant-insect interactions.

In laboratory studies (Kain et al.,1975; Kain and Atkinson, 1977) where grass grub larvae were fed the excised roots of plant species as mixtures of one resistant with one susceptible species, weight gains were found to be dependent upon the legume present. Highest weight gains were recorded on white clover mixtures, weight gains were lowest on lotus mixtures and intermediate on mixtures with lucerne. Weight gains on grasses were higher on ryegrass than

phalaris. Numbers of grass grub larvae found in small plots of mixtures in a field trial showed the results paralleled that found in the laboratory, with the highest numbers harboured by white clover mixtures, and low populations by lotus mixtures (Kain et al., 1975; Kain and Atkinson, 1977). Kain and Atkinson (1977) concluded that the effects of grass-legume mixtures on grass grub populations depend largely on the legume component.

This conclusion was reached in view of the larval locomotor and aggregation response to plant species. The roots of several legume species were preferred to ryegrass by grass grub larvae in a vermiculite medium (Sutherland and Hillier, 1974). White clover, lucerne and 'Maku' lotus were all shown to be more attractive than ryegrass and phalaris to third instar grass grub larvae in a soil medium by Kain et al. (1975), and Kain and Atkinson (1977).

In studies of third instar black beetle larval feeding behaviour by King (1977), larvae did not aggregate at plant roots in choice chamber tests in a vermiculite medium, but did aggregate at organic matter (O.M.) in the form of sieved horticultural peat. Using the criteria of larval weight gain and faecal pellet production, O.M. stimulated feeding and increased weight gain. In a comparison of grass grub and black beetle feeding behaviour, King and Kain (1974) found that grass grub was not attracted to O.M. over plant roots and that the presence of O.M. had no significant effect on grass grub feeding and weight gain. On the basis of these scarabaeid species differences, it appears likely that grass grub larvae may preferentially select and feed on living roots as was shown for S. nigrolineata by Ridsdill Smith (1975), while black beetle larvae appear to be indiscriminate feeders.

The importance of the plant effect on larval locomotor behaviour, aggregation, consumption, growth and survival to the development of pasture management practices for grass grub control was discussed by Kain and Atkinson (1977). They considered that resistant pasture species could be used in pasture systems to reduce grass grub numbers. Kain and Atkinson showed that the maintenance of 'Maku' lotus even at low levels, with grasses or white clover greatly reduced grass grub populations, due to the fact that larvae aggregate about the roots of lotus, a plant under which survival is low. A similar response was observed with lucerne. Kain et al. (1978) were able to quantify the relationship between lotus content and grass grub numbers.

In contrast to this grass grub behaviour, the apparent absence of discrimination between plant food sources by black beetle larvae may mean that the effects of an unfavourable legume such as white clover on black beetle populations may be directly proportional to the amount of clover present in the pasture (King, 1977). White clover may have to be the major component in the sward during the larval feeding period if pasture composition is to adversely affect larval survival and hence reduce population numbers.

CHAPTER 3

LITERATURE REVIEW ON POPULATION ECOLOGY AND SAMPLING

As a framework for the study of black beetle population ecology, this chapter reviews the literature on population ecology and sampling. In the first section dealing with the theoretical aspects of population dynamics, the factors responsible for the changes in population density and for population regulation, the approaches to studying populations and the analysis of population data are considered. In the second section, the techniques used and problems encountered in sampling insect populations are examined with particular reference to work on other soil-inhabiting invertebrates.

I POPULATION ECOLOGY

(1) Definitions

Morris (1957) defined population dynamics as "the measurement of population changes from generation to generation and the study of factors responsible for the changes". The mode of action of the various mortality factors is of major importance in any study of population change. Howard and Fiske (1911) distinguished three kinds of mortality factors which Smith (1935) termed density dependent, density independent and inversely density dependent. Density dependent mortalities kill an increasing percentage of the population with increases in density, an inversely density dependent

mortality kills a decreasing proportion with increasing density, while a density independent factor shows no relationship to population density (Varley et al., 1973). The relative importance of these various mortality factors has generated controversy in population theories.

Solomon (1949) defined the key factor as the main controlling factor affecting a population. Morris (1959) was the first to use the term key factor in the sense of the factor causing population change, although he also defined the key factor as the one of most use in predicting population change. Varley et al. (1973) noted that Morris's first definition, which implies direct causation, is the most useful to ecologists, and this concept of Morris has been widely adopted in insect population studies.

Some of the confusion in population theory has arisen from the use of the term 'control' to describe both the process causing population change and that causing population regulation. A regulated population is one which tends to return to an equilibrium density following any departure from this level. Solomon (1957) noted that density dependent processes account for the regulation of populations. The importance of these concepts in understanding population dynamics is considered below.

(2) Population theories

For a long period, the theory of the regulation of insect abundance was one of the most contentious ecological subjects. This tended to restrict the study of the total ecological processes in many field studies, as the proponents of the various theories

concentrated on portions of the ecosystem only. Nicholson (1933, 1954,1957,1958) and Nicholson and Bailey (1935) considered that density dependent factors influence population numbers while Andrewartha and Birch (1954) maintained that these factors were not important. Since Andrewartha and Birch concluded that there was no need to regard density dependent factors as having any special importance, Price (1975) considered them proponents of density independent population regulation.

During population increase, density dependent factors such as predation or parasitism will increase, food will decrease resulting in increased mortality or decreased reproduction and space for living or breeding will become limiting (Price, 1975). As Andrewartha and Birch (1954) considered that the insect population had insufficient time to reproduce up to the carrying capacity of the environment during favourable periods, they regarded density independent factors such as mortality caused by weather as the limiting factors. Wilson (1968) noted there was a marked tendency in population studies for researchers to arrive at different conclusions on the regulation of population density based on their "theoretical predilections", sometimes even when studying the same insect. This situation developed with the studies of Aphodius tasmaniae by Carne (1956) and Maelzer (1961a,1962,1964).

A further group of population theorists considered that population regulation was caused by a change of factors within the population that affect numbers. These include pathological effects due to crowding (e.g. Frank, 1957), processes with a genetic component (Chitty, 1960; Wellington, 1957; Pimental, 1968), social

interaction (Wynne-Edwards, 1962) and dispersal (Johnson, 1966), all of which Price (1975) notes are probably density dependent.

Huffaker et al. (1977) consider that the controversies generated by these opposing views have fortunately become less intense with the development of more holistic concepts of population dynamics. These concepts embrace factors contributing to both instability and change and those contributing to the regulation of populations at characteristic densities (Milne, 1957; Huffaker and Messenger, 1964; Clark et al., 1967; Southwood, 1975).

Price (1975) considers that for each population there is probably a unique combination of factors regulating populations, if for no other reason than because each population probably has a unique gene pool. Southwood (1977) clarifies the true situation by noting that there is a whole continuum of types of population dynamics. This continuum, termed the r - K continuum of MacArthur and Wilson (1967) is related to the duration or stability of the habitat and to various bionomic characters of the animal (e.g. size).

Southwood and Comins (1976) and Southwood (1977) presented a 'synoptic model' with three axes: population growth, population density and habitat duration stability to provide a framework within which to consider the comparative population dynamics of different species. The model is based on natality, intraspecific competition and natural enemy action which vary along the r - K continuum. At one end of the continuum are the 'r-strategists' which are species characterized by a 'boom and bust' in numbers (Southwood, 1977). These species have a high reproductive capacity.

natural enemies are absent or insignificant and intraspecific competition such as starvation, disease and migration regulates the population (Southwood and Comins, 1976). At the other extreme, Southwood and Comins categorize K-strategists as species maintaining a steady population at or near the carrying capacity of the habitat where mortality due to natural enemies is insignificant and which have low reproductive, migration and mortality rates. This concept has greatly strengthened the relevance of population dynamic theory to pest status, particularly as far as the likelihood of the success of control strategies is concerned. Southwood (1977) considers that the determination of the location of a species on the continuum suggests the sensitivity of the species to disturbance of its habitat.

(3) The regulation of populations

Extensive reviews of the factors regulating insect populations have been made by Solomon (1949,1964), Richards (1961), Clark et al. (1967), Richards and Southwood (1968), Wilson (1968), Wagner (1969), Varley et al. (1973) and Price (1975). For this reason the topic is only briefly discussed here to provide a framework for the later interpretation of the role of the mortalities observed in black beetle population studies.

The importance of density dependent processes in regulating population densities, first proposed by Nicholson after laboratory studies of the sheep blowfly Lucilia cuprina, is now generally accepted. Varley and Gradwell (1970) noted that mathematical population models which do not include density dependent mortalities

are unstable and predict that population densities must either increase or decrease indefinitely. As defined previously, a regulated population eventually tends to return to an equilibrium density. The effects of density dependent mortalities on density are determined in single species populations by the nature of the mortality. Density dependent mortalities may undercompensate and the population gradually stabilizes, exactly compensate for any population change, or overcompensate. In the latter situation, successive generations alternate above and below an equilibrium value with decreasing amplitude (Varley et al., 1973).

Hassell et al. (1976) emphasise that density dependence alone cannot only lead to stable equilibria, but can also lead to patterns of stable cyclic oscillations and even to irregular and apparently chaotic population fluctuations. These patterns can arise in both continuously overlapping and non-overlapping generations. From the modelling of life table data for a large range of insect species with non-overlapping generations where density dependence had been demonstrated in single species populations, Hassell et al. concluded that most populations did not show extreme fluctuation and rapidly assumed an equilibrium following a disturbance. Exceptions to this were the data of Harcourt (1971) with Colorado potato beetle (Leptinotarsa decemlineata Say) where because of strong density dependent larval competition and adult migration together with a high net rate of population increase, populations fluctuated markedly with a tendency for density dependent mortality to overcompensate from generation to generation. The other exception was Nicholson's data on blowflies, which having a relatively high net growth rate

and being a laboratory population freed from many outside mortalities, exhibited high population densities and dramatic crashes. In multi-species populations and where migration and dispersal occur however, Hassell et al. point out that chaotic fluctuations may arise.

Density dependent mechanisms may include the action of certain predators, parasites and pathogens and inter and intra-specific competition for resources such as food (Clark et al., 1967). This competition, as well as causing direct mortality, may result in dispersal or a reduction in fertility and competition for breeding sites.

Varley and Gradwell (1970) pointed out that a directly density dependent mortality may be regulatory in contrast to the inversely density dependent mortality, the effect of which is to add to population instability and detract from the stabilising effect of a directly density dependent mortality. They considered however that mortalities which act in an inversely density dependent way throughout the whole range of a population's density are relatively rare. A delayed density dependent mortality may be present even when a directly or inversely density dependent mortality has not been detected. The effect is simply delayed to the next generation (Varley and Gradwell). An example of this type of mortality occurs in host-parasite systems where it is the parasite's rate of increase and not host mortality that is proportional to host density.

Solomon (1964) and Holling (1968) pointed out that the term density dependent should be restricted to processes or events, rather than be used to describe mortality factors. This is because some

factors, e.g. predation, may be density dependent over a certain range of densities, but inversely density dependent or density independent at other densities. East and Pottinger (1975) demonstrated this with starling predation of grass grub.

Natural enemies are considered by De Bach (1958) to be the only regulatory processes which are usually capable of controlling populations at low densities. Although intraspecific competition for food often sets the upper limit for populations of phytophagous insects as shown by Morris et al. (1958), Clark (1964), Readshaw (1965) and Harcourt (1971), Klomp (1964) considered this situation is rare in the vast majority of insects which never become pests. At densities below where food is in limited supply, Klomp (1964) concluded that mutual interference or aggression may influence mortality, reproduction or emigration in a density dependent manner.

The influences of dispersal on insect population dynamics are worthy of some consideration in this review in view of the inherent ability of black beetle adults to disperse at two periods in the life cycle. Dispersal is adaptive in action in that it permits a population to spread as the population increases (Price, 1975), and it enables the colonization of new sites. The studies of Wellington (1957,1960,1964) on the western tent caterpillar (Malacosoma pluviale) demonstrated that in populations which were polymorphic in activity, active migrants oviposited at places away from their origin, so colonizing more severe habitats or replenishing the vigour of other populations. During harsh climatic conditions individuals in marginal areas were killed and those in favourable habitats survived to recolonize all vacant areas as conditions

permitted. Shiga (1977) found that this adult dispersal was density dependent. Similarly, the studies of Harcourt (1971) on L. decemlineata discussed previously, showed that populations were both regulated and distributed by the principal key factor, adult migration, which was density dependent and overcompensating.

Price (1975) noted that the spatial dynamics of insect species are extremely important. Wellington emphasised the importance of the spatial relationships of a species in an area in understanding the change in population numbers in any one site. Price considers that setting up a single sample plot in an area can produce some rather bewildering results and often spurious conclusions, which demonstrates the importance of sampling an extensive area to obtain a clear picture of what is happening in the population. May et al. (1974) noted that the return time for populations displaced from equilibrium can be short-circuited by migration. Taylor and Taylor (1977) proposed a concept for the regulation of populations by density dependent movement with population density being spatially dynamic and the survival of a population being determined by the balance between migratory and congregatory behaviour. They considered much environmental mortality which results in death or dispersal is transient, especially that due to predation and disease or the loss of nesting sites or food. These 'holes in the environment' eventually recover their hospitality and are re-occupied by searching migrants and the population centres are seen as mobile on an appropriate time scale. This concept may be valuable in understanding the population dynamics of an insect such as black beetle with good dispersive ability.

(4) Population change

Density independent mortalities include both catastrophic factors which produce very variable mortalities as well as those which can be described by a constant as they vary so little (Varley and Gradwell, 1970). Often these will be caused directly or indirectly by the weather through temperature or rainfall (Solomon, 1960), although Varley and Gradwell consider food availability, parasites, predators and disease can have a density independent effect. In nature, these effects are often the key factors causing population change through a disturbing effect on the population. Varley and Gradwell stress the important point however that the effects of density independent mortalities could appear to be related to density if they were acting on a population in a diversified habitat, where increasing density resulted in an increasing part of the population being forced into regions of the habitat only marginally suitable for survival. Southwood (1977) also stresses this point for r-strategists where in the movement to a new habitat, an extremely high proportion of the total mortality will be density independent and associated with migration although the level of migration itself may be density related on a regional scale.

Although density disturbing factors or key factors may be density dependent and often arise from different mortality components than those causing regulation, the attempts of the early theorists to compartmentalise mortality action can now be seen as futile (Varley and Gradwell, 1970). Richards and Southwood (1968) pointed out that the same factor may be both regulatory and disturbing.

Such a situation occurred in L. decemlineata populations where Harcourt (1971) found that the regulatory factor, adult migration, was density dependent and was also the key factor disturbing the population and so determining population change.

(5) Population dynamics studies

The ultimate aim of long term studies of the population dynamics of insect pest species has been considered by many authors to be the provision of data which will permit control based on an understanding of pest ecology (Varley, 1950; Richards, 1961; Chant, 1964; Milne, 1965; Clark et al., 1967; Pottinger, 1967; Spingett, 1970; Southwood and Way, 1970; Price, 1975). Collection of data from natural populations enables the researcher to understand their functioning and so permits what Clark et al. (1967) consider the main objective, efficient ways of manipulating the populations to be devised.

Quantitative, multifactor studies of natural, single species insect populations were developed by such workers as Morris (1955, 1957), Varley and Gradwell (1960) and Richards (1961). The demographic life table for an insect population is a convenient way of tabulating data on the population density at different stages of the life cycle within one generation, together with fecundity and different mortalities. The modification and use of the life table have been discussed by Morris and Miller (1954), Morris (1955, 1957), Southwood (1966), Harcourt (1969), Varley and Gradwell (1970) and Varley et al. (1973).

Morris (1955,1957) stressed the importance of obtaining accurate estimates of population density, which form the basis of the life table, through the use of biometrically sound sampling methods. These will be discussed in section II of this chapter. A series of such life tables from a number of generations, covering a wide range of population levels and environmental conditions, is necessary in order to understand the dynamics of the insect (Morris and Miller, 1954). The major advantage of the development of a series of age-specific life tables is that it allows those mortalities which are important in population determination to be identified and quantified as stressed by Morris (1963), Watt (1963b), Varley and Gradwell (1970 and Varley et al. (1973).

Inherent in any study of the dynamics of an insect pest population is the ultimate aim of identifying both the important density regulating parameters influencing the population and factors which may be used in the prediction of change. However, as East (1978) points out, long term life table studies have generally failed to provide a complete understanding of the subject species' population dynamics, simply because it is not possible to measure all of the independent variables which might be affecting the population. The success of the life table approach in meeting its objectives will therefore depend on which variables are measured.

An understanding of the population dynamics of an insect pest species is not possible without some knowledge of the basic biological processes involved in determining population density. The study of single ecological processes in the laboratory or the field such as carried out by Holling (1963) on predation or the large

number of process studies carried out by workers such as Davidson et al. (1972a,b), Hilditch et al. (1974), Hassan (1975), Hassan and Hilditch (1976) on the effects of soil moisture and temperature on the complex of Australian Scarabaeidae in pastures are important to the understanding of population dynamics. As noted by East (1978), further advances in insect population ecology will depend upon the interpretation of both life table studies and accompanying experimental process studies.

(6) Life table analysis and Population modelling

The presentation, analysis and interpretation of data from insect population studies has undergone considerable refinement, modification and development over a period of some 20 years, to the extent that reasonably standardized approaches are now followed in most insect studies. In this section, techniques and analyses relevant to the understanding of black beetle population dynamics will be discussed.

The life table tabulates insect population density within one generation and in conjunction with data on fecundity presents survivals between age intervals and estimates of mortalities. The form of setting out a life table was suggested by Morris and Miller (1954) and has been widely followed (Varley and Gradwell, 1970). The form of presentation of life table data is dependent on the method of analysis. There have been three main methods developed for the analysis of life table data and construction of mathematical population models based largely on correlation and regression methods.

(i) Survival analysis

Watt (1961,1963b,1964) developed a method for describing actual changes in field populations in terms of a mathematical model. The technique involved the construction of a population model of the form $I = N_{\underline{n}+1} / N_{\underline{n}}$ where I = the index of population trend proposed by Balch and Bird (1944), $N_{\underline{n}}$ is the number of eggs in generation $\underline{n}$. Although Watt initially suggested 'I' should be based on the adult stage, Morris (1963) suggested the egg stage was the most uniform with respect to quality and so was preferred.

I for a generation is a function of the survival of the various life stages in the generation, with allowance for fecundity, sex ratio and adult migration (Morris, 1963). Watt proposed the construction of a series of inductive sub-models for the survival in each age interval expressed as a function of the important independent variables operating during the age interval by using multiple regression analysis. These sub-models are then integrated into a mixed deductive-inductive model where the mortalities expected from the sub-models are compared with the actual mortality. The eventual model should describe the index of population trend in terms of the survival of the different stages as related to the various mortality factors (Watt, 1961).

Age-specific population models developed in this manner mainly from an inductive approach have generally accounted for less than 50% of the variance in population change (e.g. Morris, 1963 ; Embree, 1965; Campbell, 1967). Usually some important variables have not been incorporated into the models, or interaction has not been accounted for (Mott 1963; Watt, 1963a,b). Morris (1963) pointed

out that it is unlikely that all independent variables can be identified, let alone measured in practice and Varley and Gradwell (1970) concluded that the biological value of a population model will largely depend on those variables chosen. For the development of models which determine population change and the regulation of population level, Varley and Gradwell (1970) pointed out that it is essential that each age interval is described by a sub-model which is both mathematically satisfactory and biologically meaningful. The ultimate success will therefore depend on whether or not workers have correctly identified the important factors and are able to measure them.

(ii) Morris's Key Factor analysis

Southwood (1966) noted that this method is both less demanding mathematically than survival analysis and is less costly, since precise population measurements are necessary for only one stage in each generation. The concept of a key factor that is largely responsible for population fluctuations put forward by Morris (1959) has been widely adopted (Varley and Gradwell, 1960; Watt, 1963b). Morris (1959) suggested that the measurement of the key factor would provide a means of prediction of the population in the next generation. Varley and Gradwell (1965) showed that a major problem of the method concerns the stage selected as the basis of I, i.e. the key factor may be different if the generation is taken from egg to egg compared with late larva to late larva. They suggested that for pest outbreak prediction the generation base should be from one damage-causing stage to the same stage in the next generation.

The methods of Morris (1959) for determination of key factors and their density relationships were reviewed in detail by Southwood (1966). The method is based on simple regression analysis of log transformed data from the life tables and the key factor or factors are recognized as the factors responsible for the majority of the deviations from the regression line of population size on survivors from the previous generation. The coefficient of determination, r^2, is taken as a measure of population stability and the regression coefficient, b, provides a measure of density dependence. This method has been criticised on both biological and mathematical grounds. Varley and Gradwell (1970) considered that an approach based on linear correlation between age interval survivals as the independent variables and generation survival as the dependent variable is valid only when the worker can guarantee there is no intercorrelation between the variables. They point out that in biological systems, intercorrelations are widespread and such covariance will largely invalidate the results.

Varley and Gradwell (1960) concluded that the initial determination of the key factor should be by visual comparison of graphs showing the change in log survivals (k-values) for the different age intervals and the changes in log-generation survival (total K) for the generations, each plotted against time.

In an appraisal of the methods of Morris (1959,1963) in analysing life tables, Luck (1971) concluded that although variations in mortality between generations could be detected, the density relationships of the mortalities could not be distinguished and the method is not recommended for life table analysis.

(iii) Varley and Gradwell's method

Varley and Gradwell (1960,1963,1968) developed methods to recognize the roles of individual mortalities in a series of life tables using graphical correlation. The difference between the log density from the life tables, before and after a mortality has occurred is called the k-value for each mortality. Total generation mortality K, is given by:

$$K = k_o + k_1 + k_2 + \text{- - - - } k_i$$

When the values of K and of each of the k_i's are plotted over a number of generations, the key age interval is determined as that which is most closely correlated with changes in K. Podoler and Rodgers (1975) pointed out that while visual comparison often identifies the key factor, there is a need for a further test where the key factor is not immediately obvious and also to investigate the relative importance of changes in each mortality to changes in K.

Hassell and Huffaker (1969) and Harcourt (1971) used a high correlation coefficient between the values of K and individual mortalities to indicate the key factor. Metcalfe (1972) calculated the regression coefficients of K on individual k_i's. This latter method has the disadvantage that the regression coefficients of non-key factor mortalities have very high values (Podoler and Rodgers, 1975) while correlation methods identify the key factor as that mortality which can be used to predict total mortality or the population at some time in the future. This fits one of the two key factor definitions of Morris (1959). However, Podoler and Rodgers pointed out that the calculation of regression coefficients

is the most appropriate method to determine key factors which explai- and describe changes in population density over a number of generations. They also suggested that the regression coefficient be calculated from a plot of k-values on the y-axis against K-values or the X-axis and showed that this method identified the key factor in the data from a large number of vertebrate and invertebrate population studies.

Varley and Gradwell (1960,1963,1968,1970) and Varley et al. (1973) investigated the density relationships of the various k_i's by testing the regression of each k_i on the log of the numbers entering each age interval. If the regression is significant, density dependence may be suspected. As the two variables are not however independent, density dependence can be proved by plotting the log of the population density after the mortality has acted against the logarithm of the initial density. Both regression coefficients ($b_{y.x}$ and $b_{x.y}$) should differ significantly from 1.0 and both lines should lie on the same side of the line b = 1 (Varley and Gradwell, 1970; Luck, 1971). In addition, $b_{y.x}$ and $b_{x.y}$ should both differ significantly from zero (Benson, 1973).

The test can prove but cannot disprove density dependence (Varley and Gradwell, 1970). Benson (1973) also noted that the test fails when the slope of the regression of k on log initial density approaches closely to 1.0

Southwood (1966) concluded that Varley and Gradwell's method allows:

> The recognition of the key factor (or factors) or the period in which it acts.

The investigation of the role of mortality in population dynamics.

The consideration of the role of mortality factors at every stage of the life cycle, the recognition of the different density relationships of these factors and an indication of their mode of operation.

The population models of Varley and Gradwell (1968,1970) and Varley et al. (1973) for the winter moth have provided a satisfactory explanation for the average population level of the insect and insight into the interaction of the various mortality factors. The objective of explaining why the observed changes in population numbers takes place about a particular average level has been met by these models. It is perhaps, because of this success and the relative simplicity of the methods used, that the Varley and Gradwell techniques have been widely adopted by researchers. Metcalf (1972) eloquently summarised the situation when he stated "the reliability of the Varley and Gradwell method of analysis is now beyond doubt".

II SAMPLING INVERTEBRATE POPULATIONS

As a frontispiece to his book, "Ecological Methods", Southwood (1966) included the following extract of a review by Richards (1961), possibly intended as a warning to researchers embarking on sampling programmes as part of a study of population ecology. "Most population theories, as far as they are not purely inductive, are based on imperfect field data that are not derived from planned population studies in which all the relevant factors were measured simultaneously ....". In his comprehensive study of the sampling of populations of grass grub, Kain (1975) considers that, "usually, the main object of census sampling invertebrate populations is to obtain as accurate and precise an estimate of population density as possible with given resources, or a predetermined level of precision for the lowest possible cost."

The following sequence of events have usually been followed in the development of most sampling programmes. After deciding on the universe or habitat to be sampled, the most efficient sampling unit is determined, based on the criteria of the lowest variance and cost of different sized units. The sampling times must be chosen with a view to giving as much information as possible on population density and the various mortalities which may operate in the population. A knowledge of the spatial distribution of the population is necessary in order to allow for any stratification of habitat that must be built into the sampling plan and the possible need for transformation of the data. After deciding on the sampling plan, the sample size necessary for different stages of the invertebrate's developmental stages is estimated and sampling costs assessed to see if the study is feasible within the limits of available resources.

Inherent in any population study is the need to count the invertebrate stages present in the sampling unit, which in the case of soil insects involves the development of an efficient and accurate extraction system.

In view of the need to develop a sampling programme and extraction system to obtain population estimates for a study of black beetle dynamics, the above topics will be considered in a review of the literature on soil inhabiting invertebrates.

(1) Selection of the sampling unit

When choosing a sampling unit, it is customary to evaluate varying sizes with the optimum unit being the one which gives the lowest variance for the minimum cost. The size of the sampling unit is influenced by the distribution of the population. When the distribution of the insect is clumped or contagious, a smaller sample unit reduces the total area required to be sampled for a given level of precision (Taylor, 1953; Finney, 1946; Yates and Finney, 1942; Fleming and Baker, 1963; Burrage and Gyrisco, 1954).

When evaluating sample unit size for contagiously distributed grass grub populations, Kelsey (1967) found that a 3 inch (7.5 cm) diameter core was statistically superior to larger sampling units. Kain (1975) investigated sample unit sizes of 5 cm and 10 cm diameter soil cores and 14 x 14 cm spade squares for grass grub populations. He found that for all population densities, the 10 cm diameter core was much more efficient on a time for equal precision basis than the other sampling units.

In addition to the parameters of precision and cost, the suitability of a particular sample unit to the physical environment of the population must be considered. Although East (1972) decided a 4 inch (10 cm) diameter core was a reasonably good size for sampling grass grub populations, on stony soils where the core was not feasible, a 6 inch (15 cm) spade square was used as the sample unit.

In comparing different sized sample units, the cost (in man hours) to locate and take sample units of different size (C_u), is related to the variances of each of the different units (S_u^2) (Southwood, 1966). The relative net cost for the same precision for each unit is proportional to $C_u S_u^2$ (Finney, 1946; Lyons, 1964). For comparative purposes, the efficiencies of the different sized units are calculated and then reduced to a common base, which is usually the size of the smallest sample unit.

(2) Timing of sampling

Morris (1955) pointed out that the stage to be sampled should be present in the field for a long period or at least sufficiently long to allow the survey to be completed before an appreciable number have developed to a later stage. Also, the easier the stage is to sample and count the better. In reviewing timing, Morris (1955, 1960) considered that periods in the life cycle where high mortalities occur should be avoided.

Usually, sampling times will be dictated by the life cycle of the insect and some knowledge of this is a pre-requisite to logical timing (Graham and Stark, 1954). Timing of sampling is more difficult with multivoltine insects due to problems of overlap of generations.

Both East (1972) and Kain (1975) found that with the univoltine grass grub, overlap between stages was not very pronounced. Morris (1955) suggested pilot sampling of the population as an indicator of optimum sampling times. From pilot sampling of grass grub populations and observation of adult flight, East (1972) and Kain (1975) were able to rationalise sampling intervals in order to provide accurate estimates of populations between eggs and adults in order to collect data for life table studies. In most instances it was possible to time sampling to periods when 90% or more of the total grass grub population was in the desired age interval.

Accurate estimates of age interval mortality become increasingly difficult when the period over which numbers enter the age interval becomes very extended. For example, where oviposition continues over a long period as in black beetle it may not be possible to estimate the total egg population from a single sample. The total population may have to be estimated from a series of successive samples and a graphical method used to determine the total number of individuals. Southwood (1966) reviewed methods of obtaining age-specific population estimates for life table studies where migration or considerable overlap between stages occurs. All these techniques involve successive population estimates within the same age interval which are costly and time consuming for soil-dwelling insects such as scarabaeids.

(3) Spatial distribution

As noted by Southwood (1966), the spatial distribution or dispersion of a population is of considerable ecological significance as it affects the sampling programme and method of data analysis and

provides information on changes in the distribution during the life cycle.

(a) Frequency distributions

As most parametric statistical tests assume that the population is normally distributed with the variance being independent of the mean and its components additive, the frequency distribution of the insect studied requires examination. Waters and Henson (1959) suggest that the fitting of a frequency distribution model can be of use in planning sampling programmes and selecting transformations. The dispersion pattern of individuals in a population is seldom if ever normal (Southwood, 1966), but rather, it falls into one of three categories, random, uniform or contagious.

In a random distribution, the dispersion of which is described by the Poisson distribution, the variance is equal to the mean. Taylor et al. (1978) define spatial randomness as that disposition of individuals in space which results from a lack of response of any one individual to any other or to its environment. In many cases, random distributions are an artifact of low mean densities (Southwood, 1966). Iwao (1970) considered that this seems to arise from a statistical deficiency, in that frequency distributions may not detect aggregation at low densities. Small sample units may also induce a similar effect (Waters and Henson, 1959). In the second situation of a uniform or regular pattern of dispersion, the variance is less than the mean. These distributions are rarely found in natural animal populations (Iwao, 1970).

The third type is the contagious distribution where the population is clumped or aggregated and the variance is larger than the

mean. This is the one most commonly found in ecological studies and may result from mutual attraction between individuals, sexual attraction, heterogeneity in the habitat, reproductive behaviour and a limited ability for dispersal (Southwood, 1966; Bliss and Calhoun, 1954; Iwao, 1970).

In insect studies, the frequency distribution model that has proved most useful is the negative binomial distribution of Anscombe (1949). This distribution is described by two parameters, the mean ($\bar{x}$) and the exponent k, which is a measure of the amount of clumping and is often referred to as the dispersion parameter (Southwood, 1966). This parameter can be computed from a number of methods which were reviewed by Southwood (1966). In general, values of k are in the region of 2. Southwood noted that with increasing randomness k tends to infinity to give the Poisson series, and with increased aggregation k tends to zero to give the logarithmic series. The value of k is not a constant for a population, but often increases with the mean (Anscombe, 1949; Bliss and Owen, 1958; Waters and Henson, 1959).

East (1972) and Kain (1975) found that the negative binomial distribution was useful for describing the dispersion of some stages of the grass grub life cycle, but not others. Plunkett and Kain (1978) showed that this distribution was also useful for interpreting the causes of changes in grass grub dispersion with development.

Taylor *et al.* (1978) consider that the approach of understanding spatial distribution by analysis of the frequency distribution of insect counts, especially those based on the negative binomial have severe limitations. Finney (1941) showed that changes in the

population density of wire worms and in development can lead to changes or apparent changes in the distribution. Iwao (1970) noted that the observed distribution can be approximated by more than one model. McGuire et al. (1957) found that in various samples of European corn borer (Pyrausta nubilalis Hbn) larvae at different densities, several distributions would fit, but not always the same ones. Taylor et al. (1978) point out that the value of a fitted frequency distribution model lies largely in the graduation of data to stabilize statistics for use as population parameters and is correspondingly diminished if the model changes at different population densities or sample sizes. They consider that if k is to be used as a specific population parameter, the negative binomial must fit at all densities and the behaviour of k must be consistent.

From an analysis of population data from 102 animal species, including soil dwelling Coleoptera, Taylor et al. (1978) found that only data from two species adequately fitted the Poisson model. They concluded that spatial behaviour was density-dependent and that true randomness was a biologically rare phenomenon.

(b) Transformation

The analysis of variance of population data assumes three factors are operating which are discussed by Sokal and Rohlf (1969). These are:

(i) The sample counts are normally distributed;

(ii) The variance is independent of the mean;

(iii) Separate variance estimates are independent, i.e., the variances are additive through there being no interaction.

Insect population distributions seldom satisfy these assumptions. Transformation of the data may be carried out where the actual numbers are replaced by a function whose distribution is such that it normalises the data or stabilises the variance (Southwood, 1966). Hayman and Lowe (1961) point out that it is of greater importance to satisfy assumption (ii) than (i), and this improves the validity of (iii), (Bliss and Owen, 1958).

There are a wide range of possible transformations available for insect counts some of which were reviewed by Southwood (1966), although opinion is divided as to the necessity for transformation. Guppy and Harcourt (1970) found that the spatial pattern of a scarabaeid, Phyllophaga spp conformed to the negative binomial distribution, and sample data of eggs, larvae, pupae and teneral adults were transformed to stabilize variance (Guppy and Harcourt, 1973).

The transformation of grass grub counts was examined in detail by East (1972) and Kain (1975). In contrast to Guppy and Harcourt (1973) they decided not to transform the data. East and Kain both concluded that the consensus of opinion suggests that moderate departures from normality do not induce errors large enough to require transformation of population data. They presented the findings of Hey (1938), Bartlett (1935), Pearson (1931), Le Roux and Reimar (1959), Wadley (1967) and Scheffe (1959) in support of this. Cochran (1963) noted that good sampling practice may tend to make the approximation of the normal distribution more valid. In addition, the removal of extremes by stratification from the main body of population reduces skewness and therefore improves the normal approximation.

A major disadvantage of using transformation in life table studies arises when different transformations are used, necessitating the transformation of transformed means back to the original scale (Finney 1941; Neyman and Scott, 1960). East (1972) noted the arguments of Le Roux and Reimer (1959) and Abrahamsen and Strand (1970) for not transforming population counts for analysis of variance unless the assumptions are seriously invalidated. This is particularly so in life table construction as the arithmetic mean of the raw data, which provides an unbiased estimate of the number of insects per unit area, is the primary object of sampling (van Emden et al., 1961; Lyons, 1964).

As further support of non-transformation, the central limit theorem states that the distribution of means of large samples from any population tends to normality with a standard deviation of $\sigma/\underline{N}$ where σ is the population standard deviation and $\underline{N}$ the sample size (Cochran, 1963). To estimate how large $\underline{N}$ must be before the central limit theorem can be used safely to calculate confidence limits for samples from highly skewed populations, Cochran (1963) recommended the following equation to estimate $\underline{SN}$, the number of samples required:

$\underline{SN} = 25\ G_1^2$ where G_1 is Fisher's measure of skewness.

Kain (1975) calculated $\underline{SN}$ from this equation, and the number of samples required to give an estimate of the mean population density with a standard error equal to 10% of the mean for all stages in grass grub population development. Generally, the latter required approximately two to three times as many samples as the former. As Kain (1975) found that relative standard errors of 10% were generally attainable during his study, sample sizes large enough to assume that

the central limit theorem was applicable were not prohibitively high. East (1972) reached similar conclusions with grass grub populations in Canterbury.

Both East (1972) and Kain (1975) calculated the sample variance from the stratified population sampling they carried out, using the equation of Cochran (1963), (discussed in the next section) which does not assume homogeneity of the within stratum variance. In view of these arguments, analysis of the grass grub population dynamics studies of both these workers was carried out on non-transformed data.

(4) Sampling pattern

When the aim of a sampling programme is to obtain estimates of the mean population density for use in life tables, then it is desirable to minimise variance (Southwood, 1966). The sampling should be devoid of bias and should be random (Wadley, 1967) so that every sampling unit in the universe has an equal chance of selection. When the sample sites are being selected at random using random numbers, the majority of samples may end up from the same area which may maximise the variance (Southwood, 1966).

To overcome this problem, stratified random sampling is preferred for ecological work (Yates and Finney, 1942; Healy, 1962), i.e., the area is divided up into a number of subdivisions or strata, and at least two samples are randomly selected from each stratum. The variation between strata means is eliminated from the sampling error, and the variance of the population mean arises solely from the variation between sampling units within the strata (Sampford, 1962; Cochran, 1963). Snedecor and Cochran (1967) noted that an increase

in precision from stratification will result when the variance within individual strata is less than the overall variance of the population, and so populations should be divided into as homogeneous sub-groups as possible.

With some populations, this latter approach is not feasible. In the absence of a stratifying variable which is closely correlated with population density, it is usual to divide the habitat into equal sized strata and allocate samples proportionately between them. This does not lead to large gains in precision (Cochran, 1963; Snedecor and Cochran, 1967), but it is better than simple random sampling as it improves sample representivity (Finney, 1948; Healy, 1962; Lyons, 1964; Abrahamsen, 1969; Guppy and Harcourt, 1970, 1973).

The basic formulae for stratified random sampling as given by Cochran (1963) are as follows:

$$\bar{\bar{x}} = \Sigma W_h \bar{x}_h$$

$$W_h = \frac{N_h}{N}$$

$$s_{\bar{\bar{x}}} = \sqrt{\Sigma W^2_h \frac{s^2_h}{n_h}}$$

where $\bar{\bar{x}}$ is the estimated population mean

W_h is the weight attached to the h_{th} stratum;

$\bar{x}_h$ is the sample mean for the h_{th} stratum;

N_h is the total number of sampling units in the h_{th} stratum;

N is the total number of sampling units in the universe;

$s_{\bar{\bar{x}}}$ is the standard error of the estimated mean;

s^2_h is the sample variance for the h_{th} stratum;

n_h is the number of sampling units taken in the h_{th} stratum.

In proportional allocation, the sampling fraction is the same in every stratum, which means:

$\frac{n_h}{N_h} = \frac{n}{N}$ where n $(= \sum n_h)$ is the total number of sampling units in the sample.

Following Cochran (1963) the formulae for $\bar{x}$ and $S_{\bar{x}}$ become:

(i) $\bar{\bar{x}} = \frac{\sum n_h \bar{x}_h}{n}$ (ii) $S_{\bar{x}} = \sqrt{\frac{W_h S^2_h}{n}}$

Cochran (1963) states that if S^2_h can be safely assumed to be the same in all strata:

(iii) $S_{\bar{x}} = \frac{S^2_W}{n}$ where S^2_W is a pooled estimate of the within stratum variance calculated from an analysis of variance of the data. Yates (1965) considered that in practice with proportional allocation, it is normally quite safe to use the pooled variance estimate, even when the within stratum variances differ widely. Sampford (1962) showed that when the strata are of equal size, formulae (ii) and (iii) yield the same result. Cochran (1963) considered that at least six samples are required per stratum in order to obtain a reliable estimate of the stratum mean and variance.

An alternative to random sampling within strata is the systematic sample approach where the sample is taken at a fixed interval in space. This is more likely to be used where population density cannot be correlated with any stratifying variable, such as pest damage. Milne (1959) discussed a centric systematic area-sample and showed that if it is analysed as if it were a random sample, the resulting statistics are at least as good, if not better, than those

obtained from random sampling. With this technique a sample is drawn from the exact centre of each area or stratum.

Although the pattern has the theoretical weakness that sampling may coincide with some unsuspected systematic distribution pattern, Milne (1959) pointed out that only rarely, if ever, will unsuspected periodicity be sufficiently perfect in pattern to be a danger. Southwood (1966) pointed out that a systematic sampling programme may be carried out more quickly than the random method and so has a distinct cost advantage.

Both East (1972) and Kain (1975) carried out extensive investigations of alternative sampling programmes for grass grub populations. East (1972) found that stratified random sampling with proportional allocation where ten, 10 cm cores were taken at random from 40, one chain square plots gave no gain in precision over simple random sampling for the grass grub egg stage and only a slight gain for the first and second larval instar stages.

Kain and Atkinson (1970), East (1972) and Kain (1975) have shown that as nearly all grass grub larval populations are found in patches of visible pasture damage and in the surrounding undamaged margin, it is possible to stratify sampling on damage criteria, with large gains in precision over simple random sampling.

(5) Sample size

The total number of samples taken in a sampling plan depends on the level of precision required. Morris (1955) working with spruce budworm, first suggested that the sampling plan should be designed so that the standard error is 10% of the sample mean and this arbitrary

proposal has since been widely used in insect population sampling. The number of sampling units necessary (N) for a 10% relative standard error is given by:

$$N = \frac{\underline{s}^2}{(0.1\ \underline{\bar{x}})^2}$$

where $\underline{s}^2$ and $\underline{\bar{x}}$ are the sample variance and mean respectively.

Rojas (1964) has shown that if the dispersion of the population has been found to be well described by the negative binomial, the desired number of samples for a 10% level of precision is:

$$N = \frac{1/\underline{\bar{x}} + 1/\underline{k}}{(0.1)^2}$$

where $\underline{k}$ is the dispersion parameter of the negative binomial discussed previously in this section.

Using stratified sampling programmes both East (1972) and Kain (1975) achieved relative standard errors of less than or close to 10% of the mean for all grass grub stages apart from eggs. Only in years when egg populations were high did egg sampling provide this degree of precision (Kain, 1975), but even with low egg populations, the level obtained did not exceed a relative standard error of 20%.

(6) Extraction techniques

The extraction of soil-inhabiting invertebrates from samples and in particular methods used with scarabaeids have been reviewed in great detail by both East (1972) and Kain (1975) as a prelude to their development of an efficient extraction system for all grass grub life stages. As the techniques developed by these authors have proved so eminently successful for extracting all scarab stages from soil

samples, the literature from which their systems were developed will not be reviewed again. The grass grub extraction system which was used in this study for the small life stages of black beetle has been described in detail by Kain and Atkinson (1976). This method has a much faster processing rate in comparison with those of Salt and Hollick (1944) and Cockbill *et al.* (1945), and is ideally suited to the large number of samples required for precise estimates of population density.

SECTION 2

PRE-ADULT ECOLOGY

CHAPTER 4

INFLUENCE OF TEMPERATURE AND SOIL MOISTURE

I INTRODUCTION

Poikilotherms need heat from their environment for normal development to take place, growth rates in arthropods at least being proportional to the environmental temperatures within a given range peculiar to a species (Wigglesworth, 1965). When development rates at different temperatures of a particular stage of an insect are plotted against time, the result is usually a sigmoid curve (e.g. Matteson and Decker, 1965) with development rate linear in the normal temperature range and falling off toward the upper and lower threshold temperatures.

The literature shows the importance of soil temperature and moisture conditions to the growth and survival of scarabaeids. Although soil inhabiting insects are buffered to some extent from the wide fluctuations occurring in air temperatures, the considerable variations noted in soil temperatures have been shown to markedly influence scarabaeid life history and survival. Temperature has been shown to influence the incubation times of scarabaeid eggs, e.g. grass grub (Wightman, 1973), Amphimallon majalis (Shorey et al. 1960) and Phyllopertha horticola (Milne and Laughlin, 1956).

While low temperatures have been shown to extend the grass grub life cycle (Stewart and Stockdill, 1972), high soil temperatures are known to cause larval mortality in spite of adaptive processes in behaviour (Kain, 1975). Within the temperature tolerance range, known

to vary between scarabaeid species, development and growth generally increase with temperature, as has been shown to occur in Phyllophaga sp. (Sweetman, 1931), in Popillia japonica (Ludwig, 1932), in Phyllopertha horticola (Laughlin, 1964), in Anomala orientalis (Nakamura, 1965) and in Sericesthis nigrolineata (Cairns, 1972; Ridsdill Smith et al., 1975).

An uptake of water is characteristic of scarabaeid eggs as shown for grass grub eggs by Galbreath (1970) and Wightman (1973). This also occurs in several other groups of subterranean insects (Imms, 1964). It is usually obligatory if embryonic development is to be completed (Browning, 1967), and is presumed to be a mechanism whereby the water content of the parent insect's haemolymph is conserved in situations where water is available to the eggs, a condition usually fulfilled in the soil. First instar scarabaeid larvae, like eggs, are susceptible to extremes in soil moisture (Maelzer, 1961a; Wightman, 1973; Hassan, 1975).

In this chapter the influence of temperature and soil moisture on the growth and survival of black beetle eggs and first instar larvae is briefly examined. The study of these two physical soil factors is confined to the first two developmental stages as these are present in the soil in spring and early summer when the greatest fluctuations in moisture and temperature occur. In addition, a study was carried out of the influence of soil temperatures on the food consumption, growth and survival of second and third instar black beetle larvae which occur in the soil in summer and early autumn when soil temperatures are at their highest levels.

II EGGS

(1) Effect of temperature on development

(a) Methods

The influence of temperature on the rate of egg development and egg viability was assessed using newly laid eggs obtained from black beetle females from the Otakanini Research Area maintained with males on a carrot diet (for convenience), at Ruakura. The temperatures used in the trial were 10 ^{o}C and 25 ^{o}C maintained using water baths, and 15 ^{o}C and 20 ^{o}C using controlled temperature rooms. Eggs were taken from a soil medium immediately after oviposition, washed in a 4% solution of sodium hypochlorite and then placed in plastic phials on filter paper discs moistened with the same solution to inhibit the growth of fungi and bacteria. At each treatment temperature 50 eggs in 10 phials, each with five eggs were tested. The phials were examined at intervals to determine signs of egg development and to remove newly hatched larvae.

(b) Results and discussion

The rates of egg development and hatching at the four temperatures are shown in Table 4-1.

The fastest rate of egg development occurred at 25 ^{o}C where 58% had hatched after 17 days. The highest level of egg viability also occurred at this temperature. Development was slightly slower at 20 ^{o}C where only 36% of the eggs hatched, but development at both 20 ^{o}C and 25 ^{o}C occurred more rapidly than at the lower temperatures.

No egg hatching occurred before 40 days at 15 ^{o}C and the number of viable eggs had decreased to about half that at 25 ^{o}C. Eggs

Table 4-1 The rate at which black beetle eggs hatched and the percentage hatching at four temperatures (50 eggs in each temperature treatment).

Temperature	Number of eggs hatched - days after start of trial										% hatching
°C	10	17	23	26	30	35	40	45	50	55	in 55 days
10	0	0	0	0	0	0	0	0	0	0	0
15	0	0	0	0	0	0	0	9	5	0	28
20	0	0	16	1	1	0	0	0	0	0	36
25	15	12	0	0	0	0	0	0	0	0	58

commenced swelling as moisture was absorbed in the first few days of the trial at 20 °C and 25 °C. Some evidence of egg swelling was noted after 26 days at 10 °C. However, no hatching had occurred after 55 days at this temperature. Eggs that were still viable could be distinguished by a pearly white colouration compared with the brown shrivelled appearance of non-viable eggs. Of the 24 eggs that were viable at the end of 55 days at 10 °C, 14 of those hatched in six days after being placed in the 25 °C waterbath. At this lowest temperature, 28% of the initial number of eggs placed in the trial were able to hatch under the development stimulus of the higher temperature.

These results indicate that black beetle egg viability may be greatly reduced in cooler New Zealand spring soil conditions relative to the warmer soil temperatures found in southern Africa. The soil temperatures that were recorded during spring at the Otakanini Research Area, and the influence of this on black beetle population development are discussed in Section 4, Chapter 14.

(2) Effect of soil moisture on hatching

(a) Methods

To investigate the influence of soil moisture levels on the rate of development and viability of black beetle eggs, a laboratory trial was undertaken in January/February 1976. Male and female adults were collected in November from paddocks of maize at Ruawaro near Huntly and held in a soil medium on a carrot diet at 20 °C in a constant temperature room. As the trial involved a large number of treatments, it was carried out in two halves. The first half of the trial commenced on 12 January, the treatments being 5%, 15%, 25%, 40%

and 55% soil moistures by weight. The second half of the trial commenced on 3 February with 8.5%, 12.5%, 32.5%, 47.5% and 60% soil moisture treatments. Both halves of the trial were carried out the same way and continued for four weeks.

Eggs were separated from the soil medium by sieving. Newly laid eggs which had not commenced swelling were taken from the sample and placed in the soil moisture treatments, 100 eggs per treatment, in groups of five eggs in each of 20 small plastic pots with snap-on lids. The medium was Redhill sandy loam from the Otakanini Research Area, oven dried, then brought to the desired soil moisture level by the addition of water.

All pots in both trials were held at 20 ^{o}C and were examined at weekly intervals, the degree of egg development noted and the newly hatched first instar larvae counted. Some difficulty was experienced in recovering all the eggs from some pots and therefore the data are presented in two ways, viz.: the percentage of the total eggs which hatched over the three week trial period, and the number which hatched as a percentage of the eggs actually recovered.

(b) Results and Discussion

The effect of soil moisture on the hatching of black beetle eggs is shown in Table 4-2.

Although the two halves of the trial must be considered separately due to the time interval, there is a very good level of correlation if the two moisture series are integrated as is shown in Fig. 4-1. The most remarkable aspect of the data is the high degree of tolerance eggs have when continuously exposed to a range of moisture levels. A situation where eggs are subjected to a continuously

Table 4-2 The effect of soil moisture (by weight) on the hatching of black beetle eggs (100 eggs in each soil moisture treatment).

% Soil Moisture	Eggs hatching as % of total eggs	Eggs hatching as % of eggs recovered
Trial A		
5	0	0
15	55	70
25	60	80
40	67	86
55	60	69
Trial B		
8.5	0	0
12.5	12	20
32.5	74	91
47.5	61	70
60	0	0

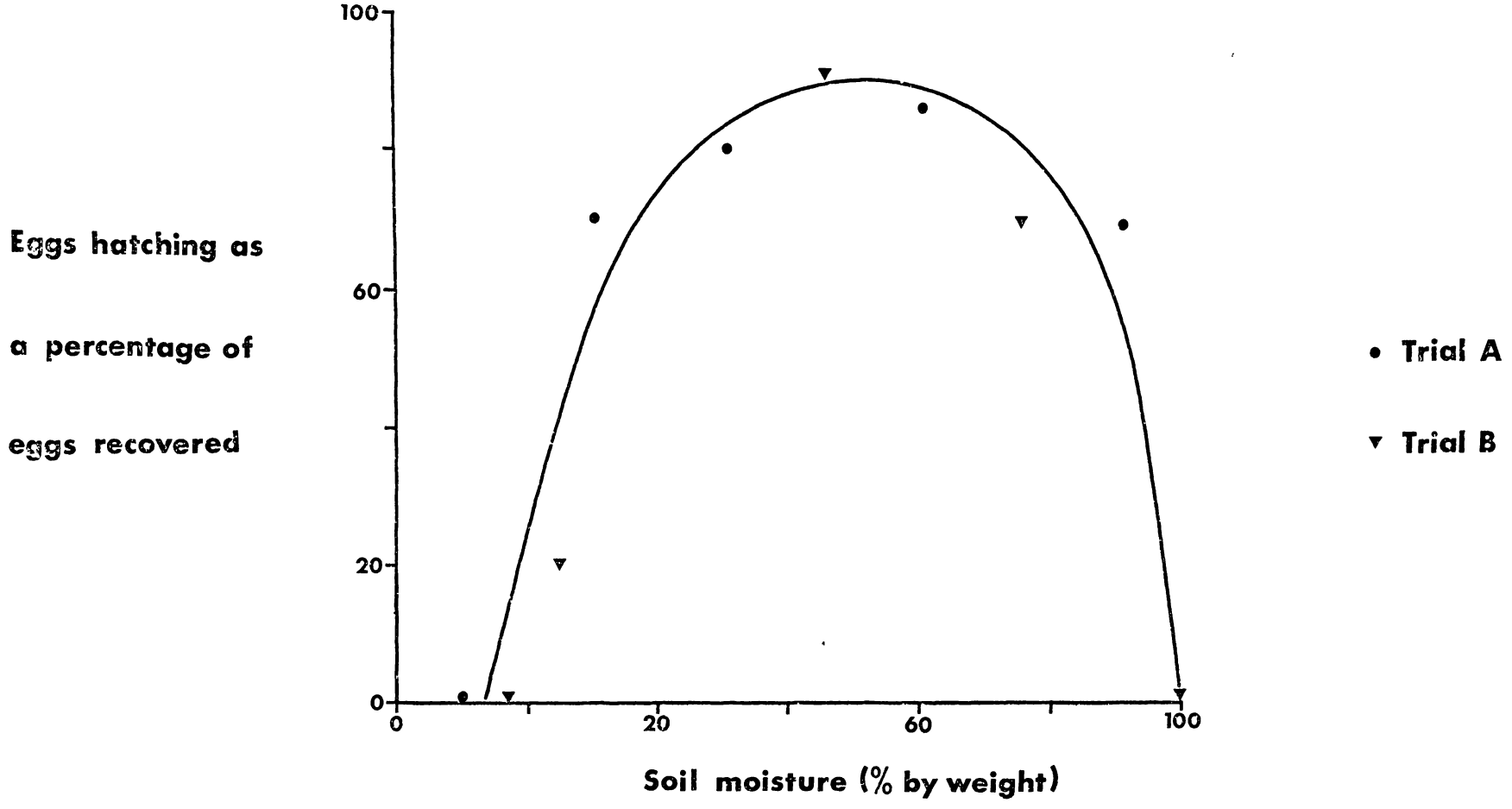


Figure 4-1 Influence of soil moisture on the hatching of black beetle eggs (results from two trials, line fitted by eye).

high level of soil moisture in the field is unlikely to occur. Monitoring of soil moistures under several pasture types for several seasons at the Otakanini Research Area has shown that levels fluctuate between 30% - 55% in the top 6 cm of the soil profile in the spring-early summer period when oviposition and egg development occur, as is discussed in Section 4, Chapter 14.

No hatching occurred at the two lowest moisture levels. Eggs rapidly desiccated and developed a brown colouration in these treatments. In trial A, the data for the number of eggs hatching expressed as a percentage of the eggs recovered suggest an optimum level lies in the 25% - 40% range. A satisfactory level of hatching was still recorded at the 55% soil moisture treatment. In trial B, peak hatching took place at the 32.5% moisture level which falls within the suggested optimum range from trial A. The zero level of egg survival recorded at 60% indicates that for the Redhill sandy loam, soil moistures above 55% have an adverse effect. At the 60% level, free water actually covered the soil, probably causing egg mortality through an oxygen deficit. Such conditions would not normally occur in field situations where black beetle is a pest as drainage usually ensures soils spend little time above field capacity.

In trial A, swelling of the eggs as moisture was absorbed had taken place in all treatments, except 5% soil moisture, after one week. After two weeks first instar larvae were recovered from all treatments except 5% and 15% showing that development was slower at 15% than at 25%. Peak egg hatching appeared to occur between two and three weeks after the start of the trial but was still slower at 15% soil moisture.

In trial B, after 13 days, 4 and 6 eggs had hatched in the 32.5% and 47.5% treatments respectively, but none were recovered from the 12.5% soil moisture level. Hatching commenced in this treatment after 17 days. Peak egg hatching occurred at the 32.5% and 47.5% levels between 14 and 17 days after the start of the trial.

In this trial run at 20 ^{o}C, the time of around 14 days before hatching commences over the favourable soil moisture range was almost a week less than that recorded at the same temperature in the trial detailed in II(1) of this chapter. The difference is most likely explained by the absence of a moist medium encompassing the eggs when placed on filter paper in the latter trial.

The relatively high tolerance of black beetle eggs to a range of soil moisture levels suggests that mortality induced by variation in this physical soil parameter is likely to be of minor importance as a component in the total pre-adult mortality.

III FIRST INSTAR LARVAE

(1) Effect of temperature on growth

(a) Methods

Black beetle male and female adults were collected from pasture at the Otakanini Research Area in spring and maintained in soil medium on a carrot diet as a convenient food source, at 20 ^{o}C at Ruakura. In January, eggs were collected and placed in petri dishes on filter paper moistened with 4% sodium hypochlorite solution. A sample of 40 newly emerged first instar larvae were weighed to establish the weight range before feeding. The mean weight was taken as the initial larval weight in the following trial.

Newly emerged larvae were placed singly in screw top phials containing Redhill sandy loam soil medium at 30% soil moisture (on a weight basis). No food source other than the soil was provided. Twenty larvae were tested at each of four temperatures. The temperatures were 10 ^{o}C and 25 ^{o}C, maintained using water baths, and 15 ^{o}C and 20 ^{o}C using controlled temperature rooms. Larval growth was monitored over the 15 day trial period by weighing individual larvae every three days and then replacing them in the phials with fresh soil medium.

Larval growth was calculated in two forms. As a mean weight gain calculated per day and then expressed as mg/larva/week, and in the form suggested by Waldbauer (1968), as relative growth rate (G.R.) which is the larval growth in mg/mg of mean fresh weight of the larva during the feeding period/week.

(b) Results and Discussion

The mean weight of newly emerged first instar larvae in the sample weighed at the commencement of the trial was 3.8 $\pm$ 0.6 mg (range 2.4-5.0 mg). To reduce unnecessary handling of the larvae mean weight was taken as the initial weight of larvae placed in each of the temperature treatments. The mean larval weight gains and growth rates at the treatment temperatures are shown in Table 4-3, and in Appendix 4-1.

Larval survival did not differ significantly over the trial period between treatments. To avoid problems with larvae evacuating the gut and ecdysing at the higher temperatures, the trial was concluded after 15 days. First instar larvae are very delicate and easily damaged during handling. Mechanical damage caused when

Table 4-3 The effect of temperature on the survival of first instar black beetle larvae, mean weight gain and mean relative growth rate (G.R.).

Temperature °C	Number of insects surviving (out of 40)	Mean weight gain mg/larva/7 days ± standard error	G.R. mg/mg larva/7 days ± standard error
10°	11	0.07 ± 0.32	0.016 ± 0.137
15°	11	0.37 ± 0.38	0.090 ± 0.092
20°	14	1.10 ± 0.28	0.251 ± 0.128
25°	12	3.36 ± 1.17	0.584 ± 0.180

retrieving larvae from the soil and during weighing has probably resulted in the relatively low survivals.

The larval weight gains and relative growth rates as a function of temperature are shown graphically in Figures 4-2 and 4-3 respectively. The data exhibit the characteristics of the exponential growth curve, both the changes in larval weight and in the growth rate increasing rapidly as temperature increases. Such growth can be described by the regression equation

$$W = (A)(B^{x})$$

where A and B are estimated constants and the exponent x = temperature ^{o}C. Applying logarithms to the equation results in the linear relationship

$$Y = \alpha + \beta X$$

where Y = log W (weight change), α = log A, and β = log B, and x = temperature ^{o}C.

This linear relationship can be seen in the figures for both larval weight gain and growth rate. Slopes of the linear regressions are significantly greater than zero in both Figure 4-2 ($P < 0.01$) and Figure 4-3 ($P < 0.05$) and the respective correlation coefficients (r) are 0.992 ($P < 0.01$) and 0.973 ($P < 0.05$). The influence of temperature on the growth of first instar larvae thus follows the exponential law, over the range of temperatures tested.

Of considerable interest in the data for the weight change of individual larvae at 10 ^{o}C and 15 ^{o}C is the occurrence of weight losses. Four larvae alive at the end of the trial lost weight over the 15 day period at 10 ^{o}C, and two larvae at 15 ^{o}C. All surviving larvae at 20 ^{o}C and 25 ^{o}C made weight gains. The weight loss of

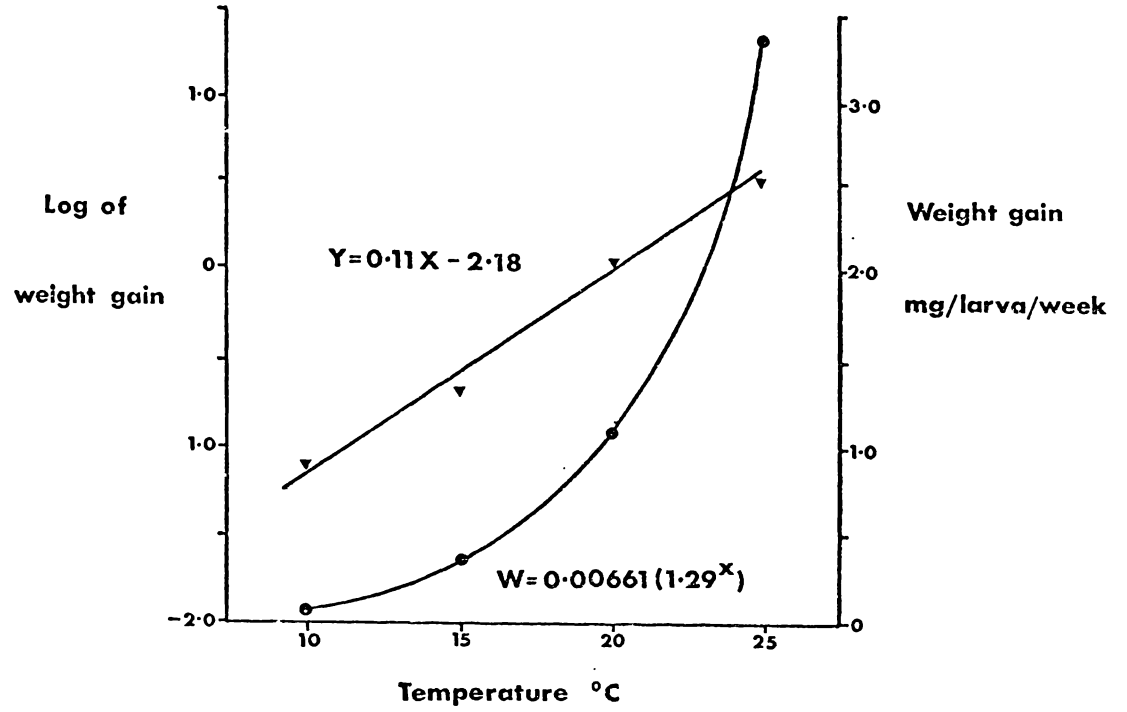


Figure 4-2 Regression of black beetle first instar larval weight gain on temperature.

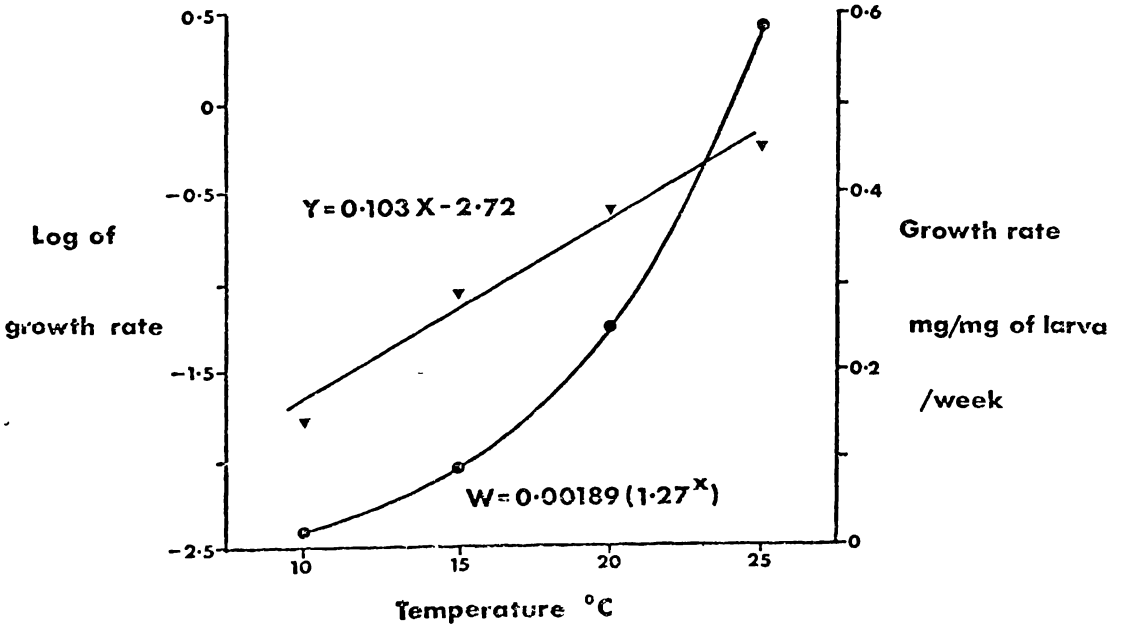


Figure 4-3 Regression of black beetle first instar larval growth rate on temperature.

some larvae and the very low mean weight gains at the two lowest temperatures, indicates the high temperature requirement of first instar larvae for satisfactory growth.

(2) Effect of soil moisture on growth and survival

(a) Methods

Black beetle eggs, obtained from the same adult population that provided eggs for the previous trial, were placed in petri dishes on filter paper moistened with 4% sodium hypochlorite solution. The petri dishes were held in a constant temperature cabinet at 20 ^{o}C until egg hatching. Newly emerged first instar larvae were placed in small plastic pots with snap-on lids containing a Redhill sandy loam medium at a range of soil moisture treatments as shown in Table 4-4. The level of organic matter in this soil was 14.9%, (where % organic matter is taken as 1.724 x % organic C, Ruakura Soil Testing Laboratory).

Five larvae were placed in each pot, with 10 pots per treatment. No food source other than the soil medium was provided. At the start of the trial in mid-January 1976, 50 newly emerged larvae were weighed to obtain an estimate of the mean weight of the larvae used in the trial. The pots were kept in a constant temperature cabinet at 20 ^{o}C for four weeks until the conclusion of the trial. At weekly intervals, the larvae surviving in the pots were counted, weighed to determine the rate of development and then replaced in the pots with fresh soil at the treatment soil moisture level.

(b) Results and Discussion

The mean weight of the newly emerged first instar larvae was 4.6 ± 0.9 mg. The survival and growth of the larvae at the various moisture treatments are shown in Table 4-4.

After six days all larvae were dead in the two extreme treatments. Larvae at the 5% level had a shrivelled appearance due to desiccation while those at 60% soil moisture where water lay on the soil surface had presumably succumbed from a lack of oxygen. Even after six days, survival was highest at the 25% treatment.

After 14 days, survival was still relatively high in this treatment and mean larval weight at 15% and 25% had increased by about 80% on the initial weight. One larva at the 40% moisture level weighed 17.0 mg which inflated both the mean and S.E.. No larvae remained alive after 14 days in the 55% treatment. Considerable mortality occurred between 14 and 21 days in the three remaining treatments, possibly because of the continual handling. Relatively large differences in larval weight were found within the 15% and 25% levels as shown by the S.E.'s. The two individuals alive in the 40% moisture level had similar weights.

After 30 days, survival was highest in the 25% soil moisture level and this treatment contained one second instar larva. The remaining larva at 40% was in the second instar, while the three larvae in the 15% treatment were all first instar.

The trial results show considerable heterogeneity of first instar response to soil moisture. Soil moisture levels are known to fluctuate markedly in the field over short periods before and after rainfall. In addition no study has been made of the interaction

Table 4-4 Survival and growth of first instar black beetle larvae at six soil moisture levels.

% Soil Moisture	after 6 days		after 14 days		after 21 days		after 30 days	
	% survival	Mean wt (mg) ± S.E.	% survival	Mean wt (mg) ± S.E.	% survival	Mean wt (mg) ± S.E.	% survival	Mean wt (mg) ± S.E.
5%	0	-	0	-	0	-	0	-
15%	50	4.7 ± 0.9	44	8.2 ± 2.0	8	12.6 ± 4.6	6	17.2 ± 1.8
25%	68	5.1 ± 1.1	64	8.3 ± 1.9	26	11.6 ± 4.2	16	18.1 ± 4.9
40%	48	4.8 ± 1.1	32	8.5 ± 4.1	4	24.6 ± 1.8	2	39.3
55%	40	4.3 ± 0.6	0	-	0	-	0	-
60%	0	-	0	-	0	-	0	-

of soil moisture with temperature. This prevents any extrapolation of these results to the prediction of possible field mortalities although they do suggest that fluctuation from 30-50% soil moisture could cause much greater mortality of first instar larvae than eggs. In laboratory studies of larval ecology requiring the rearing of populations of first instar larvae, a soil moisture level in the region of 25% is likely to give the highest survival and rate of growth. The removal of the frequent handling and weighing causing damage that was necessary in this trial, would result in a probable increase in larval survival.

IV SECOND AND THIRD INSTAR LARVAE

(1) Temperature - Mortality Interaction

(a) Methods

Second instar larvae (200) and third instar larvae (300) were collected from a black beetle population in paspalum dominant, grass/legume pasture at Elstow, near Te Aroha. The larvae were held in sandy loam soil medium from the pasture site at 20 ^{o}C for four days. The influence of a range of temperatures on the survival of these larvae was investigated in a laboratory trial. Similar sized larvae were confined singly in plastic phials with screw on lids containing the same soil medium at either 10% or 20% soil moisture levels (by weight). The temperatures tested were 25^{o}, 30^{o}, 35^{o}, 40^{o} and 45 ^{o}C. Twelve second instar larvae and 20 third instar larvae were exposed per temperature per soil moisture level.

For a four hour period each day (between 1300 and 1700 hours) larvae were held at the five treatment temperatures. Larvae were

then placed in a 20 °C 'control' temperature for the next 20 hours before the procedure was repeated. This continued for a period of four days. During this time an additional 12 second instar (L_2) and 20 third instar (L_3) larvae per soil moisture treatment were held constantly at 20 °C to serve as a control. The treatments were therefore as follows:

1. 12 L_2 larvae and 20 L_3 larvae/soil moisture level at 20 °C
2. 12 L_2 larvae and 20 L_3 larvae/soil moisture/temperature 25--45 °C) for 4 hours and then at 20 °C for 20 hours.

At the end of the four day period, all larvae were held at 20 °C for a further 48 hours, after which the surviving larvae in each treatment were counted.

(b) Results and Discussion

The mortality of larvae at the treatment temperatures in each soil moisture level is shown in Table 4-5.

The results show that both second and third instar black beetle larvae are tolerant of exposure to high soil temperatures. With both instars there is a suggestion that the higher soil moisture level had a moderating influence on the effect of soil temperature.

The results also indicate that third instar larvae are more tolerant of high temperatures than the second instar. This result would fit in with field conditions where the majority of the larval population would be in the more resistant third instar stage when low soil moistures and the highest summer soil temperatures occur. No significant mortality of third instar larvae occurred at or below 25 °C. However, at 35 °C, 50% of the second instar larvae died in the 10% soil moisture medium.

Table 4-5 The mortality of second instar and third instar black beetle larvae held at a range of temperatures for four hours per day over a four day trial period.

Temperature °C	Second instar larvae Mortality +		Third instar larvae Mortality	
	10% *	20% *	10%	20%
20°	1	1	0	0
25°	0	1	0	0
30°	0	1	1	0
35°	6	4	1	0
40°	8	7	11	5
45°	12	12	20	20

* soil moisture level (by weight)

\+ number dead out of $12L_2$ or $20L_3$ larvae.

Studies of the distribution of black beetle populations in the soil profile under pasture which are discussed in Section 4, Chapter 13, have shown that during the life cycle the majority of the population undergo growth and development in the top 3 cm. In mid February, 52% of larvae and pupae in ryegrass pasture were found in the top 3 cm of the soil profile.

During the summer, soil temperatures are known to rise to very high levels in the top few cm's of the soil. Soil temperatures under ryegrass and mixed ryegrass/white clover pasture at the Otakanini Research Area were found to reach a level of 41.5 ^{o}C and 38.5 ^{o}C at 2 cm depth, under bare soil and stubble respectively in February 1978.

Further investigation of the 40^{o} - 45 ^{o}C critical temperature range was not possible due to the unavailability of test larvae after this trial was completed. Because of this it is not possible to determine the nature of the temperature-mortality threshold curve. Davidson et al. (1972a) observed that the curve was exponential for Sericesthis nigrolineata, while Kain (1975) found that the mortality response curves for grass grub were sigmoid. The investigation of the temperature-mortality relationship for black beetle that was possible contrasts markedly with the results of Kain (1975) as discussed further in Chapter 7.

After correcting for control mortality, no mortality of third instar black beetle larvae occurred in this study below 35 ^{o}C and mortality was less than 50% below 40 ^{o}C. Although both second and third instar larvae are reasonably well adapted to withstand the high soil temperatures found in the northern North Island regions during summer, some larval mortality is possible when soil temperatures either approach or exceed 40 ^{o}C in the top few cm's of the profile

over several successive days. This will be further discussed in Section 4 of the thesis, dealing with population ecology.

(2) Influence of temperature on food consumption and growth

(a) Methods

In a preliminary study carried out in 1977, the influence of temperature on the carrot consumption and larval growth of 30 third instar black beetle larvae was monitored at four temperatures using similar techniques to those described by Ridsdill Smith et al. (1975) with S. nigrolineata larvae. Weighed larvae were each provided with a weighed portion of carrot, allowed to feed at the treatment temperatures for either a three or four day period after which the remaining carrot was weighed and the larval weight change over the feeding period calculated by re-weighing the larva.

At the start of each feeding period a sub sample of 30 carrot food portions was placed in each of four treatment temperatures without larvae for the duration of the feeding period. The carrot pieces were then re-weighed and the loss in weight recorded in the absence of feeding. Significant weight losses were noted at each temperature ranging from 0.076 mg/1 mg initial carrot weight at 10 ^{o}C to 0.148 mg/1 mg initial carrot weight at 25 ^{o}C.

When this weight loss was related to the initial weight of the carrot portion before feeding (about 300-400 mg) it was found that taking a mean initial carrot weight of 350 mg, the loss in weight of uneaten carrot over the feeding period attributable to desiccation would vary between 25 mg to 50 mg depending on the temperature. Such a weight loss could be allowed for as a correction factor if a

constant. However it was further found that the magnitude of the weight loss varied between carrots and between different batches of carrots.

The occurrence of this weight loss was of minor significance where all the carrot was eaten over the feeding period. This did in fact take place to a large extent at 25 ^{o}C when as much as 400 mg of carrot was consumed by the larvae over a four day feeding period. At the 10 ^{o} and 15 ^{o}C treatment temperatures where consumption was much lower, it became difficult to partition the smaller decrease in carrot weight into the components of loss through ingestion by the larva and loss by desiccation. Instances did occur where the decrease in carrot weight over the feeding period was less than the calculated carrot desiccation correction factor in spite of obvious signs of feeding activity.

There are inherent inaccuracies in this method using carrot wet weights entirely as well as an apparent inability of the technique to measure consumption accurately at lower temperatures. In view of this the procedures described in the following section were adopted in the trial carried out in 1978.

Second and third instar larvae were collected from a population of black beetles under paspalum dominant, grass/legume pasture at Elstow, in January 1978. Larvae were held in a soil medium at 20 ^{o}C and pre-conditioned on a carrot diet for four days. At the start of the trial, larvae were selected for uniformity of weight and visible fat content. Twenty five, second instar and 20 third instar larvae per treatment temperature were placed singly in the compartments of ice-cube trays after being weighed. The temperatures used were 10^{o}, 15^{o}, 20^{o}, 25^{o} and 30 ^{o}C, maintained in constant temperature cabinets.

Each larva was provided with a piece of weighed carrot as a food source. Carrot pieces were of as near uniform size as possible, approximately 0.5 cm in diameter and 1 cm in length, being cut from equal width slices with a cork borer. The pieces were cut at equal radii from the carrot slice centre to ensure uniform tissue composition and were dried on tissue paper before weighing. From each carrot used as food, 25 pieces were selected at random and treated in the same way as the food pieces. This aliquot of the supplied food was then oven dried at 55 ^{o}C to a constant weight and then weighed to give a measure of the dry weight of each carrot piece fed to a larva. This procedure was followed at each feeding interval to give a measure of the variability between carrots of the same batch.

Every two days, each larva was weighed, the remaining carrot oven dried and weighed and fresh weighed carrot supplied. Larval weight change was the difference between the weight at the start and end of the feeding period. The consumption of each larva was determined by the dry weight difference between the carrot supplied and the carrot remaining after two days of feeding. The trial continued for a period of 16 days and was discontinued before any influence of change from second larval instar to third, or third instar to pre-pupa could occur.

The consumption and utilisation of food by insects is outlined in the literature review in Chapter 2. As no determination of larval dry weight was made during the trial, consumption and growth are expressed on a wet weight basis for both larval and carrot weights in the forms suggested by Waldbauer (1968).

(b) Results and Discussion

(i) Larval survival

The survival of second instar larvae at the 30 °C temperature treatment was poor. At the end of 13 days all larvae had died and so no consumption and growth data were obtained at this temperature. All other calculations were made on the larvae in both instars alive at the end of the trial period.

Survival of third instar larvae over the 16 day trial period was greater than that of second instar larvae as shown in Table 4-6. This may have been partly due to the more fragile nature of the second instar resulting in handling damage during weighing. It is likely however that temperature was the major factor limiting survival.

The results suggest that the third instar is more tolerant of higher temperatures. Peak survival was 100% at 20 °C and was as good at 30 ° as at the 10 °C treatment. In contrast, highest second instar survival occurred around 15 °C and rapidly declined above 20 °C. This result confirms the trend of the higher temperature tolerance of third instar larvae demonstrated in IV (1) of this chapter. Although no second instar larvae were alive at 30 °C after 16 days, some larvae were alive at the end of five days as was shown in the previous trial in Table 4-5.

(ii) Consumption Index

The consumption of carrot by both instars is expressed in terms of the Consumption Index (C.I. = consumption in mg/mg of mean larval weight/day). Analysis of variance was carried out on untransformed

Table 4-6 The survival of second and third instar black beetle larvae at five treatment temperatures on a diet of carrot.

	% Survival over trial at each temperature*				
	10°	15°	20°	25°	30°
L_2 larvae	52	80	72	48	0
L_3 larvae	85	80	100	90	85

* 25 L_2 and 20 L_3 larvae at each temperature

Table 4-7 The mean C.I. per day for second and third instar black beetle larvae at five temperatures, feeding on carrot.

Temperature °C	Second instar larvae		Third instar larvae		Significance of difference between L_2 & L_3 larvae
	Mean C.I.	± S.E.	Mean C.I.	± S.E.	
10°	.041	.0069	.031	.0023	N.S.
15°	.150	.013	.068	.0032	* * *
20°	.234	.022	.135	.0063	* * *
25°	.203	.014	.174	.0081	N.S.
30°	-*	-	.176	.0081	-

* no second instar larvae survived at 30°C

* * * $P < 0.001$

N.S. non-significant

data. The relationship between C.I. and temperature for both instars is shown in Fig. 4-4.

The C.I. shown in Table 4-7, was significantly greater ($P < 0.001$) for second instar than for third instar larvae at the 15° and 20 °C temperatures and the reasons for this will be discussed in the section dealing with utilisation. The C.I. of second instar larvae increased linearly with temperature reaching an upper threshold at 20 °C. There was some evidence for a slight decrease in the index at 25 °C, but this was not significant. The C.I. for third instar larvae also increased linearly with temperature, but a significant increase ($P < 0.01$) in the index occurred between 20° and 25 °C, giving a threshold temperature of 25 °C. The data suggest that there is an upper threshold between 25° and 30 °C.

(iii) Utilisation

The utilisation of the diet at the different temperatures can be expressed in terms of the efficiency of conversion of ingested food to body weight (E.C.I.) which is larval weight gain/weight of carrot consumed both measured on a wet weight basis, expressed as a percentage.

The relationship between mean E.C.I. and temperature is shown graphically in Fig. 4-5 and the mean E.C.I. for second and third instar larvae at each temperature, feeding on carrot is shown in Table 4-8.

The relationship between second and third instar larvae for E.C.I. is the inverse of that for C.I. Although third instar larvae consumed less, their utilisation as expressed by the E.C.I. was higher than that of the second instar, and this difference was significant at the 20° and 25 °C temperatures.

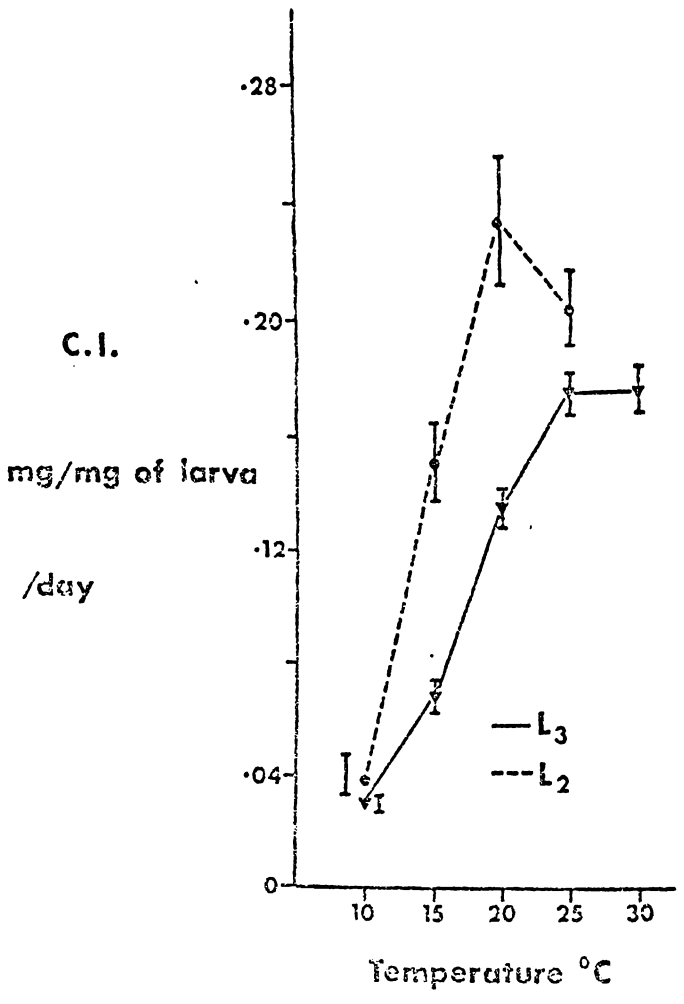


Figure 4-4

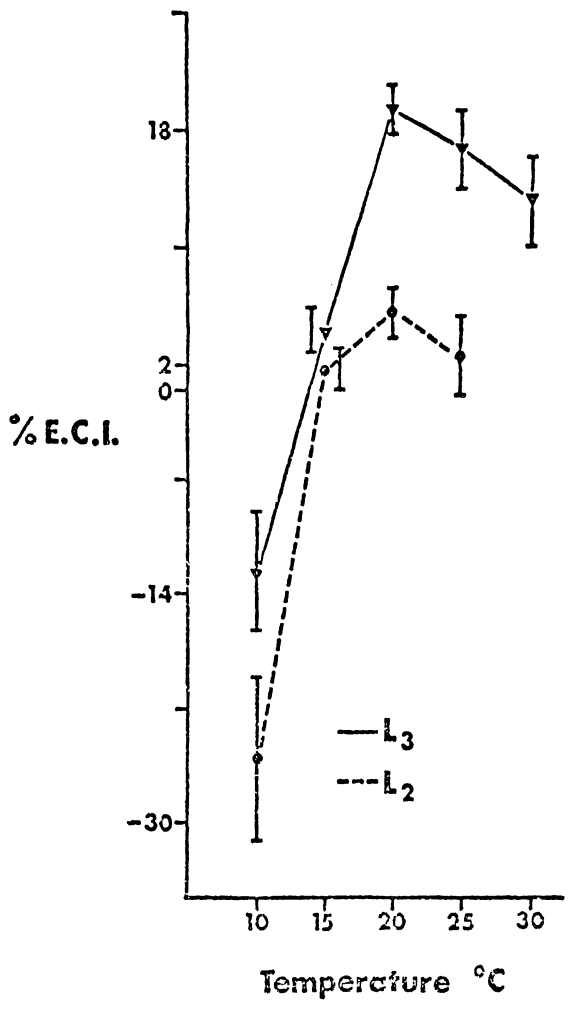


Figure 4-5

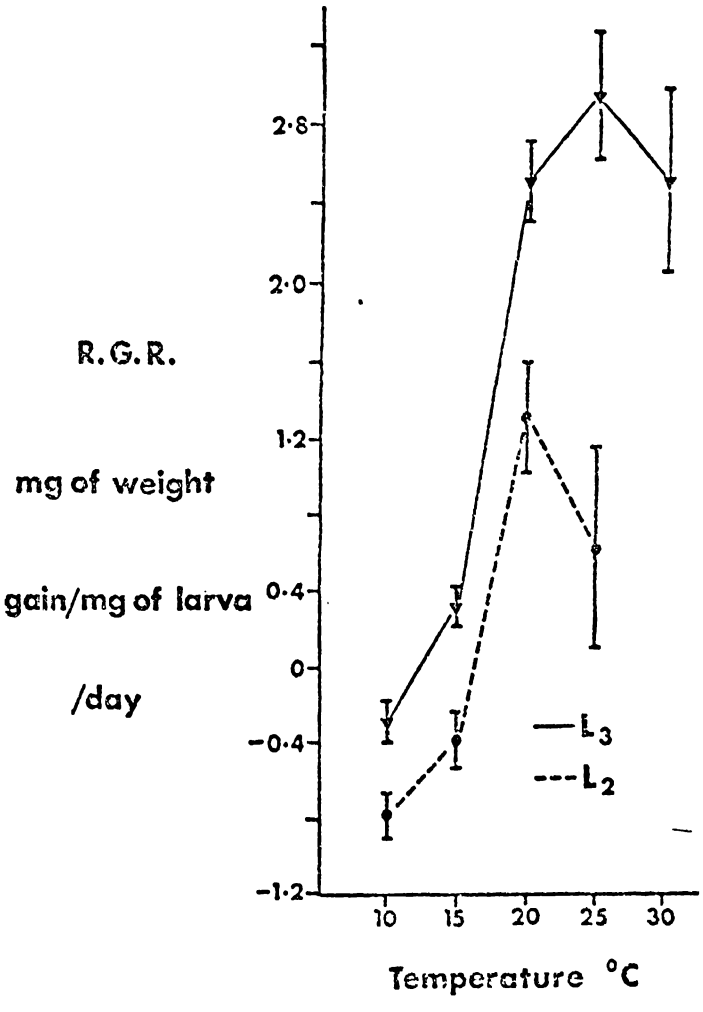


Figure 4-6

Table 4-8 Mean E.C.I. of carrot by second instar and third instar black beetle larvae at five temperatures.

Temperature	Second instar larvae Mean E.C.I.	± S.E.	Third instar larvae Mean E.C.I.	± S.E.	Significance of difference between L_2 & L_3 larvae
10°	-25.7	6.1	-12.4	4.3	N.S.
15°	1.8	1.5	4.5	1.5	N.S.
20°	5.4	1.9	19.1	1.7	* * *
25°	2.6	2.8	16.8	2.6	* *
30°	-	-	13.2	2.8	-

* * * $P < 0.001$

* * $P < 0.01$

N.S. non-significant

Table 4-9 The mean R.G.R. per day for second and third instar black beetle larvae at five temperatures, feeding on carrot.

Temperature °C	Second instar larvae Mean R.G.R.	± S.E.	Third instar larvae Mean R.G.R.	± S.E.	Significance of difference between L_2 & L_3 larvae
10°	-0.79	0.12	-0.29	0.11	* *
15°	0.39	0.16	0.32	0.11	N.S.
20°	1.31	0.29	2.51	0.21	* *
25°	0.63	0.54	2.95	0.34	* * *
30°	-*	-	2.50	0.49	-

* no second instar larvae survived at 30°C

Other symbols as in Table 4-8

The optimum temperature for utilisation appears to differ between the instars. For second instar larvae it appears to be approximately 20 ^{o}C, but the increase in utilisation from 15 ^{o}C to 20 ^{o}C is much less than for third instar larvae. Utilisation increased significantly ($P < 0.01$) between 15^{o} and 20 ^{o}C for third instar larvae, with peak conversion of food ingested to body weight occurring at about 20 ^{o}C.

(iv) Growth

Larval growth can be expressed as the relative growth rate (R.G.R.) in mg of weight gain/mg of mean larval weight. The relationship between R.G.R. and temperature is shown graphically in Fig. 4-6 and the mean R.G.R. for second and third instar larvae at each temperature, feeding on carrot is shown in Table 4-9.

The R.G.R. was significantly greater in third instar larvae than second instar at the 10^{o}, 20^{o} and 25^{o}C temperatures. This reflects the higher efficiency of utilisation of ingested food by third instar larvae. There was a linear increase in R.G.R. with increasing temperature for both instars up to 20 ^{o}C which appears to be the upper threshold. There is some evidence that growth of third instar larvae is not as adversely affected by temperatures above 20 ^{o}C as growth of second instar larvae. These results fit those observed for E.C.I. very well. Both instars had a negative R.G.R. at 10 ^{o}C showing once again the detrimental effects on black beetle larvae of temperatures below 15 ^{o}C.

These studies of the influence of temperature on the consumption and growth of black beetle larvae demonstrate the warm climate origins of this insect and the physiological adaptations to high temperature

it appears to possess. Using the indices discussed in this section, consumption, utilisation of food and subsequent growth of third instar larvae is optimum in the 20°–25 °C range, with that of second instar larvae occurring at about 20 °C. As third instar larvae usually develop later in the summer when soil temperatures are highest, this difference in temperature tolerance of the two instars will have significance only when development of second instar larvae has been delayed due to unfavourable climatic conditions earlier in the season. Larval development, which has been shown to take place in the top 3 cm of the soil profile where soil temperatures are highest, (see Section 4, Chapter 13), is well adapted to field conditions.

CHAPTER 5

INFLUENCE OF PLANT SPECIES ON CONSUMPTION AND UTILISATION

I INTRODUCTION

Much of the reported work in the literature deals with consumption and utilisation of plants by foliage feeding Lepidoptera and Orthoptera (e.g. Waldbauer, 1964; Soo Hoo and Fraenkal, 1966; Mukerji and Guppy, 1970). This work and the techniques involved in the measurement of consumption and utilisation has been reviewed by Waldbauer (1968) and was summarised previously in Chapter 2 of Section 1.

Little research has been undertaken on the Scarabaeidae, although Hurpin (1960) measured consumption by Melolontha melolontha and recently Ridsdill Smith et al. (1975) investigated the consumption and utilisation of carrot by third instar larvae of Sericesthis nigrolineata. In addition Ridsdill Smith (1975) used a marker technique to assess the passage of a carrot food source through the gut of S. nigrolineata larvae in the presence and absence of plant roots.

There appears to be no attempt reported in the literature to measure the relative consumption and utilisation of the roots of different plant species by scarabaeids. Plant roots form a major portion of the diet of economically damaging black beetle larvae, and any investigation of their ecology would not be complete without some understanding being gained of the suitability of some of the plant species, typically found in pastures, as diet components.

In this chapter, the influence of two grasses and a legume species on black beetle larvae is investigated using both the marker technique of Ridsdill Smith (1975) and the gravimetric techniques reviewed by Waldbauer (1968).

II RELATIVE CONSUMPTION OF PASPALUM, RYEGRASS AND WHITE CLOVER

(a) Methods

A technique using glass beads, similar to that of Ridsdill Smith (1975) was used in this study to provide an estimate of relative black beetle larval consumption of three plant species. Third instar black beetle larvae were collected from a paspalum dominant, grass/legume sward at Elstow near Te Aroha in February and held at Ruakura in soil at 20 ^{o}C for several days. From this population, 100 similar sized larvae were selected and placed singly in the compartments of plastic ice-cube trays. Each compartment contained a small piece of freshly cut carrot, moistened with water and then dipped in glass beads to give a complete covering of the beads on all the carrot surface. The beads used were BDH, approximately 60 mesh, normally used for gas chromatography column packing.

The larvae were allowed to feed on the carrot for 17½ hours at 20 ^{o}C in darkness, which was the time established from preliminary studies that was necessary to ensure all sections of the larval gut were packed with glass beads. The larvae were stimulated to feed by the carrot and they ingested glass beads from the coating at the same time. After the initial feeding period, the larvae were removed from the carrot source, and 25 were immediately deep frozen for later assessment of the amount of gut fill with beads. This group acted as the control.

The remaining 75 larvae were subdivided into three groups and transferred to fresh ice-cube trays containing the roots of one of three plant treatments. These were 'Grasslands 15' paspalum, 'Nui' ryegrass and 'Pitau' white clover. The genus and specific names for plant species are given in Appendix O-1. A small portion of freshly harvested and washed plant root with crown attached was placed in each compartment. After 8 hours in darkness at 20 ^{o}C, larvae were then deep frozen to prevent further feeding and gut activity.

At a later stage, the larvae were dissected under water using a stereo microscope and the gut removed. The gut was then divided into four sections on an anatomical basis: foregut and anterior midgut, posterior midgut 1, posterior midgut 2 and hindgut. In addition faecal pellets within the posterior portion of the hindgut were removed as a fifth category. The sections were then opened on a white ceramic slab within concave depressions and the gut contents carefully dissected out. The abundance of beads in each section of the gut was ranked on a 0 - 4 scale, for each larva, with a score of 0 indicating no glass beads present and a ranking of 4 used where the gut was completely packed with beads. A ranking of 1 was used for very few beads (up to 6) and scores of 2 and 3 were intermediate, 2 where the volume of organic matter exceeded the volume of glass beads, and 3 for the reverse situation. Using this method it was possible to rank the relative abundance of beads within the gut of each larva in each plant treatment. By comparison of the total scores in each plant treatment with that of larvae which had fed only on carrot coated with glass beads, the extent of food ingestion which would push the beads through the gut could be assessed.

(b) Results and Discussion

The distribution of glass beads in the guts of the larvae on the various treatments is shown in Table 5-1. The numbers in each category are the total from the ranking of all larvae in the treatment.

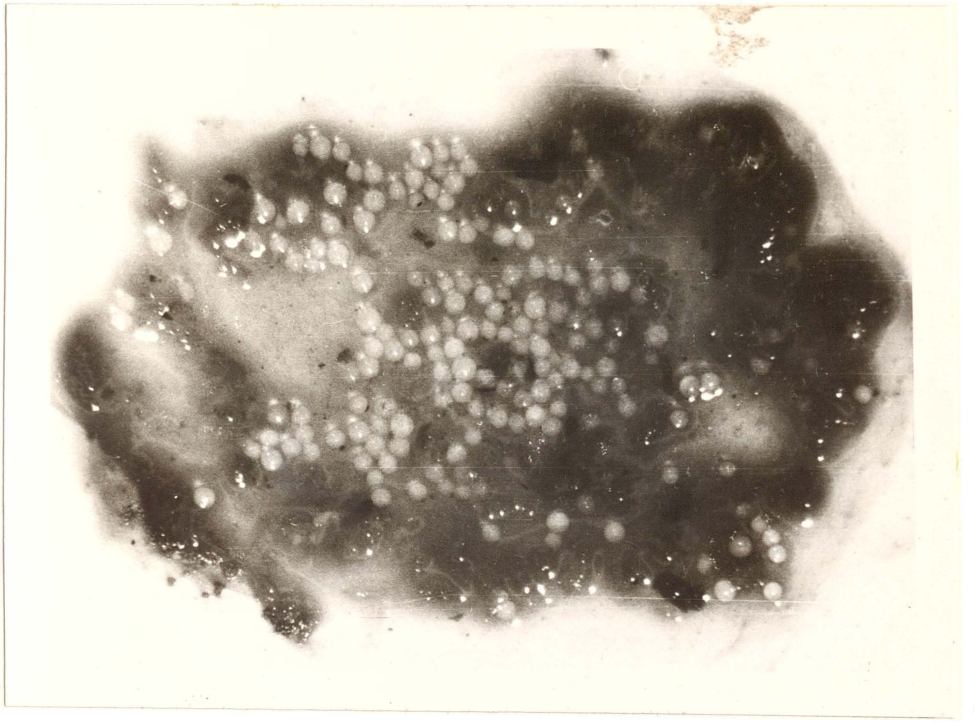
Analysis of the data was carried out by non-parametric methods using the Kruskal-Wallis 1-way ANOVA by ranks (Sokal and Rohlf, 1969, Chapter 13). Considering firstly the mean total of the rankings in the three sections of the midgut, there are significant ($P < 0.001$) overall treatment differences. The mean glass bead score in the control insects is significantly greater ($P < 0.01$) than the three-plant treatments which suggests larvae ingested plant root material which moved beads along the gut. The white clover ranking is significantly greater ($P < 0.05$) than that of the two grasses indicating that more ingestion occurred on the grasses. It should be noted that as larvae were not held for 8 hours in the absence of root material after feeding on the glass-bead coated carrot it cannot be stated with any certainty that larvae did actually feed on the white clover. The decrease in the ranking score in the midgut of larvae in the white clover treatment may be due solely to peristaltic movement during digestion. To this extent the trial design was deficient, and will be examined further in the next section. The decrease in the ranking score of larvae feeding on the grasses is however due to ingestion moving the beads through the gut as shown in the plates.

Dealing next with the mean total of the rankings in hindgut and faecal pellets, the overall treatment differences are significant ($P < 0.01$). The white clover ranking is not significantly different

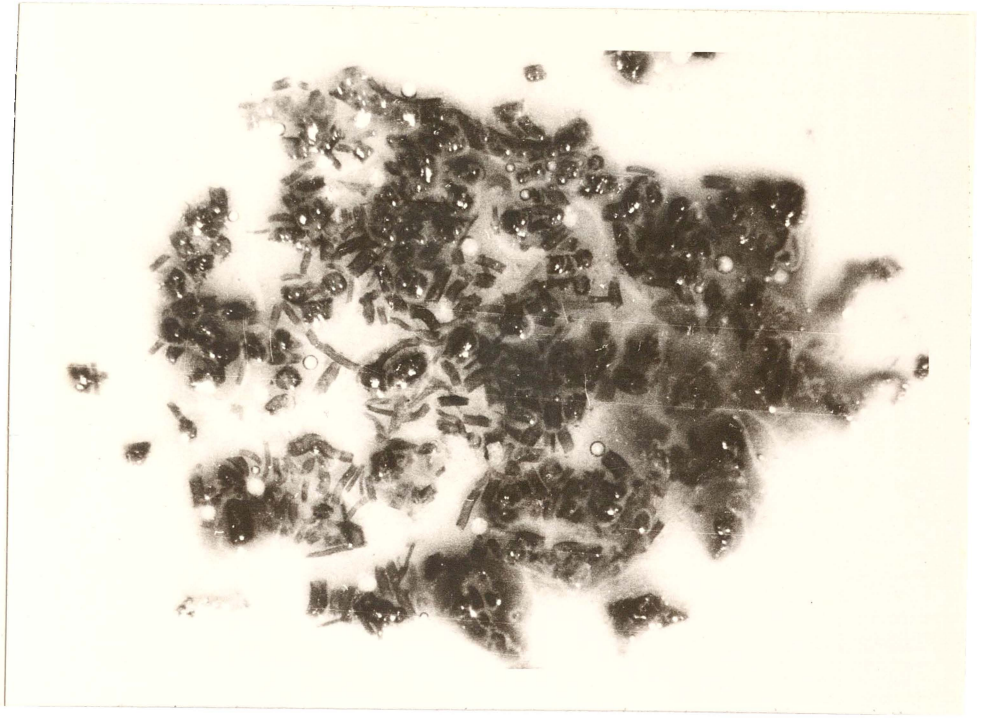
Table 5-1 The distribution of glass beads in the gut of third instar black beetle larvae after feeding on four diet treatments.

Treatment	Anterior mid-gut	Posterior mid-gut 1	Posterior mid-gut 2	Hindgut	Faecal pellets	Ranking Index (mean bead score per larvae)
Control (carrot and beads only) n = 24 *	6	73	76	78	25	10.75
White clover n = 25	4	47	63	75	30	8.76
paspalum n = 24 *	4	33	49	59	21	6.92
ryegrass n = 25	3	35	49	59	10	6.24

* One larva on each of the carrot and paspalum treatments failed to ingest any glass beads.

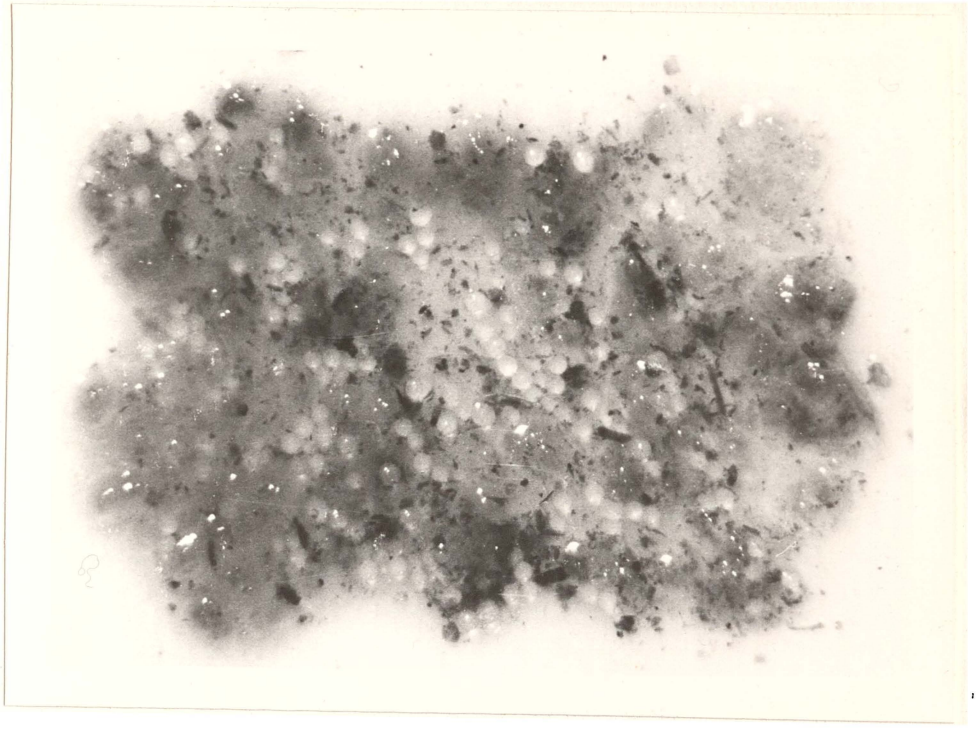


White clover diet

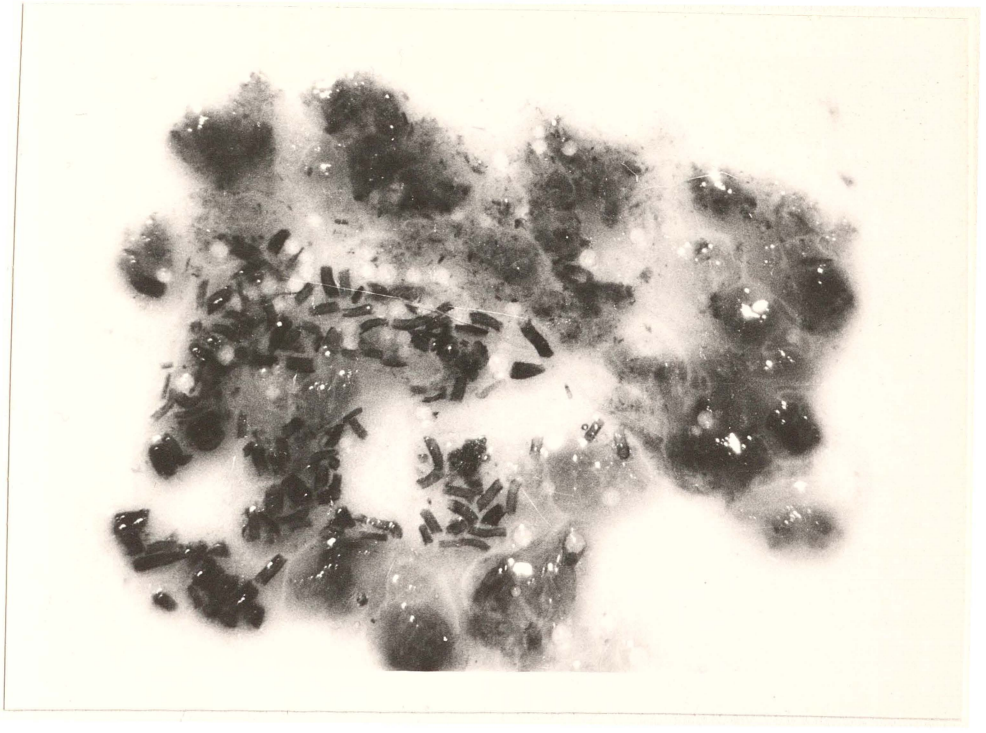


Paspalum diet

Plate 5-1 Glass beads in posterior midgut l section of third instar larvae after feeding on a white clover or a paspalum root diet.

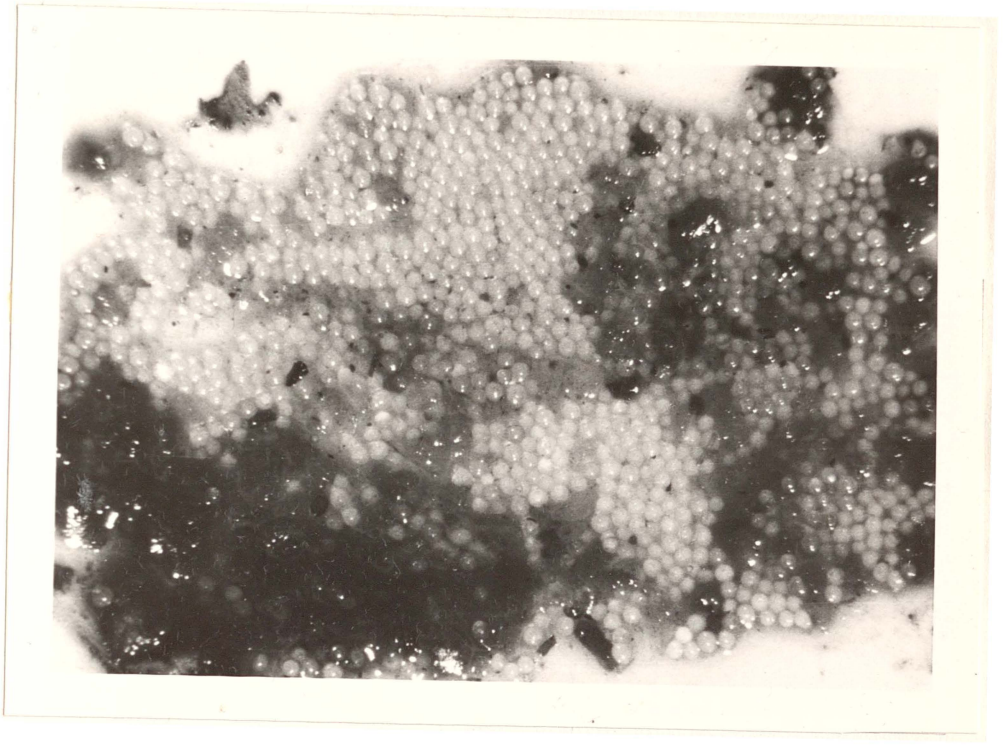


White clover diet

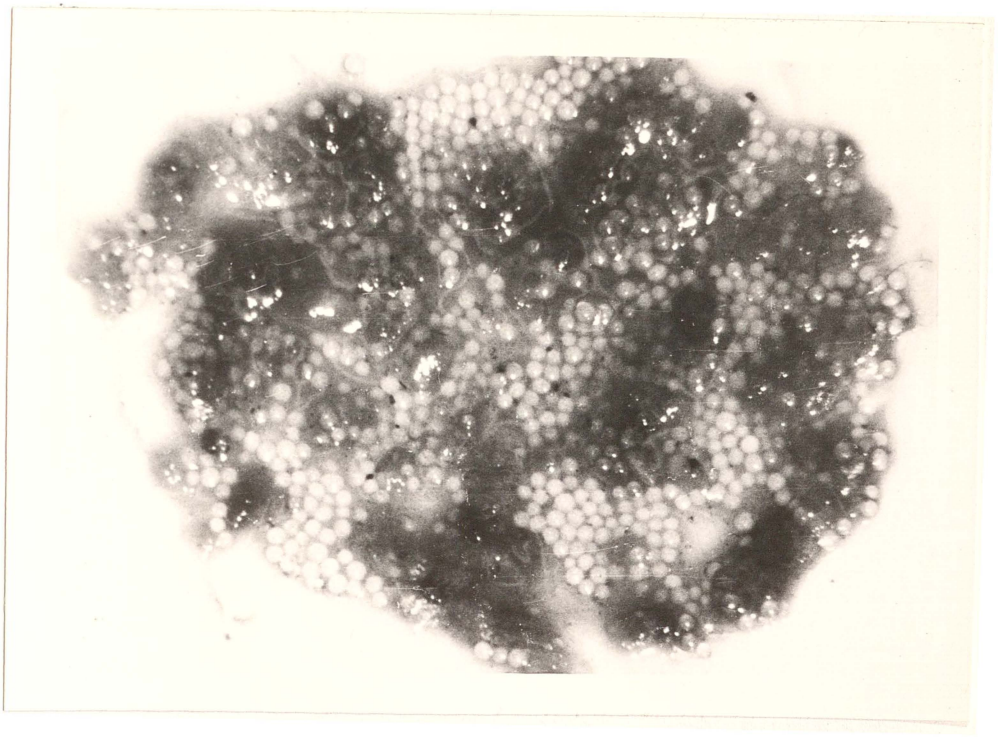


Paspalum diet

Plate 5-2 Glass beads in posterior midgut 2 section of third instar larvae after feeding on a white clover or a paspalum root diet.



White clover diet



Paspalum diet

Plate 5-3 Glass beads in hindgut section of third instar larvae after feeding on a white clover or a paspalum root diet.

from the control. This shows that although feeding appears to have moved glass beads from the foregut and midgut into the hindgut of larvae on white clover, egestion of beads in the faeces has maintained a similar level in the hindgut to that in the control. The mean score in the larvae feeding on the two grasses was significantly lower ($P < 0.05$) than the control and white clover treatments. This result shows that not only were beads that were moved into the hindgut from the anterior portions egested, but a significant proportion of those in the hindgut at the commencement of feeding were voided also over the 8 hour feeding period.

Considering lastly the ranking indices in the last column (the mean bead scores per larva), the ranking on white clover is significantly lower ($P < 0.01$) than the control, and that on the two grasses is significantly lower ($P < 0.001$) than on white clover. The paspalum and ryegrass indices do not differ significantly.

The results confirm the technique as a reasonable index of feeding activity and show that ryegrass and paspalum appear more favoured food plants when consumption is used as an index of acceptability.

The typical differences found in the abundance of glass beads between white clover and paspalum in the posterior midgut 1, posterior midgut 2, and hindgut are shown in Plates 5-1 to 5-3. Severed portions of paspalum root can clearly be seen in the midgut sections.

III LARVAL CONSUMPTION, UTILISATION AND GROWTH ON PLANTS

(1) Third instar larvae

(a) Methods

The methods used in this study were adapted from those used to measure food consumption by Pseudaletia unipunctata (Mukerji and Guppy 1970) and by two species of grasshoppers (Bailey and Mukerji, 1976).

Black beetle third instar larvae were collected from a paspalum-dominant mixed grass/legume pasture at Elstow near Te Aroha in February 1978. The population was then held in soil at Ruakura at 20 ^{o}C in a constant temperature cabinet for several days to allow any larvae damaged during collection to be identified. At the commencement of the trial 60 active larvae with uniform visible fat content were selected, weighed and then placed singly in numbered compartments in plastic ice cube trays.

Freshly harvested plants of paspalum, ryegrass and white clover were washed and then separated into 50 portions of roots with crown attached for each species. In the case of paspalum, the rhizome storage organs of the plant were included with attached roots. The portions were rigorously selected for uniformity of size and composition and were kept at a similar moisture content within moist paper towels. Twenty portions of each species were then weighed and placed singly in the compartments of ice-cube trays with the larvae.

At the same time a further sample of 25 portions of each species, selected at random from the main sample and of similar

weight and composition were weighed and then dried to a constant weight in an oven at 55 ^{o}C. This aliquot of each species allowed a measure of the dry weight of the food provided for each larva at the start of the feeding period.

The feeding larvae were kept in darkness at 20 ^{o}C for two to three days after which they were removed from the trays, weighed and fresh weighed food portions provided in clean trays. The remaining plant material was separated, oven dried to a constant weight and then weighed. This permitted consumption to be determined as the dry weight difference between the food supplied and the food remaining usually after two days of feeding but for three days over a weekend. At each feeding period a fresh aliquot of each plant treatment was taken to determine the fresh weight:dry weight relationship of the food, and to reduce the effect that variation in the composition of the plant source would have on the accuracy of the consumption index. The trial continued over a period of 14 days, but due to handling damage to the larvae and subsequent mortality, analysis of the data was carried out from the initial three feeding periods only, totalling 7 days when larval survival was high.

The criteria used to measure larval consumption, utilisation and growth on the three plants, namely consumption index (C.I.), relative growth rate (G.R.) and efficiency of conversion of ingested food to body substance (E.C.I.) have been discussed by Waldbauer (1968) and are reviewed in Chapter 2 of this thesis.

(b) Results and Discussion

Although larval weight change, and root consumption data were obtained for each larva in the trial every two days, all results gathered over the trial period were converted to weekly totals. Regression analysis of the data was carried out using an existing programme through the Ruakura Research Centre computer terminal.

(i) Consumption

The regression of the fresh weight of root consumed on mean larval weight over the seven day period is shown in Figure 5-1 and the regression equations in Table 5-2.

The slope of the regression lines for the two grasses is not significantly different, the linear relationships being virtually identical. The pooled slope value of the regression for the grasses is significantly different ($P < 0.05$) from that of white clover. The non-significant value of 'r' for the white clover regression equation illustrates the lack of correlation between consumption and mean larval weight. Very little consumption occurred at any larval weight over the feeding period, and there is no suggestion of consumption increasing as larval weight increases.

When consumption is expressed as the C.I. which is consumption of fresh root in mg/mg of larval wet weight/week, a similar plant species effect to that described by the above regression equations is obtained. Mean larval weight calculated from the data shows mean weight over the trial period was significantly greater on ryegrass than paspalum or white clover, although this is partly due to a higher mean initial larval weight on ryegrass (162.6 ± 22.4 mg

Table 5-2 The regression equations for the relationship between plant root consumption per week and mean third instar black beetle larval weight, $Y = a + bX$ where Y = consumption (mg fresh weight) and X = mean larval wet weight (mg).

Food plant	Intercept (a)	Slope (b + S.E.)	Correlation coefficient (r)
paspalum roots and rhizomes	-108	1.25 ± 0.45	0.57 ($P < 0.05$)
ryegrass roots	-102	1.26 ± 0.58	0.49 ($P < 0.05$)
white clover roots	+7	0.14 ± 0.20	0.16 NS*

* NS = non significant ($P > 0.1$)

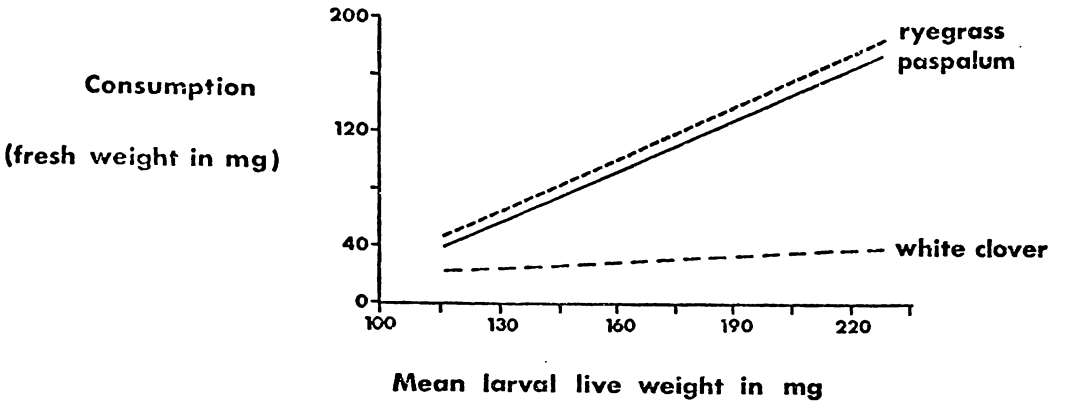


Figure 5-1 Relationship between consumption of plant roots and mean larval weight of third instar black beetle larvae.

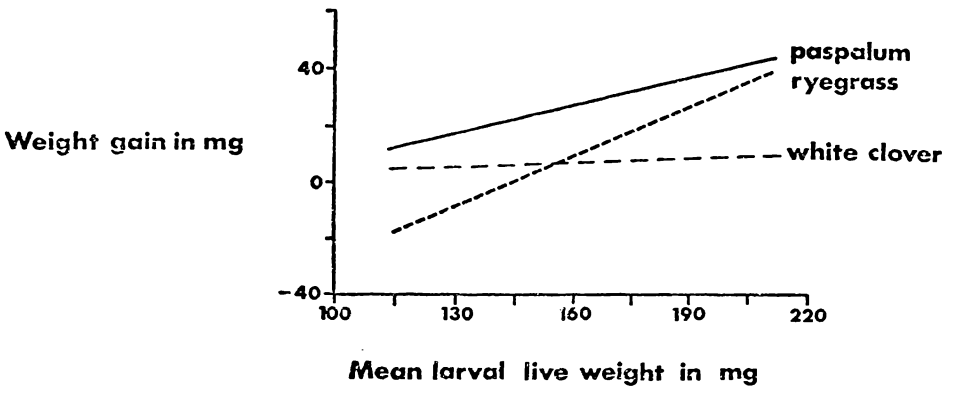


Figure 5-2 Relationship between third instar black beetle larval weight gain and mean weight when feeding on plant root diets.

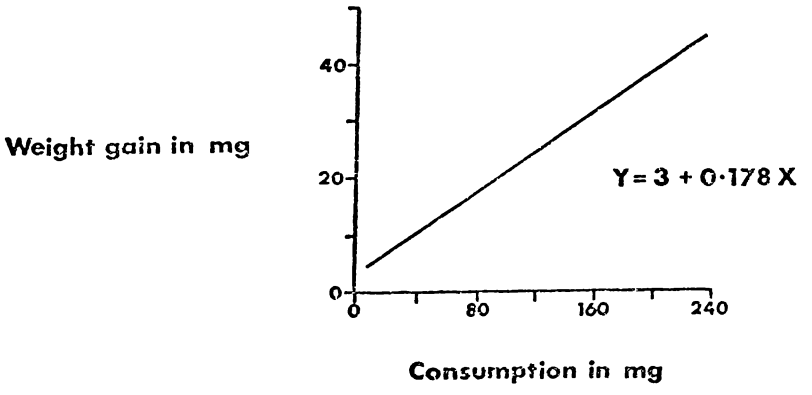


Figure 5-3 Relationship between third instar black beetle larval weight gain and the consumption of plant roots.

compared with paspalum (138.4 ± 25.8 mg). From the regression equations, mean fresh weight of food consumed is calculated and thus the consumption index (C.I.).

Significantly more food was consumed by larvae feeding on ryegrass roots than on paspalum as shown in Table 5-3. In view of the higher mean larval weight on ryegrass and the linear relationship already shown between consumptions and larval weight, this consumption difference between the two grasses is not surprising. Both actual consumption and the C.I. were significantly lower on white clover than on the two grasses, showing the latter were much more favourable as a food source.

These results determined gravimetrically are in close agreement with those from the study of the passage of glass beads through the gut to obtain a measure of relative consumption. The slower passage of the beads through the gut in larvae feeding on white clover also indicated much lower consumption of the legume than the grasses.

(ii) Growth of larvae

The regressions of weight gain on mean larval weight over the seven day period (both calculated on a mg fresh larval weight basis) are shown in Fig. 5-2 and Table 5-4.

There was a high level of variability shown in individual larval weight gain and this is evident in the regression lines. Two larvae feeding on ryegrass actually lost weight over the feeding interval, with one larva losing 20 mg. This, in conjunction with the significantly higher mean larval weight on ryegrass, has resulted in the higher slope value of the regression relationship which gives weight losses at mean larval weights of less than 145 mg.

Table 5-3 Mean wet weight of third instar black beetle larvae, mean fresh weight of plant roots consumed and the C.I. per week.

Food plant	Mean larval wet weight (mg)	Mean fresh weight of food consumed (mg)	C.I. mg/mg of larva/week
ryegrass	185	138	0.75
paspalum	155	85	0.55
white clover	164	29	0.18
Average S.E. of difference	9	18	0.10
Significance of differences	(P< 0.01)	(P< 0.001)	(P< 0.001)

Table 5-4 The regression equations for the relationship between third instar black beetle larval weight gain and mean larval weight, Y = a + b X where Y = larval weight gain and X = mean larval weight.

Food plant	Intercept (a)	Slope (b ± S.E.)	Correlation coefficient (r)
ryegrass roots	-86	0.59 ± 0.15	0.71 (P< 0.01)
paspalum roots and rhizomes	-25	0.32 ± 0.11	0.59 (P< 0.05)
white clover roots	- 3	0.06 ± 0.08	0.17 NS*

* NS = non-significant (P> 0.1)

As with consumption, there was no significant linear relationship between weight gain and mean weight of larvae feeding on white clover. The slopes of the regressions for the two grasses were significantly different ($P < 0.01$), which means that for a given mean weight, larval weight gain will be smaller in insects feeding on a ryegrass food source than a paspalum food source.

Using the mean larval weights, the mean weight gains on each of the plant diets can be calculated from the regression equations (Table 5-5).

The higher mean larval weight over the trial period on ryegrass is allowed for in the calculation of the relative growth. The G.R. is significantly smaller ($P < 0.01$) on white clover, but does not differ significantly between the two grasses. Only two larvae gained more than 20 mg on the white clover diet over the trial period compared with 10 and 9 larvae on paspalum and ryegrass root material respectively.

The results suggest that the paspalum roots and rhizomes ingested by the larvae may have been more efficiently utilised than the ryegrass. The very poor larval growth on the white clover diet relates well to the low consumption data from the previous section. Very little white clover root material was ingested and this has resulted, as would be expected, in low weight gains relative to the grasses.

(iii) Efficiency of utilisation

The relationship between the weight gained by larvae and the food consumed gives a measure of utilisation or the efficiency of conversion of ingested food to body weight (E.C.I.). Following

Table 5-5 Mean third instar black beetle larval weight gain and relative growth rate (G.R.), as larval growth in mg/mg of larva/week on plant root diets.

Food plant	Mean wet larval weight (mg)	Mean wet weight gain (mg)	G.R. mg/mg of larva/week
paspalum	155	24.5	0.158
ryegrass	185	23	0.124
white clover	164	7	0.043

Waldbauer (1968), the E.C.I.'s for paspalum, ryegrass and white clover were 29%, 18% and 24% respectively. Regression analysis of the data showed however that the slopes of the relationships derived for each plant species were not significantly different. Although there was some evidence of intercept differences, suggesting that for a given amount of consumption there was variation in the amount utilised, they were not significant ($0.05 < P < 0.1$). In view of this a single line was fitted to the relationship.

The regression of larval weight gain on consumption is shown in Fig. 5-3. The regression equation is:

$$\text{Weight Gain} = 3 + 0.178 \ (\pm 0.0464) \times \text{Weight consumed}$$

$$(r = 0.592, \quad P < 0.001)$$

Bailey and Mukerji (1976) also found a significant linear relationship between weight gain and food consumed for two species of grasshopper nymphs feeding on a range of host plants. In their study, none of the slopes of the regression lines differed significantly, illustrating that utilisation of the various food species was similar.

From Fig. 5-3, it is evident that the plot of the linear relationship would intersect the abscissa to the left of the origin although the intercept is not significantly different from zero. On the assumptions that at zero ingestion, either zero weight gain or alternatively a weight loss would occur, then the intercept might be expected to go through the origin or to the right of the origin. The latter was observed by Mukerji and Guppy (1970) for Pseudaletia unipunctata and by Turnbull (1962) for Linyphia triangularis Clerck, and these workers concluded that a threshold rate of energy intake is necessary before growth can take place.

Due to the extreme variability of some of the black beetle feeding data, evident from the figure, such a conclusion cannot be drawn from this study. In view of this variability it would be unwise to make deductions on the growth situation at zero ingestion, although a similar situation to that noted by Mukerji and Guppy and by Turnbull would seem logical for black beetle also.

It is of interest in the comparison of utilisation of the three plant species that although consumption of the legume was low relative to the grasses, the E.C.I.'s did not appear to differ. In view of the finding that utilisation does not differ significantly from that of the grasses, slower growth and lower survival on white clover roots is more likely to be the result of low consumption induced by the presence of feeding deterrents.

The results of this study provide a basis for understanding the low larval weight gains and poor survival on white clover, relative to paspalum and ryegrass, when larvae are fed plant roots in a soil medium as discussed in Chapter 6.

(2) Second instar larvae

(a) Methods

In a trial conducted prior to that carried out with third instar larvae (III(1) of this chapter), second instar larval consumption and growth were investigated on the roots of paspalum, ryegrass and white clover. Larvae were collected from the same site at Elstow and treated similarly to the third instar larvae. Twenty five second instar larvae per plant treatment were fed as in the previous trial and larval weight change, faecal pellet production and consumption recorded every two days over a 14 day trial period. Using aliquots

of each treatment species to assess the dry weight of food provided, consumption was determined as the difference between the food supplied and the dry weight of that remaining after feeding as in the third instar trial.

(b) Results and Discussion

When analysis of the consumption data commenced it was evident that a wide variation had been permitted in the wet weight of the plant roots at the start of the feeding period. This was especially so with the paspalum treatment where the wet weight of the food provided at the start of the feeding period varied from 200-1200 mg in some instances. The weight range of the aliquot taken at the same time for dry weight determination was often much smaller, resulting in a very inaccurate estimate of the wet weight:dry weight relationship. The overall effect of this was to give irrational estimates of consumption, with roots apparently gaining large amounts of weight even though considerable feeding activity had occurred.

To overcome this problem with the third instar larval trial, strict control was exercised over the weight range of both the plant root food portion and the aliquot. This enabled more accurate determinations of consumption to be made. Unfortunately, the unavailability of further supplies of second instar larvae prevented a repeat of this trial using the improved technique. However, the larval weight change data from the trial represents an accurate index of second instar growth on the plants and is shown in Table 5-6, and in Appendix 5-1.

Analysis of variance of the G.R. data showed that there were significant ($F = 11.029$, $P < 0.01$) treatment differences. The G.R.

Table 5-6 The mean weight gain and growth rate (G.R.) of second instar black beetle larvae feeding on plant roots.

Treatment	Weight gain ± S.E. (mg/larva/week)	G.R. ± S.E. (mg/mg of larva/week)
paspalum	8.90 ± 3.46	0.102 ± 0.06
ryegrass	7.72 ± 6.72	0.072 ± 0.056
white clover	0.469 ± 5.08	0.004 ± 0.066

was significantly greater ($P < 0.001$) on paspalum, and on ryegrass ($P < 0.01$), than on white clover. There was no significant difference between the two grasses. Over 50% of the larvae in the white clover treatment alive at the end of the trial actually lost weight over the trial period, compared with only one individual in the ryegrass and none feeding on paspalum roots and rhizomes.

The results illustrate the unfavourable influence white clover root material has on second instar larval growth compared with the two grass species. They also show good correlation with those obtained for third instar larvae, so that there is considerable justification for predicting that consumption and utilisation of the three species by second instar larvae would also follow the pattern shown for third instar larvae.

CHAPTER 6

INFLUENCE OF SOIL, ORGANIC MATTER AND PLANTS ON GROWTH AND SURVIVAL

I INTRODUCTION

The role that soil organic matter (O.M.) plays in the diet of soil inhabiting scarabaeid species has been a subject of considerable interest to researchers studying larval feeding damage to pasture species. Wensler (1971) states that "soil O.M., made up of undecayed plant and animal tissues and their derivatives in the process of decay to soil humus, constitutes the major source of nutrients for soil inhabiting scarabaeid larvae." Of this total soil O.M. complex, living plant root material forms a relatively small percentage (Wensler, 1971). Russell (1961) found that living plant root material comprised only 8.5% of the total weight of O.M. in the top 14 cm of a prairie soil.

There appears to be considerable variation in the reported literature dealing with scarabaeid feeding behaviour on the role of O.M. and plant roots in the larval diet. Some species now considered as having major pest status were thought to be solely O.M. feeders. Cumpston (1940) reported that larvae of black beetle were considered to subsist upon decaying vegetable matter in the soil, and consequently not to cause damage to the roots of pasture species. Cumpston however noted the roots of a large area of turf had been so completely damaged by larvae of black beetle that the turf could be pulled away. In spite of this observation, Cumpston (1940) and

Harrington (1953) considered that plant damage caused by black beetle may be due to a very poor content of decaying vegetable matter or humus in the soil.

There is evidence to indicate that scarabaeid larvae are able to obtain their nutritional requirements from different sources of O.M. in the soil. Ritcher (1958) noted that the larvae of Melolonthinae feed on both humus and live plant material. The addition of O.M. in the form of cow manure to the soil has been shown to stimulate the growth of a number of scarabaeid species (e.g. Davidson and Roberts, 1968a; Wensler, 1971; Radcliffe, 1970; Wightman, 1972a). The larvae of several scarabaeids however grow better in soil with living roots as shown by Pham Binh Quen (1969), Smith (1922), Swartz and Jurimas (1970), Wightman (1972b). The larvae of Sericesthis nigrolineata were shown by Ridsdill Smith (1975) to preferentially select and feed on living roots.

Some species can be reared satisfactorily from eggs for long periods in the absence of plants as shown by Fox and Ludwig (cited in Cumpston, 1940) with Popillia japonica, by Cumpston (1940) with black beetle and by Carne (1957) with Sericesthis geminata. The available evidence on scarabaeid larval feeding and the interaction between soil O.M. and plants, would suggest that both soil O.M. and living plant root material can form the basis of the larval diet.

In the previous chapter, it was established that the consumption and utilisation of plant roots by black beetle larvae varied between plant species. This chapter presents the results of a number of laboratory and field studies of the interaction of soil O.M. and plants on the growth and survival of black beetle larvae.

II INTERACTION OF ORGANIC MATTER AND PLANTS

(1) Influence of the medium on first instar larvae in the absence of plants

(a) Methods

The importance of soil organic matter (O.M.) to the survival and growth of newly emerged first instar larvae was examined in four media with varying levels of O.M. Black beetle male and female adults, collected in the spring from pasture at the Otakanini Research Area, were maintained at Ruakura in a soil medium on carrot diet at 20 ^{o}C. In January, newly laid eggs were collected from the soil by sieving, surface sterilized with 4% sodium hypochlorite solution, and placed in petri dishes on filter paper moistened with the same solution. Newly emerged larvae were taken from the dishes and placed in small plastic pots with snap-on lids containing the treatment medium. Treatments were vermiculite (horticultural grade), Horotiu sand, Redhill sandy loam and sieved peat (horticultural grade, Hauraki Plains spaghnum peat).

Each medium was maintained at a 25% moisture level (on a weight basis). One larva was placed in each pot, with 50 pots per treatment medium. No food source was present other than the medium. At the commencement of the trial, a sample of 50 newly emerged larvae was weighed to establish mean weight. As suitable larvae hatched over a period, it was not possible to start all trials on the same day. The Horotiu sand treatment commenced on 14 January, vermiculite and peat on the 16 January and Redhill sandy loam on 19 January. Surviving larvae from all pots were weighed at several intervals between the start of the trial and the conclusion on 16 February. The level of

O.M. in the media (excluding vermiculite) was determined by the Ruakura Soil Testing Laboratory. The Horotiu sand and Redhill sandy loam were analysed for percent organic C (% O.M. = 1.724 x % organic C), and percent loss on ignition was carried out on the peat medium, using the standard laboratory method for determining percent O.M. in peat soils.

(b) Results and Discussion

The percent organic matter in the treatment media is shown in Table 6-1.

Vermiculite being an artificial medium contained no O.M. and acted as a control, while the level of O.M. in Horotiu sand was very low, in comparison with the other two media.

The survival and growth of the first instar larvae on each of the media are shown in Table 6-2.

The mean weight of the sample of newly emerged first instar larvae at the start of the trial was 3.8 $\pm$ 0.6 mg (range 2.4-5.0 mg). Survival was highest on the peat medium throughout the trial, with 10 larvae still alive at the end of the trial. Of these larvae, six were in the second larval instar. Although larval survival on the vermiculite and Horotiu media was good at the first assessment, considerable mortality occurred in both treatments by the end of January. All larvae in these two media were dead by the 5 February. This was to be expected due to the complete lack of nutritive status of vermiculite. The inability of the Horotiu sand to sustain larvae however, indicates the level of 3.6% O.M. in the medium is inadequate also. Survival in the Redhill sandy loam followed a similar pattern to the vermiculite and Horotiu sand media with the exception that two

Table 6-1 The % organic matter (O.M.) in four treatment media used in a study of the importance of O.M. to the growth of first instar black beetle larvae.

Medium	% Organic C	% loss on ignition	% O.M.
Vermiculite	- +	-	0
Horotiu sand	2.1	-	3.6
Redhill Sandy loam	11.3	-	19.5
Peat	- +	55.9	55.9

+ = no determination carried out.

Table 6-2 The survival and growth of first instar black beetle larvae on media with varying levels of organic matter.

	Trial Assessment Dates									
	23.1 (1)		27.1 (2)		30.1		5.2		16.2	
Medium	*%S	** $\bar{x}$ wt.	% S	$\bar{x}$ wt.	% S	$\bar{x}$ wt.	% S	$\bar{x}$ wt.	% S	$\bar{x}$ wt.
Vermiculite	72	3.4±0.7	-	-	16	3.7±1.1	0	-	0	-
Horotiu sand	60	4.6±1.0	-	-	14	7.5±2.7	0	-	0	-
Redhill sandy loam	-	-	62	6.0±1.0	24	6.7±4.3	4	12.1± 0	4	16.3± 0
peat	92	5.0±1.6	-	-	62	7.0±2.4	30	12.8±3.2	20	21.3±6.5

(1) Redhill sandy loam treatment not assessed this date

(2) Only Redhill loam treatment assessed.

*%S = % Survival, n = 50

** $\bar{x}$ wt = mean weight of surviving first instar larvae (mg)

larvae were still alive at the end of the trial, one of which was in the second instar. This poor survival was surprising in view of an organic matter level of almost 20%.

These data cannot reflect the survival of first instar larvae under field conditions due to the depressive effect of handling stress, at weighing, on survival. They do show however the importance of O.M. in the medium to the growth and survival of first instar larvae, and the favourable nature of peat as a diet source.

(2) Influence of the medium and plants on first instar larvae

(a) Methods

To further examine the importance of the medium to first instar larval growth and survival, a trial was carried out with plant roots provided, in addition to the two best media from the trial described in (1) previously, peat and Redhill sandy loam. The two plant treatments were the roots of 'Nui' ryegrass and 'Pitau' white clover.

Plant material was grown in a pumice nursery bed, plants were harvested as needed and the roots, with crown attached, were washed free of pumice. A portion of plant root was placed in a small plastic pot containing the medium at a 25% moisture level, so that the roots were covered by the medium. Two black beetle eggs, on the point of hatching, were placed in each pot, with 30 pots per plant treatment per medium kept in a constant temperature cabinet at 20 ^{o}C. As soon as the eggs hatched, one larva was removed from each pot to prevent mortality from larval aggression, and the remaining larva placed adjacent to the roots, and examined at weekly intervals until ecdysis to the second instar occurred. The number of larvae in each treatment surviving to the second instar stage was recorded.

(b) Results and Discussion

The number of larvae surviving to reach the second instar was 50% greater on the peat medium than the soil medium (Table 6-3). The percent O.M. levels of these media were as detailed previously in (1) of this chapter. There was no significant difference in the numbers surviving on each of the media between the two plant species. In addition, the development time to second instar larvae did not differ significantly, means being 36.3 $\pm$ 2.7 and 37.5 $\pm$ 5.0 days on ryegrass in the peat and soil mediums respectively and 34.0 $\pm$ 4.0 and 34.6 $\pm$ 3.5 days on white clover in the two media. This is of considerable interest as white clover has been shown to be an unfavourable diet source for second and third instar larvae (Parts III and IV of this chapter, also Chapter 5).

These results provide strong evidence for the conclusion that first instar larvae feed primarily on soil organic matter rather than plant roots, and that the level of survival and rate of growth is dependent on the percent O.M. in the medium. In this respect peat was a more favourable medium than the Redhill sandy loam.

(3) Larval instar development and survival in peat

(a) Methods

The ability of black beetle larvae to develop beyond the first instar in a peat medium in the absence of any living plant roots was assessed in a further trial. Fifty newly emerged first instar larvae were placed singly in small lidded pots containing the same peat medium used in trials (1) and (2) previously at 25% moisture level. Pots were kept in a constant temperature cabinet at 20 ^{o}C and the stage

Table 6-3 The influence of the level of organic matter in the medium and of plant species on the growth of first instar black beetle larvae to the second instar.

Medium	Number of larvae reaching second instar on plant treatments (out of 30)	
	Ryegrass	White clover
Redhill Sandy loam	13	14
Peat	28	26

of larval development assessed every two weeks, until all larvae had either died or ecdysed to the third instar stage. Fresh medium was provided in each pot at these inspection times.

(b) Results and Discussion

Of the 50 first instar larvae at the start of the trial, 35 survived and underwent ecdysis to second instar larvae, taking a mean period of 21.4 $\pm$ 10.1 days (range 17-52 days) to complete the first instar stage. Development of the 22 larvae which survived to the third instar stage took 67.6 $\pm$ 14.2 days (range 52-117 days) from the start of the trial. These development times must only be approximate as with assessment occurring only every two weeks, ecdysis may have taken place soon after one inspection and not noted until the next assessment occasion. The results obtained for both development periods however illustrate the high degree of heterogeneity of the population. Under standard diet, moisture and temperature conditions, the development time to the third instar ranged from just over 7 weeks to over 16 weeks. If such variation can occur under laboratory conditions then considerably more is possible in the field.

The survival results indicate the highly favourable nature of the peat diet as a food source for larval growth, with over 40% reaching the third instar. King (1977) showed that in addition to causing third instar larval aggregation in laboratory studies, O.M. (sieved horticultural peat) may play a phagostimulant role in larval feeding. In addition adults have been recovered from pots of peat as the end point of development from newly emerged first instar larvae, in the absence of any other food source (King, unpublished information).

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These findings suggest that in pasture on high O.M. content soils, the unfavourable nature of some plant species, (discussed in parts III and IV of this chapter and in Chapter 5 previously), may be negated by the ability of black beetle larvae to develop satisfactorily in the absence of a plant root component in the diet. King (1977) showed in laboratory studies that third instar larvae were not attracted to plant roots when these were present in a peat medium.

III INFLUENCE OF PLANTS ON GROWTH

(1) Third instar larval growth on grasses and legumes

(a) Methods

A range of grass and legume plant species was screened against third instar black beetle larvae in the laboratory, using weight gain as an indicator of the influence of the plant on the insect. The plant species listed in the table of treatments were grown in a pumice medium nursery bed, to provide a constant source of plant material for testing. Third instar black beetle larvae were collected from a population in pasture at Ruawaro near Huntly and held in soil for a week in a constant temperature cabinet at 20 ^{o}C at Ruakura.

Plants of the test species were taken from the nursery bed, washed to remove the pumice, and then small portions of roots with crown attached were surrounded by a soil medium contained in small, lidded plastic pots.

In treatments consisting of a mixture, equal root portions of the two species were woven together so that larval feeding on one species only would be difficult.

The medium used was sieved Redhill sandy loam (% O.M., 19.5%) at 30% moisture level. Larvae of a similar size were selected and one was placed in each pot after being weighed. The 50 pots in each plant treatment were held at 20 ^{o}C during the two week trial period. Larvae were supplied with fresh root material and soil twice a week. The weight change of larvae alive at the end of the trial was computed on a daily basis as an index of growth on the different species.

(b) Results and Discussion

The larval weight gains (mg/larva/day) over the trial period are shown in Table 6-4. Analysis of variance carried out on transformed means, $\log_e(1 + x)$ revealed significant treatment differences, $F = 7.1276$ ($P < 0.001$). Tests for significance between treatments were made by Duncan's Multiple Range Test (Duncan, 1955).

Larval weight gain was significantly higher ($P < 0.01$) on paspalum and ryegrass than on the other treatments. The three legumes screened all produced low larval weight gains which were not significantly different from that on phalaris. The results show the unfavourable influence legumes appear to have on larval growth compared with grasses, with phalaris being an exception to this division. Further grasses are examined in the next trial. Sutherland and Greenfield (1978) have shown the presence of feeding deterrents in legume species including white clover, lotus major and lucerne, which accounts for poor larval growth in these species.

Reservations are held on the suitability of the screening technique described for evaluating mixtures, owing to possible variations in the degree of interminqling of the roots. In addition,

Table 6–4 Third instar black beetle larval weight gains on a diet of plant roots. (Treatments with letters in common do not differ significantly, ($P < 0.01$)).

Treatment	Larval weight gain (mg / larva / day)	
'G 15' paspalum	6.7	A
'Nui' ryegrass	6.5	A
'Maku' lotus	2.5	B
ryegrass / lotus	2.4	B
'Pitau' white clover	1.8	B
'Seedmaster' phalaris	1.3	B
ryegrass / white clover	1.1	B
'Wairau' lucerne	0.8	B
phalaris / white clover	0.5	B

Table 6–5 Third instar black beetle larval weight gains on a diet of grass roots.

Treatment	Larval weight gain mg / larva / day
'Nui' ryegrass	9.4
'Apanui' cocksfoot	11.1
Kikuyu (unknown selection)	15.9
'G 4710' tall fescue	17.8
'Matua' prairie grass	18.7
Average S.E. of differences	1.32 (Significant at ($P < 0.001$))

the extent to which preferential feeding occurred on one species in a mixture is unknown. It would appear however that larval weight gain on a grass/legume mixture is influenced primarily by the presence of the legume, as growth on the mixture did not differ significantly from that on the legume alone.

(2) Third instar larval growth on grasses

(a) Methods

To further evaluate larval growth on grasses, weight gain on ryegrass, shown to be favourable from the previous trial was compared with another four grass species. The techniques used were identical to those described in trial A, with the exception that 30 larvae were screened per species compared with 50 in the previous trial. The genus and specific names of the species are shown in Appendix 6-1.

(b) Results and Discussion

The larval weight gains on the five grasses are shown in Table 6-5. Covariance analysis relating weight gain to initial larval weight was carried out on untransformed data and showed significant treatment differences. Using a graphical method to test for the non-normality of data, larval weight gain on kikuyu, tall fescue and prairie grass was found to be significantly greater ($P < 0.001$) than on the other two treatments. There were no significant differences between daily weight gains on the treatments within these two groups.

This trial was carried out in February when due to high summer temperature, growth of the ryegrass and cocksfoot plants was slower than the other three species due to senescence of plants. Kikuyu is a summer-active subtropical species and both tall fescue and prairie

grass have shown considerable summer activity in field trials at the Otakanini Research Area, possibly due in part to a deeper and more vigorous root system than species such as ryegrass. It is possible that the greater larval growth on these three species is a reflection of better nutrient levels, compared with those in ryegrass and cocksfoot where high temperatures have induced a degree of senescence.

This trial also shows that relative to ryegrass (which was shown to be a 'favourable' plant species for larval growth in the previous trial III (1) of this chapter), these four grass species can also be termed favourable. The reason for the higher weight gain on ryegrass in this trial than in trial A is unknown, but is likely to be a factor of both variations in plant growth and larval populations as the two studies were carried out in successive years.

From these screening studies, phalaris emerges as the only grass species tested on which larval growth is poor, and in fact not significantly different from that on the legume species examined.

IV INFLUENCE OF PLANTS ON SURVIVAL

(1) Survival from eggs and second instar larvae on grasses and legumes

(a) Methods

Seedlings of the following plant treatments were individually raised, in a pumice potting mixture, in 8 cm diameter black polythene bags in a glasshouse, until planting as small plants in the field at the Otakanini Research Area in October.

1. 'G 15' paspalum
2. 'Nui' ryegrass

3. 'Seedmaster' phalaris

4. 'Pitau' white clover

5. 'Maku' lotus

6. ryegrass/lotus 50:50 mixture

7. phalaris/white clover 50:50 mixture

Swards of constant species composition, spacing and plant numbers were produced by hand planting in 0.5 m^2 plots, with each plot enclosed by boundaries of asbestos sheeting strips as shown in Plate 6-1. The strip was 20 cm wide, sunk 15 cm into the soil leaving a 5 cm high margin around each plot. Each plot was planted at a total density of 36 plants per m^2. Fertiliser was applied pre-planting and plots were watered until the plants were established. All treatments were trimmed to a height of 6 cm at weekly intervals by hand-clippers. There were five replicates of each treatment arranged in a randomised block design. Each plot was further sub-divided into two areas of 0.25 m^2 by a strip of asbestos sheeting.

Into one 0.25 m^2 area in each plot, 30 black beetle eggs were seeded on 23 December. The eggs were taken from a population of black beetle adults maintained in a soil medium on a carrot diet at 20 ^oC at Ruakura. Eggs were placed in small holes in the soil made by a spatula, at a depth of 2 cm, by the base of plants and then covered by soil. The egg distribution was uniform in each plot. On the 4 February, the entire 0.25 m^2 area of the plot (half of each treatment) was dug up, and the insect stages present removed by hand sorting and counted.

Into the other 0.25 m^2 area of each plot, 15 second instar larvae were seeded on 17 December. The larvae were collected from



Plate 6-1 Small pasture plots used to determine the survival of black beetle larvae on a range of plant species in the field.

an area of pasture at Ruawaro near Huntly, and then held in a soil medium at 20 ^{o}C at Ruakura for several days to allow any damaged during collection to be identified. Similar sized larvae were distributed uniformly on the plot surface adjacent to plants and any that did not immediately burrow into the soil were replaced. On the 24 January, the whole 0.25 m^2 of each plot was dug up as for the area seeded with eggs, the insect stages present collected by handsorting the soil, and then counted.

(b) Results and Discussion

Table 6-6 shows the percentage survival from eggs on each plant treatment. Analysis of variance was carried out on transformed data, $\log_e(1 + x)$. Significant treatment differences were identified using Duncan's Multiple Range Test.

Survival was very low over the whole trial which indicates the difficulties in establishing black beetle populations artificially from eggs. Although recovery was higher from paspalum and ryegrass than from the other treatments, F = 1.92 which is not significant, showing that no treatment differences were present. This is due to the high variability in individual replicate totals (see Appendix 6-1).

The various plant treatments had no consistent effect on the rate of development of the black beetle population after hatching from the egg stage as shown in Table 6-7.

The recovery of black beetle from the treatments seeded with second instar larvae and the percent of the total recovered in each development stage are shown in Table 6-8.

In this trial, no black beetle were present in the plots at the time of planting the various treatment species. However, adults may

Table 6–6 The recovery and % survival of black beetle larvae in February from plant treatments seeded with 150 eggs in December.

Treatment*	Number of black beetle recovered	% survival
ryegrass	43	29
paspalum	31	21
ryegrass / lotus	22	15
lotus	12	8
white clover	12	8
phalaris	11	7
phalaris / white clover	6	4

* cultivars as shown previously

Table 6–7 The % of the total black beetle recovered in each development stage from a range of plant treatments seeded with 150 eggs.

	% of total recovered				
Treatment	L_2 larva	L_3 larva	pre-pupa	pupa	Adult
ryegrass	15	66	19	0	0
paspalum	0	56	22	7	15
ryegrass / lotus	10	70	10	5	5
lotus	33	56	0	11	0
white clover	36	27	9	9	18
phalaris	22	33	0	33	12
phalaris / white clover	0	100	0	0	0

Table 6–8 The numbers of black beetle recovered and the stage of development in January from plant treatments seeded with 75 second instar larvae in December.

Treatment	Number of black beetle recovered	% of total recovered				
		L_1 larvae	L_2 larvae	L_3 larvae	pre-pupa	pupa
paspalum	147	2	23	67	2	6
ryegrass	92	11	48	35	4	2
ryegrass/ lotus	46	0	17	67	13	3
lotus	44	0	2	75	9	14
phalaris/ white clover	42	0	5	57	36	2
phalaris	41	4	12	54	20	10
white clover	32	9	3	72	13	3

have dispersed into the plots by flight during the period between planting and seeding. No attempt was made to remove black beetle present in the plots at this stage, or to prevent flight into the plots after seeding. The results show that more black beetle were recovered from the paspalum and ryegrass treatments than were seeded in initially (75 second instar larvae per treatment). The individual replicate totals are shown in Appendix 6–2. In addition first instar larvae were recovered from four of the treatments. These findings support the conclusion that oviposition by immigrant females occurred on at least some of the plots after the treatments were established.

Analysis of the data shows that more black beetle were recovered from paspalum ($P < 0.05$) than from the other treatments. From an analysis comparing the paspalum and ryegrass group with the group comprising all other treatments, there were significantly more ($P < 0.05$) black beetle recovered from the former group. This could have resulted from a number of factors:

- More eggs were laid in the paspalum and ryegrass treatments.
- More adults dispersed from adjacent pasture into these two grass treatments.
- Immigrant adults lived longer in these treatments.
- Larval survival was greater on paspalum and ryegrass.

The favourable effects of the two grasses on oviposition preference, adult longevity and fecundity are demonstrated in Section 3, Chapters 8 and 9. Regardless of what combination of factors operated in this trial, the conclusion from the results remains that the recovery of black beetles was greater on the paspalum and ryegrass treatments.

As a further aspect of this investigation of the influence of plant species on survival, third instar larvae were seeded with the same treatments in March in an identical trial design (see Section 3, Chapter 10). In this study, significantly more black beetle were recovered from the paspalum and ryegrass treatments in the following July.

In each of these three trials, the trends are the same; greater black beetle population density on the paspalum and ryegrass species. For the reasons already discussed it is not possible to attribute these differences solely to survival which was the initial aim of the investigation. However, when larval weight gain on the treatments as detailed in III (1), earlier in this chapter is correlated with population density in treatments seeded with black beetle using a non-parametric rank test, $r = 0.61$ ($P < 0.05$). Larval weight gain on pasture species in the laboratory appears therefore to be a reasonably good indicator of the effects of pasture species on population density in the field.

(2) Larval growth and survival from eggs on a grass, a legume and a grass/legume mixture

(a) Methods

As part of a simulated field study of the effect of plant species on fecundity which is described fully in Section 3, Chapter 8, II (2) (iv), the effect of pasture composition on larval survival was also investigated using the same trial layout. On the 16 November 1976, male and female black beetle adult pairs were placed in 15 cm diameter PVC cylinders, sunk in the ground and containing either ryegrass, white clover or a ryegrass/white clover mixture as pasture

treatments. The level of oviposition in the treatments was determined by removing half the cylinders in each treatment on 20 December 1976 and extracting the eggs and first instar larvae from the enclosed soil.

The remaining 14 cylinders in each treatment were left in the soil at the Otakanini Research Area until 1 February 1977 when they were carefully dug up so that the soil and pasture within the cylinder was intact, placed in plastic bags and then taken to the extraction laboratory at Ruakura. Here the larvae within the cylinders were extracted by hand-sorting, and then counted and weighed. A sample of the larvae from each of the treatments was deep frozen and held until determination of the level of fats was carried out using the methods detailed in Section 3, Chapter 8.

(2) Results and Discussion

The mean level of white clover and ryegrass in the pasture mixture treatments as determined on a percent cover basis by point analysis was 60 $\pm$ 8% and 40 $\pm$ 8% respectively.

Analysis of these results showed that there were no significant treatment differences. It is assumed for the purposes of the evaluation of plant species on larval survival, that these populations represent the mean level in each treatment.

The number of larvae recovered from the treatments in February is shown in Table 6-9. Replicate totals are shown in Appendix 6-3.

There was a wide variation recorded in the number of larvae per cylinder, ranging from 0-13. Analysis of the data shows that there are no treatment differences. The percent decrease in the larval population over the period from 20 December to 1 February was 75.7%,

Table 6-9 The number of black beetle larvae recovered in February from three plant treatments seeded with 14 male and female adult pairs in November.

Treatment	Number of black beetle recovered			
	First instar larvae	Second instar larvae	Third instar larvae	Mean per cylinder
ryegrass	0	5	17	1.57 ± 3.0
white clover	0	16	0	1.14 ± 1.4
ryegrass/ white clover	1	15	11	1.93 ± 2.4

Table 6-10 The mean weight of second and third instar larvae recovered in February from three plant treatments.

Treatment	mean larval weight (mg)		
	Second instar	Third instar	Second and Third overall
ryegrass	109.3 ± 39.0	236.2 ± 105.2	172.8 ± 238.1
ryegrass/ white clover	77.4 ± 43.0	189.2 ± 70.0	133.3 ± 149.4
white clover	71.3 ± 37.6	-*	71.3 ± 37.6

* = no larvae in the third-instar

Table 6-11 The mean % fat level in the second and third instar black beetle larvae recovered from three plant treatments.

Treatment	Mean % fat / larva	
	Second instar	Third instar
ryegrass	21.2 ± 5.2	21.1 ± 8.4
ryegrass/white clover	20.4 ± 2.3	16.0 ± 5.4
white clover	24.1 ± 11.9	-

70% and 76.5% on the ryegrass, white clover and ryegrass/white clover treatments respectively, showing that larval survival over this period was not significantly affected by the plant treatments.

The most striking aspect of the data is the effect that the treatments have had on the development of the larvae (Table 6-9). In the ryegrass treatment, 77% of the population is in the third instar stage, compared with 40% in the ryegrass/white clover, and none in the white clover treatment. Conversely, only 23% of the larvae are in the second instar stage in ryegrass, compared with 56% and 100% on the ryegrass/white clover and white clover treatments respectively. The increasing level of white clover component in the treatments has had a negative effect on the rate of larval development.

The larval weight data shown in Table 6-10 suggests that both second and third instar larvae developing on ryegrass in the absence of white clover, grow at a faster rate and so weigh more after a given period of time than larvae on a diet containing the legume. Considerable variation was present in the data as shown by the very large S.E.'s of the means. Analysis of variance of data for both second and third instars shows no significant treatment differences exist. However, analysis of variance of mean overall larval weight (i.e. pooled second and third instar data), showed that significant treatment differences existed ($F = 13.4$, $P < 0.001$). The presence of the legume reduced the rate of larval growth.

Fat levels in the larvae recovered from the trial are shown in Table 6-11. There were no third instar larvae recovered from the white clover treatment so no fat determination was possible. All

extractions were carried out on larvae from rep 3 of the trial only as most larvae were recovered from this replication. Considerable variation was found in the fat levels within a treatment as shown by the relatively large S.E.'s. Analysis of variance carried out on arcsin transformed proportions showed that there were no significant treatment differences.

Although survival from eggs and first instar larvae in December to second and third instar larvae in February was not significantly influenced by the treatments in this trial, the presence of legume in the pasture diet did reduce the larval rate of development. These results would suggest that larvae are having to feed longer on a diet containing the unfavourable legume component than in the ryegrass diet to achieve the same increase in weight.

CHAPTER 7

DISCUSSION OF PRE-ADULT ECOLOGY SECTION

The aspects of pre-adult ecology examined in this section involve some of the factors influencing growth and survival of the various developmental stages. These are soil moisture and temperature and the larval diet. Although the main emphasis of the section was on the interaction between the insect and various food sources, results gained on the influence of the physical soil parameters have allowed comparison with other scarabaeids to be made.

I SOIL MOISTURE AND TEMPERATURE

Black beetle eggs were shown to be relatively tolerant of a wide range of soil moisture levels when continually exposed to these levels. Although the optimum range for hatching occurred between 25% and 40% soil moisture (by weight) in Redhill sandy loam, egg viability was not greatly reduced between 15% and 55%. It can be concluded that as spring soil moisture conditions recorded on the same soil type under pasture at the Otakanini Research Area, fluctuated between 30% and 55% over several seasons, egg mortality induced by variation in this parameter is likely to be of minor significance between seasons. Grass grub eggs are also known to be able to survive a wide range of soil moisture conditions (Kelsey, 1951; Galbreath, 1970).

In contrast to black beetle eggs, first instar larvae appeared to be much less tolerant of extremes of soil moisture levels

(Table 4-4). It has been shown by Davidson et al. (1972b) for first instar Sericesthis nigrolineata larvae and by Wightman (1974) for grass grub larvae, that survival decreased as soil moisture levels approached plant wilting point and soil saturation point. Hassan (1975) found that all first instar larvae of Anoplognathus porosus died after three days in very dry soil, and Wightman (1973) concluded that first instar grass grub larvae were less tolerant of low soil moisture levels than the egg stage. The greater tolerance to extreme soil moistures of eggs than of first instar larvae in black beetle is therefore similar to other scarabs. Although survival of first instar black beetle larvae was highest at 25% soil moisture level, considerable heterogeneity of response was evident in the population tested.

The most striking characteristic of the black beetle - temperature interaction was the high temperature necessary for growth and survival and the high temperature tolerance relative to some other scarabaeids (e.g. grass grub, Sericesthis nigrolineata). The highest level of egg viability and the fastest rate of hatching occurred at 25 ^{o}C compared with 20 ^{o}C for grass grub eggs (Wightman, 1973). No hatching occurred at 10 ^{o}C, although eggs held at this temperature for 55 days hatched when transferred to 25 ^{o}C indicating that eggs laid early in the spring may develop slowly until soil temperatures increase.

First instar black beetle larvae exhibited an exponential increase in growth rate between 10 ^{o}C and 25 ^{o}C. Although some larvae at 10 ^{o}C and 15 ^{o}C lost weight over the trial period, no weight loss occurred at the higher temperatures. Second and third

instar larvae were also found to be tolerant of exposure to high soil temperatures with the third instar being more tolerant than second instar larvae. Larvae appeared to be less tolerant of high soil temperatures at lower soil moisture levels. A similar interaction was observed by Davidson et al. (1972a) for S. nigrolineata larvae.

No third instar black beetle larval mortality occurred below 35 ^{o}C and mortality was less than 50% below 40 ^{o}C. Second instar mortality was below 50% at 35 ^{o}C in both soil moisture regimes. As shown in Chapter 6 however, long periods of continual exposure of second instar larvae to 35 ^{o}C caused 100% mortality.

These results are in marked contrast to those for grass grub obtained by Kain (1975) who showed that the thermal death point threshold range of second and third instar larvae, exposed to high temperature conditions in the laboratory, extended from 31.1-33.9 ^{o}C, with 100% mortality at the higher temperature. Although some overlap in the distributions of the two insects does occur, black beetle is more northerly and so grass grub is not found over much of the black beetle range. This difference in distribution probably reflects the difference in temperature tolerances.

The response of other scarabaeid larvae to temperature has been shown to vary between species. The results of Hassan (1975) and Davidson et al. (1972a) showed that at 37.5 ^{o}C, survival of S. nigrolineata larvae was low after a 3 h exposure, while 80% of Anoplognathus porosus larvae were alive after a 6 h exposure. This suggested that A. porosus larvae seemed able to tolerate higher temperatures than S. nigrolineata even though both species occur in the same general area.

The finding that temperatures between 15 °C and 20 °C appear to be the critical range for black beetle eggs and first instar larval development and growth is also mirrored in the interaction of temperature with second and third instar food consumption and growth. When carrot was provided as a food source, third instar larvae were found to be more tolerant than second instar larvae of higher temperatures. The consumption index (C.I.) increased linearly with increasing temperature with an upper threshold at about 20 °C for second instar larvae and between 25 °C and 30 °C for third instar larvae. Although Ridsdill Smith *et al.* (1975) using similar techniques found the upper threshold for third instar *S. nigrolineata* larvae was 30 °C, the C.I. for this insect at 20 °C, was 0.13 mg/mg of larva/day, similar to that found by Hurpin (1960) for third instar *Melolontha melolontha* larvae on a carrot diet at 20 °C, and to the black beetle figure of 0.135 obtained in this study.

Both black beetle larval instars had a negative efficiency of conversion of ingested food (E.C.I.) at 10 °C, with a peak utilisation at 20 °C. The results with third instar larvae contrast with those of Ridsdill Smith *et al.* (1975) who found a peak E.C.I. for *S. nigrolineata* larvae at 14 °C and a 6% E.C.I. level at 10 °C, illustrating a marked difference in cold-hardiness. In addition, the E.C.I. for black beetle at 20 °C is almost double the figure for *S. nigrolineata*. The E.C.I. for the latter species declined from 10.9% at 14.9 °C to less than 1% at about 28 °C, compared with a decline from 19.1% at 20 °C to 13.2% at 30 °C for black beetle.

For both insects, utilisation declines at higher temperatures in spite of increasing consumption. Cairns (1972) noted for *S. nigrolineata* larvae, that at temperatures above the optimum, the

amount of assimilated energy lost through respiration increased, thus reducing the proportion of energy that could be channelled into growth. Utilisation of carrot by third instar black beetle larvae was greater than for the second instar. This increase in the E.C.I. between instars has been observed in other insects (e.g. Pseudaletia unipuncta, Mukerji and Guppy, 1970; Stalia major, Fewkes, 1960; Phaleria bucephala, Evans, 1939).

The growth rate (G.R.) was significantly higher for third instar larvae than for the second instar which reflects the higher E.C.I. by larvae of the later instar. The G.R. for third instar black beetle larvae peaked at 25 ^{o}C, compared to a figure of 17.5 ^{o}C obtained with S. nigrolineata larvae by Ridsdill Smith et al. (1975).

These temperature interaction results illustrate the warm climate affiliations of black beetle as outlined in Chapter 1, and the greater degree of cold-hardiness exhibited by S. nigrolineata which is adapted to the cold winter conditions of the New England tablelands in New South Wales. The relatively high temperature requirements of black beetle probably give some indication as to the likelihood of an eventual limit to a southern spread of the distribution. As consumption, utilisation and subsequent growth of the larvae appear to be optimum in the 20^{o}C to 25 ^{o}C range, the insect is likely to build up to pest status numbers following warm seasonal conditions in northern New Zealand. The distribution may be limited to areas of New Zealand where these soil conditions regularly occur, which would follow the present black beetle distribution shown by Watson (1978).

II THE ROLE OF ORGANIC MATTER

As was pointed out in the introduction to Chapter 6, organic matter (O.M.) is known to play an important role in scarabaeid larval feeding. Black beetle larvae have been shown able to obtain their nutritional requirements from the soil O.M. complex in this study. First instar larvae survived best in the medium with the highest level of O.M. in the absence of plants, with peat being a more favourable medium than soil or sand. When ryegrass or white clover plant roots were provided in either a peat or a soil medium as food for first instar larvae, there was no difference in larval survival between the two plant species, but survival was found to be twice as high in the peat medium as in soil.

This finding is of particular interest as white clover was shown to be an unfavourable diet for second and third instar black beetle larvae in Chapters 5 and 6. In view of this, the results suggest that first instar larvae feed primarily on O.M. with the rate of growth and survival being influenced by the level of O.M. in the soil. Carne and Chinnick (1957) also considered that young larvae of Sericesthus geminata fed primarily on O.M. with larger larvae feeding on the roots of grasses. In contrast, Kain and Atkinson (1977) showed that first instar grass grub larvae are primarily root feeders.

Black beetle were shown to be able to develop from eggs to third instar larvae on a diet high in O.M. in the absence of any living plant material. Cumpston (1940) also noted this ability with black beetle. Miller (cited in Sutherland, 1971) and Kain (1975) concluded that in the absence of live plant tissue, grass grub could also exist on soil O.M.

The actual role that O.M. plays in the feeding behaviour and nutrition of later instars of black beetle larvae is still a matter of conjecture. King (1977) concluded that as O.M. was shown to stimulate third instar larval feeding in the presence of plant roots, larvae were both O.M. and plant feeders. This finding is in agreement with the feeding behaviour of a number of other scarabaeids reported in the literature and reviewed in the introduction to Chapter 6. The point remaining unresolved is whether larvae preferentially ingest either living or dead components of the soil O.M. complex. Power (1968) suggested that grass grub larvae did not eat plant roots selectively and these were simply ingested with soil and O.M., while Kain and Atkinson (1977) considered it was still unclear if actively feeding larvae discriminate between soil and dead or live tissue. Wensler (1971) however found that S. geminata larvae aggregated in the presence of O.M. when placed in a soil with a low O.M. level but preferred living ryegrass roots to dead O.M. As feeding activity was increased by the addition of either form of O.M. to the soil, Wensler concluded that larvae fed selectively on O.M., but did not specify any preference for the form of O.M. In contrast, Ridsdill Smith (1975) found that S. nigrolineata larvae also selected and ingested O.M. in soil in both the presence and absence of plant roots, but that larvae were better able to feed and grow when plant roots were present. He concluded that larvae of this species preferentially select and feed on living roots.

In contrast to the findings of Wensler and Ridsdill Smith, Davidson (1969) and Davidson and Roberts (1968b) suggested that the larvae of some other Australian Scarabaeidae, namely Rhopaea spp. and

Anoplognathus spp. are soil ingestors which only incidentally eat plant roots and as such are more general feeders, being primarily saprophagous. As King (1977) was able to show aggregation of black beetle larvae at sites high in O.M. but not at plants, it is likely that this species may also be primarily saprophagous. Black beetle larvae are known to develop in the top few centimetres of the soil profile (Chapter 13), where soil O.M. levels are highest and where feeding activity would inevitably involve plant roots.

III EFFECTS OF PASTURE SPECIES ON LARVAL GROWTH AND SURVIVAL

The results of the work reported in this section on the food consumption, utilisation and subsequent growth and survival of black beetle larvae, illustrate some striking differences between plant species in the plant-insect interaction. An excellent correlation was found between the consumption and utilisation of plant species by larvae and growth and survival in both the laboratory and field. As pointed out in the introduction to Chapter 5, little research has been undertaken on the measurement of feeding by Scarabaeidae. Ridsdill Smith *et al.* (1975) noted that until larval consumption of grass roots can be measured directly, their results on the consumption of carrot by larvae of *S. nigrolineata* represent the best estimate of scarabaeid intake available for root feeding species. The data presented on consumption and utilisation in this section are therefore a positive contribution not only to an understanding of black beetle ecology, but also to the feeding behaviour of scarabaeids generally.

Using the glass bead ingestion technique to provide a measure of relative acceptability, it was found that considerably more feeding by

black beetle third instar larvae occurred on ryegrass and paspalum than on white clover, showing that the two grass species were more favoured food plants. Ridsdill Smith *et al.* used the technique to assess differences in feeding rates of *S. nigrolineata* larvae in soil with and without plants. The results with black beetle larvae show that it can also be used to examine differences in feeding rates between plant species.

The gravimetric techniques used showed that the C.I. of third instar black beetle larvae was greater on ryegrass and paspalum than on white clover, which is in agreement with the results obtained using the glass bead technique. Sutherland and Greenfield (1978) showed the presence of a black beetle larval feeding deterrent in white clover roots, which would explain the lower consumption on this species.

C.I. expressed in mg/mg of larva/day for the grasses was between 0.08 and 0.11, compared with 0.135 for carrot. This suggests a lower consumption of pasture plant roots than carrot. In his review of consumption by insects, Waldbauer (1968) presents C.I.'s for Lepidopteran species ranging from 1.2 to 2.2 when consumption of plant foliage is expressed on the same fresh weight of food, fresh weight of insect basis as was used for the scarabaeids. This suggests that larvae of root feeding insects may have lower C.I.'s than foliage feeding insects, possibly because the former are normally adapted to the simultaneous ingestion of O.M. present in the soil within the natural feeding environment.

The significantly higher black beetle larval growth rate on grasses, compared with white clover was expected in view of the consumption results. Surprisingly there were no significant

differences in utilisation of the three species by third instar larvae, which suggests that the low growth rate on white clover is simply an artifact of low consumption. Sutherland and Greenfield (1978) demonstrated the presence of a toxin in white clover root extracts, but the dose of root extract injected to induce larval mortality was equivalent to a fresh weight of root seven times greater than larvae consumed in seven days in the consumption trial. Unless the toxin in white clover roots acts in a cumulative manner, it would appear very unlikely that sufficient root would be ingested in a field situation, where organic matter is also consumed, to cause mortality.

Although no data were obtained on consumption and utilisation of plant roots by second instar larvae, the much higher growth rate on grasses than on white clover suggest that the feeding response is similar to that shown for third instar larvae.

The relationships established between plant species for the growth of larvae feeding on them in the absence of soil, were also found to exist when the same species were provided as food in a soil medium. Larval growth in terms of weight gain was greater on rye-grass and paspalum than on white clover. All other legumes tested were also as unfavourable as white clover for larval growth. White clover has also been shown to have an adverse effect on other scarabaeid species (Davidson and Roberts, 1968b) although Farrell and Sweney (1972,1974b) and Kain and Atkinson (1977) showed high grass grub larval weight gains and survivals on white clover relative to other legume species.

Of the range of grass species provided as black beetle diets, all except phalaris could be termed favourable for growth. This

species has been shown to have an adverse effect on the growth of a number of other scarabaeids (Davidson and Roberts 1968b; Wensler, 1971; Kain and Atkinson, 1977). Davidson and Roberts concluded that toxic alkaloids may be responsible although Sutherland and Greenfield (1978) could find no evidence for a toxin affecting black beetle larvae in phalaris root extract.

Black beetle larval survival tested in the field on the range of grass and legume species followed the same pattern established for weight gains in the laboratory. This close relationship was also shown for grass grub by Kain et al. (1975) and Kain and Atkinson (1977). The growth and survival of black beetle larvae on a grass/legume mixture (e.g. ryegrass/white clover) was found to be lower than on the grass species alone. A field study reported in Chapter 6 revealed that this may be the result of a retardation of growth as the rate of larval development was shown to be slower on white clover and a white clover/ryegrass diet, than on ryegrass alone.

Kain et al., and Kain and Atkinson found that the grass grub larval weight gain and survival on a grass/legume mixture diet were also influenced more by the nature of the legume than the grass species. Their evidence showed however that the effects of grass/legume mixtures depends on the fact that since grass grub larvae are attracted to legumes (whether they are favourable or unfavourable to growth and survival), a small amount of unfavourable lotus in a grass/lotus mixture may have a large detrimental effect. In contrast, this does not appear to be the case with black beetle where no larval attraction or aggregation at plant species has been demonstrated. If black beetle is a non-selective feeder, then the effects of a legume in a mixture may be directly proportional to the amount of legume present.

The studies reported in this section have highlighted the importance of the host plant to larval ecology. Although adult behaviour has a major influence on the area of occurrence of black beetle populations (see Section 3), the level of feeding, growth and survival of larvae is largely an artifact of plant diet and of temperature. This aspect is extended in Section 4 where the effect of pasture composition on black beetle population numbers is examined.

IV SUMMARY

1. Black beetle eggs were more tolerant of a range of soil moisture conditions than first instar larvae.
2. The highest level of egg viability occurred between 20 ^{o}C and 25 ^{o}C. First instar larvae exhibited an exponential increase in growth rate between 10 ^{o}C and 25 ^{o}C.
3. After four hour exposure periods to high temperatures over a four day period, little second and third instar mortality occurred at 35 ^{o}C suggesting a greater tolerance of high soil temperatures than exhibited by temperate scarabs such as grass grub.
4. The consumption index (C.I.), efficiency of conversion of ingested food (E.C.I.) and growth rate (G.R.) for second and third instar larvae increased linearly with increasing temperature, with peak values occurring above 20 ^{o}C, before decreasing again between 25^{o}C and 30 ^{o}C. Third instar larvae were tolerant of higher temperatures than the second instar. The C.I. for third

instar black beetle larvae on carrot at 20 ^{o}C was similar to that for Sericesthis nigrolineata and Melolontha melolontha at the same temperature.

5. Black beetle were shown to be able to develop from eggs to third instar larvae on a high organic matter (O.M.) diet in the absence of any living plant material.

6. First instar larvae appear to feed primarily on O.M. with the rate of growth and survival being influenced by the level of O.M. in the soil.

7. It is concluded that later black beetle larval instars are primarily saprophagous, similar to larvae of Rhopaea spp. and Anoplognathus spp. but that as larval development takes place in the top few centimetres of the soil profile where O.M. levels are highest, plant roots will also be ingested.

8. Consumption of ryegrass and paspalum roots by third instar larvae and the subsequent growth rate was greater on these species than on white clover roots. No difference was noted in the E.C.I. between the three plant species.

9. Consumption of pasture plant roots appeared to be lower than that of carrot.

10. Larval weight gain in the laboratory and survival in the field was low on all legume species tested and high on all grass species with the exception of phalaris.

11. The presence of a legume in a grass/legume mixture was shown to reduce larval growth rate and survival, although the operative mechanism appears to differ from that causing the response of grass grub larvae to grass/legume mixtures.

SECTION 3

ADULT ECOLOGY

CHAPTER 8

ADULT FAT LEVELS, OVARIAN DEVELOPMENT AND FECUNDITY

I INTRODUCTION

Although Johannesson (1975) and Mercer and King (1976) investigated the sexual development of black beetle adults as outlined in the literature review in Chapter 1, there is no published research on the interaction of biological parameters such as diet on the nutrition, longevity and reproductive potential of adults. This is an aspect of adult ecology of considerable importance as the adult stage which is present in the soil for the greater part of the insect's life cycle, possesses great mobility; being able to disperse both within and between sites in autumn and again in spring. As a consequence of this mobility, the type of diet may vary greatly between adult emergence and oviposition in the spring.

In this chapter, the results of an investigation of seasonal changes in the pattern of female sexual development, body fat levels and the influence of diet on fat level are presented. Black beetle fecundity was also examined with particular emphasis being placed on the influence of diet on potential and actual fecundity.

II ADULT FAT LEVELS AND OVARIAN DEVELOPMENT

The levels of fat reserves in adult black beetle were assessed in a series of experiments designed to provide information on the following points:

(i) The importance of the duration of hot-solvent extraction to the weight of fat removed using a standard technique.

(ii) The seasonal changes in fat levels and the relationship of these to female sexual development.

(iii) Fat levels in male and female adults.

(iv) The influence of diet on female fat levels.

(1) Methods

(a) Technique used in determining adult fat levels

Black beetle adults were dried overnight to a constant weight in an oven at 56 ^{o}C. The dry weight of the adult was recorded on an H 16 Mettler balance. The adult was then placed in a 'Whatman-25 x 100 cellulose' extraction thimble, and the beetle was crushed at the bottom of the thimble using a 10 cm long glass rod which was left in the thimble during extraction. The thimble was then placed in a micro-Soxhlet extractor above a 100 ml 'Quick fit' flask containing a mixture of 20 ml 40:60 petroleum spirit and 20 ml of diethyl ether with a few 'BDH' anti-bumping granules. A condenser was attached to the top of the micro-Soxhlet. With the apparatus supported by a stand, the flask was placed in a 'Isopad' heating mantle and the solvent was boiled for three hours at a heat setting of 8 on an 'Isopad ERNI' control unit.

To investigate the effect of time of extraction on adult fat recovered, a fresh flask of solvent was placed below the micro-Soxhlet after three hours in the initial extractions. A further three hours extraction was then carried out. This allowed an estimate of the extra fat removed by a further three hour extraction

period. All subsequent studies involved only a single three hour extraction period.

At the conclusion of the extraction period the flask was removed from the heating mantle, the solvent was allowed to cool and then transferred to a clean weighed flask through 'Whatman IIIV' filter paper. This removed the anti-bumping granules. Both the first flask and the filter paper were flushed with ether solvent to remove any traces of fats. The solvent in the weighed flask was then evaporated off using a'Jobling Type 319' vacuum rotary evaporator leaving the extracted fat behind. After the evaporation procedure, flasks were placed in an oven at 56 ^{o}C overnight. In the morning, the oven was turned off, the door opened, and flasks left to cool for three hours before weighing on an H 16 Mettler. This allowed calculation of the weight of fat extracted and relative to the oven dry weight of the insect, the percent fat extracted.

(b) Seasonal changes in fat levels

To determine the pattern of fat build-up by the teneral adult female in the autumn, and utilisation over the winter and spring periods during sexual development, samples of adults were taken from a black beetle population at intervals between March and November 1977. The population was in a 0.2 ha paspalum pasture at the Otakanini Research Area. Samples were taken from the same area of the paddock at each sampling occasion to minimise pasture damage. The number of adults collected varied, depending on the time taken to recover females from the sward.

Adults were returned to Ruakura for processing. To establish the relationship between time of sampling, and ovarian development of

the females, the ovaries and other sex organs were dissected out under a stereo microscope. Only adults which were visibly free from disease, particularly Adelina sp. were used to determine fat levels. An ovarian development ranking was given to each female using the system of Mercer and King (1976) and the presence of the mated condition and any visible disease was recorded. After dissection, individual females were then held in a deep freeze until fat analysis could be undertaken using the procedure detailed in (a) of this chapter. This allowed both seasonal changes in fat levels and ovarian development to be established on the same females.

(c) Male and female fat levels

Although most of the work on adult fat levels was carried out on females because of the interest in diet, fat levels and fecundity, the relationship between the levels of male and female fat reserves was investigated. On 26 July 1977, ten male and twelve female adults were taken from the paspalum paddock at the Otakanini Research Area. On 27 July, ten male and 21 female adults were taken from an area of paspalum dominant pasture with a northerly aspect on the property of Mr P. Waugh, Te Kowhai, near Hamilton.

Dissection of females from both sites was carried out to determine sexual development as described in (b) of the methods. All females used were visibly free of Adelina sp. Extraction of the fat reserves was then carried out on the males and the females from both sites using the methods outlined in (a).

(d) Influence of site and diet on fat level

In this study, the importance of diet was investigated by several techniques.

(i) To investigate the variation in fat level that can occur between geographically separate sites at the same time of the year, populations of black beetle were sampled between July and November 1977. The sites were: the paspalum paddock at the Otakanini Research Area, the property of Mr P. Waugh, Te Kowhai and the property of Mr D. Spring, Elstow, Te Aroha. The last two sites comprised paspalum dominant pasture.

Only females were collected at each sampling occasion and both the mean stage of ovarian development and the level of fat reserves were established on females free from Adelina sp. infection, using the methods described in (a) and (b) of the Methods. In July and September females were collected from the Otakanini and Te Kowhai sites. In October, females were collected from all three sites and in November the Otakanini and Te Aroha sites were sampled.

(ii) To investigate the influence of diet on fat levels, adult females were taken from the paspalum paddock and an adjacent area of maize stubble at the Otakanini Research Area on 1 June 1977. The levels of ovarian development and fat were established by the methods previously outlined.

(iii) The influence that the type of diet between early spring and oviposition has on fat levels was studied by collecting male and female adults from both the paspalum paddock at Otakanini and the paspalum dominant pasture at Mr P. Waugh's, Te Kowhai, in September 1977. The levels of ovarian development and of fat were established

on a subsample of females from both sites which were free from Adelina sp. infection. The population from Otakanini was then maintained as separate male and female pairs on a carrot diet with soil, in small lidded plastic pots maintained in an insectary until the commencement of oviposition when the average fat level was established. The population from Te Kowhai was maintained until oviposition in a similar fashion on either a diet of 'G 15' paspalum or 'Nui' ryegrass or 'Pitau' white clover roots, obtained from a plant nursery bed. The level of fat in ovipositing females was then established by the methods previously described. This enabled the suitability of the carrot and pasture plant diets for sexually maturing females to be assessed.

(2) Results and Discussion

(a) Extraction technique

The total dry weight of fat, in five females fed on a carrot diet between 11 April and 11 July, removed by solvent extraction was 64.9 mg. The average dry weight per beetle was 80.3 mg. The percent fat per beetle removed in the first three hours was 14.6% and that extracted in the second three hours, 1.5%.

The weights of fat in ten females fed on a diet of paspalum or ryegrass roots over the same period were 106.8 mg and 95.0 mg respectively. Of this total, 92.4 mg of fat was removed in the first three hour extraction period and 14.4 mg in the second three hour period from those on a paspalum diet. Expressed in terms of percent fat/beetle on paspalum (on a dry weight basis), the level as determined by three hours extraction is 11.6% and by six hours extraction 13.4%. On the ryegrass diet the level of fat from the

first three hours extraction was 10.5% and 11.7% from six hours extraction.

On the diets tested, between 87% and 90% of the fat removed by six hours of hot solvent extraction was removed in the first three hour period. When fat levels are assessed singly on individual adults, these results suggest that three hours extraction will remove most of the fat present, speed up the extraction process, and still give an accurate measure of relative differences between populations.

Thin layer chromatography of the fat extracted was carried out by the Organic Chemistry Group at the Ruakura Research Centre. This revealed that in common with most other insects as reviewed by Gilbert (1967), the major component of the fats extracted from black beetle adults by the method used were triglycerides.

The technique used by Johannesson (1975) involved drying adults over silica gel before extracting with petroleum ether for 24 hours. This present study followed the method of Mukerji and Guppy (1973) where in a study of the lipid content of Pseudaletia unipunctata, insects were oven dried at 55 ^{o}C to a constant weight. Comparison of the percent fat on a dry weight basis obtained by Johannesson with those obtained in this study reveals very much higher levels from the latter. This difference however is not a function of any difference in insect dry weight between the two techniques as the mean dry weights of adults found by Johannesson are very similar to those of this study. Rather the amount of fat actually extracted in this study appears much greater. No mention is made by Johannesson of whether the extraction was carried out on intact beetles. It is considered that the crushing of the adults in the extraction thimbles in this study

has permitted more complete extraction of lipid reserves than in the investigation by Johannesson.

(b) Seasonal changes in fat levels

The percent of the population mated was determined by the presence of one or more spermatophores in the bursa copulatrix at the various sampling times. This was 0% in March and June, 17% in July, 85% in October (46% had mated more than once) and 100% in November (all had mated more than once).

As ovarian development proceeds the ranking index increases. Table 8-1 shows that the level of fats initially increases and then decreases. ANOVA carried out on the percent fat for each sampling occasion (given in Appendix 8-1), using an arcsin transformation showed that the increase in fat levels from March to June was highly significant ($P < 0.001$) as was the decrease from June to July. The decrease at the time of oviposition in the spring, from October to November was also highly significant ($P < 0.001$). Using a non-parametric test, the increase in the mean ovarian development ranking between March and November was found to be highly significant ($P < 0.001$).

These results have some similarities with those of Johannesson (1975) who found percent fat level as determined by solvent extraction increased from March to July and then decreased again by November. In the present study, fat level peaked in June. Using a visual assessment of fat level, Johannesson concluded that after peaking in mid-May, it remained static until the end of August and then declined from September. This contrasts with the present results where the fat levels (as determined by solvent extraction), declined after June. Difficulties have been noted (King, unpublished results) in relating

Table 8-1 The mean level of sexual development and % fat in black beetle adult females without disease, taken from the paspalum paddock at the Otakanini Research Area in 1977.

Mean sexual development and fat reserves at various sampling times ± S.E.

	30 March *(n=16)	1 June (n=15)	27 July (n=12)	13 October (n=9)	16 November (n=8)
**ovarian development ranking	1.9 ± 0.3	2.4 ± 0.6	2.6 ± 0.6	3.8 ± 0.8	4.9 ± 0.4
percent fat (dry wt basis)	17.8 ± 4.4	40.0 ± 5.2	19.6 ± 10.1	14.2 ± 5.6	5.5 ± 2.8

* Number of adults at the various sampling times

** Ranking on a 1-5 scale (Mercer and King, 1976)

Table 8-2 The % fat level in adult male and female black beetle from two paspalum pasture sites in July 1977.

Sampling site	Sex	% Fat (dry weight basis) and Range
Otakanini	Male	13.3 7.5 - 21.7 (n = 10)
	Female	19.6 5.8 - 39.4 (n = 12)
Te Kowhai	Male	27.2 13.7 - 37.4 (n = 30)
	Female	30.6 12.4 - 45.4 (n = 21)

visual rankings of fat body to those determined by quantitative methods. As ovarian development proceeds during the over-wintering period, when feeding and activity decrease, it could be expected that some fat reserves would of necessity be utilised as an energy source.

(c) Male and female fat levels

None of the females from the Te Kowhai site were mated compared with a level of 17% mated in the population from the Otakanini paspalum. Females from Te Kowhai had a mean ovarian development ranking of 2.3 ± 0.4 compared with a level of 2.6 ± 0.6 in the Otakanini population as shown in Appendix 8-2, not significantly different, but the difference in mated status suggests the latter population was more sexually developed.

Analysis of variance of arcsin transformed data showed that the level of fats in the male and female populations shown in Appendix 8-2, differed significantly ($P < 0.05$) between the sexes at the two sites (Table 8-2). Johannesson also found a sex difference in adult fat levels in July, with males and females having mean fat levels (air dry adult weight basis) of 9.8% and 11.2% respectively.

The level of fat in both the male and female adults was significantly higher ($P < 0.001$) in the population from Te Kowhai than in the Otakanini population. As the level of sexual maturity did not differ, it must be concluded that the Te Kowhai site was more favourable for overwintering populations and that the difference in fat level may reflect the influence of a more nutritionally adequate diet. Alternatively, the females from Otakanini may have been infected with pathogens that were not evident during screening of the population, which resulted in a lowering of the fat level.

(d) Influence of site and diet on fat level

(i) The variation in fat level sites is shown in Table 8-3.

Analysis of variance of arcsin transformed data showed that the mean percent fat level of female adults from Te Kowhai (Table 8-3) was significantly higher ($P < 0.01$) than that of beetles from Otakanini at the July and September sampling occasions. In October, the fat level in females from Otakanini was still significantly lower ($P < 0.05$) than those from Te Kowhai, although the level in those from Te Aroha did not differ from the other two sites. The high percent fat level in females at Te Aroha in November was significantly greater ($P < 0.01$) than that from the Otakanini population. The apparent increase in fat levels at Te Aroha between October and November was not significant. Using non-parametric tests, ovarian development was found to differ significantly ($P < 0.05$) between the geographically separated populations only in September.

Although considerable variation exists in sexual development and fat levels within a population at various times of the year (see Appendix 8-3), the results reveal significant differences in fat levels between populations.

(ii) The influence of different sites and diets on female fat levels is shown in Table 8-4. Ovarian development and fat levels are given in Appendix 8-4. Although the ovarian development rankings did not differ significantly (Table 8-4), analysis of variance of arcsin transformed data showed that fat levels in paspalum were significantly higher ($P < 0.01$), with a much smaller range than in females from maize stubble. This result suggests that the paspalum pasture is a more favourable diet for adult females over the autumn to early winter

Table 8-3 The influence of site on mean black beetle female sexual development and fat levels.

Site	Time of sampling	% Fat dry weight basis	Range and number in sample	Ovarian Development Ranking
Te Kowhai	26.7.77	30.6 ± 8.6	12.4 - 45.4 (n = 21)	2.3 ± 0.4
Otakanini	27.7.77	19.6 ± 10.1	5.8 - 39.4 (n = 12)	2.6 ± 0.6
Te Kowhai	13.9.77	26.7 ± 4.7	15.7 - 38.2 (n = 20)	3.4 ± 0.5
Otakanini	8.9.77	16.6 ± 4.3	12.9 - 25.1 (n = 8)	2.9 ± 0.4
Te Kowhai	4.10.77	21.1 ± 6.7	12.2 - 37.5 (n = 12)	3.5 ± 0.4
Te Aroha	21.10.77	18.9 ± 6.3	6.2 - 27.9 (n = 12)	4.2 ± 1.0
Otakanini	13.10.77	14.2 ± 5.6	6.5 - 24.1 (n = 9)	3.8 ± 0.8
Te Aroha	17.11.77	28.2 ± 6.5	15.5 - 36.2 (n = 12)	4.8 ± 0.5
Otakanini	16.11.77	5.5 ± 2.8	3.6 - 12.3 (n = 8)	4.9 ± 0.4

Table 8–4 The mean level of ovarian development and fat in female black beetle adults from maize stubble and paspalum pasture at Otakanini in June.

Site	% Fat (dry weight basis) ± S.E.	Range and number in sample	Ovarian Development Ranking ± S.E.
maize stubble	23.5 ± 13.5	8.7 – 45.1 (n = 8)	2.3 ± 0.9
paspalum pasture	40.0 ± 5.2	26.6 – 48.2 (n = 15)	2.4 ± 0.6

Table 8–5 The % fat in female black beetle adults at September and at oviposition for populations fed on either a carrot diet or pasture plant roots in an insectary trial.

Diet	% Fat (dry weight basis) At start of trial	At Oviposition
Carrot	16.6 ± 4.3	26.3 ± 6.9
Paspalum roots	26.7 ± 4.7	8.9 ± 4.3
Ryegrass roots		9.4 ± 2.9
White clover roots		11.2*

* Only 2 females survived on the white clover diet.

period although the influence of factors such as soil structure, moisture and temperature may also play a role.

(iii) The influence of diet over the period from early spring to oviposition is shown in Table 8-5. Analysis of variance was carried out on arcsin transformed data.

Fat levels over the trial period are shown in Appendix 8-5. The level of fat at the commencement of the feeding periods in September was significantly higher ($P < 0.01$) in the population to be confined to a pasture species diet than the population to be fed on carrot. At the commencement of oviposition this situation had been reversed (Table 8-5), and the percent fat of females on the carrot diet was significantly greater ($P < 0.01$) than those on the pasture species roots diet. The significant increase ($P < 0.01$) in fat levels of those confined on carrots and the significant decrease ($P < 0.001$) of those females on the pasture species diets illustrates the relatively favourable nature of carrot as a food source for adult black beetle. Fat levels at oviposition on the pasture species diets did not differ significantly between species. The decrease in fat levels with increasing ovarian development shown in section II (b) of this chapter also occurred in this trial on the pasture species diets. On the carrot diet, fat levels actually increased during ovarian development showing the very favourable nature of this diet.

III ADULT FECUNDITY

(1) The importance of food to ovipositing females

The importance of food over the pre-oviposition and the oviposition period to both potential and actual black beetle fecundity

was investigated in a series of trials. Potential fecundity was assessed as the total number of oocytes present in the ovaries and oviducts at the commencement of oviposition. Actual fecundity was taken as the total eggs laid by a female before senescence.

(a) Methods

Black beetle male and female adults were collected from an area of maize stubble at the Otakanini Research Area at the beginning of August 1976. The males and females were maintained separately on a diet of carrots in 30% soil moisture (by weight) Redhill sandy loam in a constant temperature room at 10 ^{o}C $\pm$ 1 ^{o}C with an 11:13 h, light:dark ratio.

In early September, 140 male and female pairs were placed individually in 10 cm high x 8 cm diameter white plastic pots with snap-on lids containing soil medium at a 30% soil moisture level. Adults were fed ad. lib. on carrot which was replaced twice a week. Fresh soil medium was provided every two weeks and the pots were maintained in a screened, outdoor insectary in a randomised pattern at ambient temperature. Adult males which died during the trial period were replaced. As it was not possible to determine if live adults were infected with disease which (as is shown in Chapter 11), was present at Otakanini, the results of this study may have been influenced by the incidence of pathogens, particularly Adelina sp. known to be present in the population.

At the time the 140 male and female pairs were set up from the main population, two subsamples of ten females were taken from this same population. One subsample was dissected to determine the stage of ovarian development and the presence of the mated condition following

Johannesson (1975) and Mercer and King (1976). The fat reserve level of the other subsample was determined on individual females, using the methods described previously in Section II.

When the carrot diet was replaced, the soil was sieved to determine the presence of eggs. At the commencement of oviposition, a sample of 20 females that had deposited their first eggs was dissected and the oocytes present within the ovarioles and oviducts counted to determine potential fecundity. All oocytes which had been differentiated within the ovarioles and which appeared likely to develop and be deposited by the female were included.

A further sample of 20 females which had also commenced oviposition were maintained in the soil medium in the absence of food until the death of the population. This enabled the importance to longevity and fecundity of access to food by ovipositing females to be assessed. Oviposition was monitored in the remainder of the population (100 male and female pairs) until the conclusion of the trial at the end of March 1977.

(b) Results and Discussion

(i) Female fat reserves and stage of sexual development.

The mean percentage fat on a dry weight basis for the subsample of females at the start of the trial was 30.3 $\pm$ 10.7%. Considerable variation in fat level was found (Appendix 8-6) with a range of 14.0 - 48.2%. The dry weight of the female was found to be significantly correlated with the percentage fat ($r = 0.747$, $P < 0.01$), shown in Fig. 8-1. At this stage in the spring, the dry weight of the female is evidently influenced greatly by the level of fat in the insect.

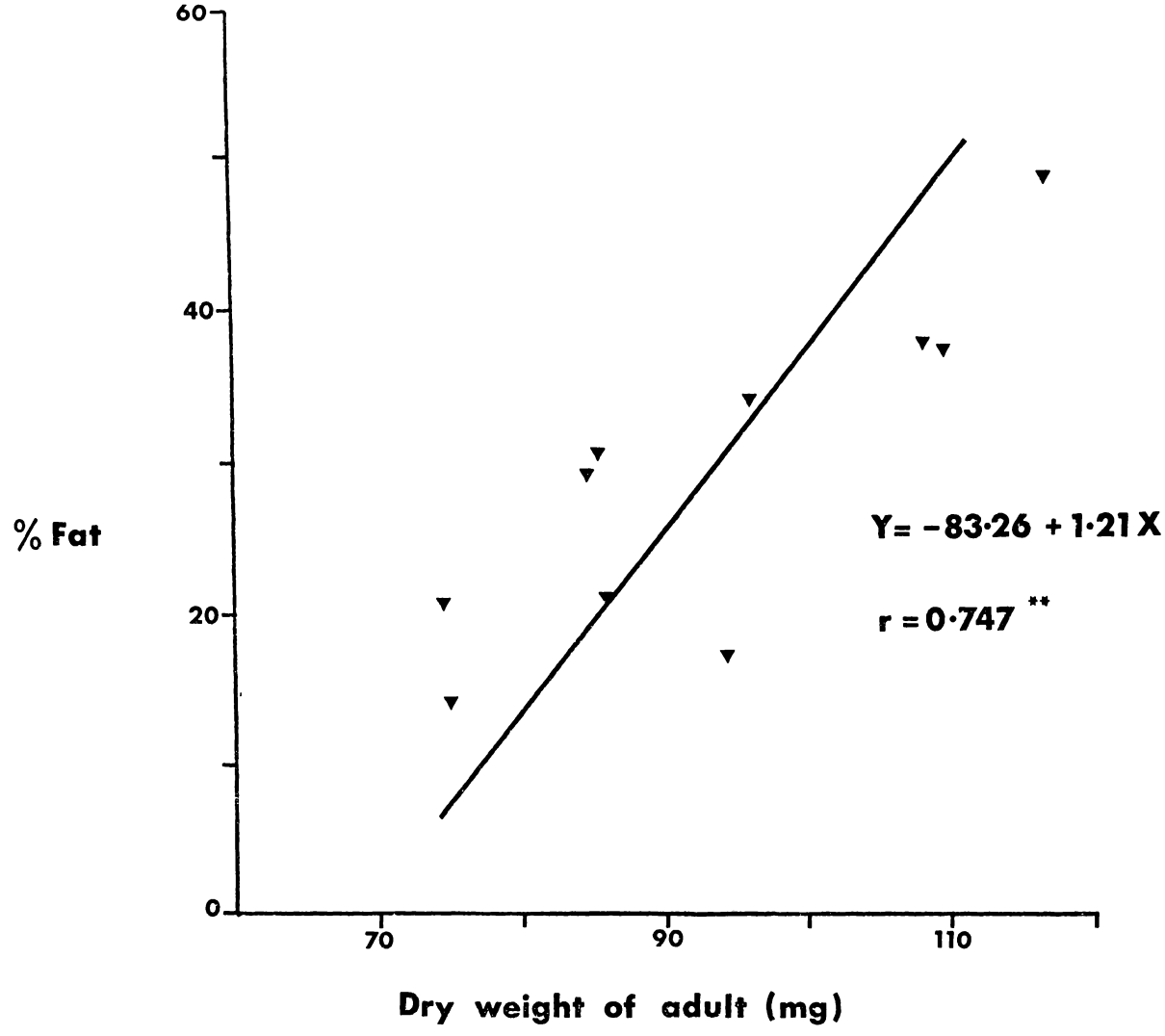


Figure 8-1 Relationship between the dry weight of female black beetle adults in September and the % fat. (** = P< 0.01).

The results of the dissection of the adult female subsample at the commencement of the trial also revealed considerable variation in the stage of sexual development. Using the ovarian ranking scheme of Mercer and King (1976), the variation was found to extend from Stage 1 - 4 with only 30% in the mated condition. Four females were found to be in Stage 1, two in Stage 2, three in Stage 3 and only one in Stage 4. As no fat analysis was carried out on dissected individuals, no correlation between fat level and ovarian development is possible in this trial. The relative sexual immaturity in the population is reflected in the slow rate of oviposition in the trial. On the 12 October, one month after the start of the trial, only one female had commenced oviposition, and by the end of October, only four of the 140 females had deposited eggs.

(ii) Potential fecundity

Data on fecundity are given in Appendix 8-7. All females dissected had laid their first batch of eggs which had a mean value of 3.2 eggs/female (range 1-10). The mean number of oocytes present in the ovaries at dissection was 48.1 $\pm$ 10.9 (range 26-69), per female giving a total mean potential fecundity of 51.3 $\pm$ 11.7 eggs/female (range 28-70), assuming no further oocyte differentiation takes place after the beginning of oviposition. With this proviso and under conditions favourable for adult survival, a mean fecundity of 51.3 eggs/female is possible for this population on the carrot diet.

(iii) Fecundity in the absence of food

The fecundity of individual females is given in Appendix 8-8. A mean of 2.4 eggs/female (range 1-10), was laid in the first batch

of eggs before the carrot food source was removed. This figure is not significantly different from that of the first batch of eggs of the population which was dissected to obtain the total potential fecundity. After the food was removed from the population, oviposition continued over a mean period of 47 ± 14 days (range 4-71) until adult death. In the absence of food, a further 5.9 ± 4.3 eggs/female (range 0-14) were produced, 71% of the total eggs laid. This figure is significantly different ($P < 0.01$) from the number laid prior to food removal. The total fecundity for this population was 8.3 ± 5.4 eggs/female with a range of 2-24 eggs/female.

(iv) Fecundity in the presence of food

Of the 100 females in this population at the start of the trial, 96 laid eggs over the five month trial period as shown in Appendix 8-9. The four females which did not commence oviposition were alive at the end of the trial and were observed mating on either one or two occasions. These individuals must be considered sterile. Johannesson (1975) found that 15% of females were sterile and failed to oviposit in a laboratory trial. At the conclusion of the trial, 59% of the population was still alive and 29% of these females produced eggs at the last occasion the soil was sorted before the trial was ended. The females alive and ovipositing at the end of the trial had been producing eggs over a mean period of 106 ± 12 days per female.

The mean number of eggs laid in the first batch per ovipositing female was 2.6 with a range of 1-15. This was not significantly different from the other two figures from the trial of 3.2 and 2.4 eggs/female in the potential fecundity and fecundity in absence of food sections respectively. The mean number of eggs laid per ovipositing

female after the first batch up to the end of the trial was 42.5 ± 26.0 with a range of 0-89 eggs/female. The total fecundity per ovipositing female was 45.1 ± 26.6 eggs/female (range 1-97). The fecundity of those females alive at the end of the trial and which had oviposited was 56.5 ± 22.7 eggs/female (range 2-97).

(2) The influence of pasture plant species on adult longevity and fecundity

A series of three insectary and one field study were carried out to examine the influence of different plant species on potential fecundity, adult longevity and actual fecundity.

(a) Methods

(i) Insectary screening of the effect of a range of plant species on actual fecundity.

Black beetle male and female adults were collected from a paddock of maize stubble at the Otakanini Research Area in August and held in a controlled temperature room at 10 °C in a soil medium on a carrot diet. The population was known to be infected with disease, in particular the pathogen Adelina sp. At the commencement of the trial in September, adults were placed in white plastic pots 10 cm high x 8 cm diameter, one male and female pair per pot. A Redhill sandy loam medium at 35% (by weight) soil moisture was used to half fill each pot. Plant root material (crown with roots attached) of a range of pasture species obtained by raising seedlings in a nursery area using a fertilised pumice medium was placed in the pots with the root system buried in the soil. The plant material used was taken from established plants at least 6 months old. The genus and specific names of the plants used are given in Appendix 0-1.

The plant treatments were:

'G 15' paspalum

'Nui' ryegrass

'Seedmaster' phalaris

'Slender Stem' digitaria

'Pitau' whiteclover

'Wairau' lucerne

'Maku' lotus

ryegrass/white clover (50:50 mixture)

ryegrass/lotus (50:50 mixture)

phalaris/white clover (50:50 mixture)

The roots in the three plant mixture treatments were entwined together to reduce selective feeding. In addition, adults were maintained on the soil medium in the absence of any plant roots as a further treatment. There were 30 replicates of each treatment. The pots were held in a randomised layout in a controlled environment room at 20 ^{o}C with a 14:10 light:dark hours ratio. New soil medium was supplied every two weeks. Fresh root material was supplied twice a week and the eggs laid by each female assessed and recorded by hand-sorting. The trial was carried out from 23 September to 17 December. Adult males which died during the trial were replaced.

(ii) Adult longevity and actual fecundity on paspalum, ryegrass and white clover.

In a later insectary trial, the two best treatments from the previous trial, paspalum and ryegrass, were compared with white clover from the less favourable group over a longer oviposition period. This trial was carried out in a screened, outdoor insectary where the

more natural conditions of a diurnal temperature fluctuation occurred. Black beetle adults were once again collected from maize stubble in August as for the carrot diet trial. All experimental details were the same as III (1), with the following exceptions:

The treatments were 'G 15' paspalum, 'Nui' ryegrass and 'Pitau' white clover, taken from a plant nursery bed. The roots with crown attached were placed in the soil and fresh material was supplied twice weekly. Redhill sandy loam at 30% soil moisture was the medium used. There were 30 replicates of each treatment. The trial began in early September and concluded at the end of February.

(iii) Effect of plant species on female longevity and potential fecundity.

To investigate the effect of diet on the longevity of the female in the spring, and on potential fecundity, adults were fed on three plant species in an insectary trial. The plant treatments 'G 15' paspalum, 'Nui' ryegrass and 'Pitau' white clover were obtained from a nursery area of established plants of each species.

Black beetle male and female adults were collected from a population known to be free of Adelina sp. in a paspalum dominant pasture at Te Kowhai near Hamilton in September. The stage of ovarian development and level of fat reserves of the population were determined by dissection and solvent extraction respectively of a subsample of 20 females. Commencing on 13 September, 30 male and female pairs per treatment were maintained in an insectary with the experimental details and design being the same as for the previous trial with the following exceptions. The soil medium used in the trial was Hamilton clay loam at 30% soil moisture. Pots were examined twice weekly for the presence

of eggs and as soon as the first eggs were laid, individual females were first dissected to determine potential fecundity by counting all differentiated oocytes within the ovarioles and oviducts. The level of fat reserves was then determined by solvent extraction. Some of the females that died before oviposition were dissected to determine the state of the ovaries.

(iv) Actual fecundity on plant species in the field.

To simulate a field study of the effect of plant species on fecundity, a trial was carried out at the Otakanini Research Area. An area of existing pasture was sprayed with paraquat to remove existing vegetation, cultivated and then sown into 1 m x 2.5 m plots of the following pasture treatments in September, 'Nui' ryegrass, 'Pitau' white clover and a mixture of 50:50 ryegrass and white clover. The seeding rate of the last treatment was adjusted in relation to percent germination in order to give a sward of approximately this composition. There were four replicates of each treatment randomised within four blocks. Diazinon insecticide at 2.2 kg/ha was applied after pasture germination in an attempt to remove any black beetle present at the site.

At the end of October, P.V.C. cylinders, 15 cm in diameter and 23 cm long were buried 15 cm into the soil of the plots so that pasture was enclosed inside the cylinder (Plate 8-1). Seven cylinders were placed within each plot, care being taken in the mixture plots to site cylinders in areas typical of the treatment composition.

In mid-November, black beetle adult males and females were collected from a population known to be free of Adelina sp in a cultivated area of paspalum-dominant pasture at Elstow near Te Aroha.



Plate 8-1 Cylinders placed in pasture to investigate the effects of pasture type on adult fecundity and larval development and survival.



Plate 8-2 Cylinders covered with a nylon mesh cover to prevent dispersal of black beetle adults during oviposition.

A subsample of 12 females from the population was dissected to determine the mean stage of ovarian development. Determination of fat reserve levels was subsequently carried out on the same females by solvent extraction.

Im mid-November, the relative ryegrass: white clover composition of the mixture treatment was determined by point analysis of the pasture within cylinders of each of the four replicates.

On the 16 November, one male and female adult pair was introduced into each cylinder. Adults which did not burrow into the soil were replaced. Cylinders were then immediately covered by a fine nylon mesh cover, 20 cm high x 16 cm in diameter which was held against the outer rim of the cylinder by rubber bands. The cover completely enclosed both cylinder and pasture to prevent dispersal by the adults as shown in Plate 8-2. This cover remained in place until the end of the trial, except for removal every ten days to allow clipping of the enclosed pasture to a height of 5 cm.

On 20 December, 14 cylinders per treatment with enclosed pasture and soil intact were removed from the plots, placed in plastic bags and returned to the extraction laboratory at Ruakura. The soil cores and pasture within the cylinders were hand sorted to remove adults, and eggs and small larvae were subsequently extracted by wet sieving after using a salt flotation system and counted. The remaining cylinders in each treatment were left as the basis of a study of pasture composition on larval rates of growth.

(b) Results and Discussion

(i) Effect of a range of plant treatments on fecundity.

Analysis of variance was carried out on transformed means,

$\log_e (1 + X)$. The variance ratio 'F' was 3.08 which was highly significant ($P < 0.001$). The mean fecundities shown in Table 8-6 were compared using Duncan's Multiple Range Test. At the 5% level of significance, fecundity on paspalum was greater than on phalaris, white clover, lotus and the ryegrass/white clover mixture. Fecundity on the latter four treatments plus lucerne was not different from that on soil alone. When the two best treatments, paspalum and ryegrass are compared by 'F' test (Sokal and Rohlf, 1969, Chapter 9) with lucerne, white clover, lotus and phalaris, there were significantly more ($P < 0.001$) eggs/ovipositing adult in the first group.

Comparison by 'binomial test' of the number of females ovipositing on paspalum and ryegrass with those on lucerne, white clover, lotus and phalaris shows that significantly more ($P < 0.01$) laid eggs on the former group. Few adults survived to commence oviposition in the soil treatment in the absence of plants and mean fecundity was only 1.1 eggs/female.

(ii) Adult longevity and fecundity on paspalum, ryegrass and white clover

The range of individual fecundity is given in Appendix 8-10. Significantly more eggs were laid on a paspalum diet ($P < 0.01$) and a ryegrass diet ($P < 0.05$) than on white clover (Table 8-7). There was no significant difference between the paspalum and ryegrass treatments ($P > 0.1$). More adults oviposited ($P < 0.01$) on the two grass treatments than on white clover. Although only two females laid ten or more eggs on white clover compared with nine on paspalum and five on ryegrass, one individual on the legume diet produced

Table 8–6 The total number of eggs laid, the mean fecundity and the number of black beetle adult females actually ovipositing per treatment. (30 females per treatment. Means without letters in common are significantly different at $P < 0.05$).

Treatment	Total eggs laid	Number of females ovipositing	Mean Fecundity (eggs/ovipositing female)		Females alive at end of trial
paspalum	153	24	6.4	a	17
ryegrass	98	19	5.2	ab	14
ryegrass/lotus	66	18	3.7	abc	8
phalaris/white clover	64	18	3.6	abc	10
digitaria	46	13	3.5	abc	6
lucerne	37	11	3.4	abcd	5
phalaris	51	18	2.8	bcd	6
white clover	33	12	2.8	bcd	5
ryegrass/white clover	42	16	2.6	bcd	14
lotus	46	18	2.6	cd	10
soil only	10	9	1.1	d	6

25 eggs in the first batch and then died. This has markedly affected the fecundity figures for white clover.

When mean fecundity is expressed in terms of the eggs laid per female starting the trial, significantly more eggs were produced by females feeding on the grass diets ($P < 0.05$) than on white clover However, when fecundity is expressed as eggs laid per female actually ovipositing on the diet, there are no significant differences between treatments.

The diet also appeared to have an influence on the rate at which oviposition commences. By the end of November all females which eventually oviposited on the white clover diet had laid their first eggs, compared with only 50% and 57% on the paspalum and ryegrass diets respectively.

The significant effect of diet on fecundity operates through the influence of the plant on adult longevity. All the females on the white clover diet had died by the 21 January, whereas at this time, 40% and 24% of the adults were still alive on the paspalum and ryegrass diets respectively.

(iii) Effect of plant species on female longevity and potential fecundity.

At collection from the field in September, the subsample of females had a mean ovarian development ranking of 3.4 ± 0.53, which on the 1-5 scale with 5 showing the oviposition stage (Mercer and King, 1976) indicates the relative sexual immaturity of the population. Fat levels in the subsample of females in September are shown in Appendix 8-11.

At oviposition, fat levels did not differ significantly on the three diets. Over the period from September to the commencement of

Table 8-7 The total number of eggs laid, the number of ovipositing black beetle females and the mean fecundity for each plant treatment (30 females per treatment).

Treatment	Total eggs laid	Number of females Ovipositing	Mean Fecundity Eggs/30 Females	Eggs/Ovipositing female
paspalum	252	25	8.4 ± 7.0	10.1 ± 6.5
ryegrass	163	22	5.4 ± 7.5	7.4 ± 7.9
white clover	61	9	2.0 ± 5.1	6.8 ± 7.7

Table 8-8 The number of black beetle adult females commencing oviposition and the mean potential fecundity at oviposition ± S.E. when fed on pasture plant diets (30 females per treatment).

Treatment	Number of females ovipositing	Mean no. eggs laid in first batch	Mean no.of oocytes/ female in ovaries	Mean potential fecundity/ovipositing female
paspalum	17	1.5 ± 0.9	35.5 ± 5.3	37.0 ± 5.1
ryegrass	5	1.6 ± 1.3	31.2 ± 8.3	32.8 ± 9.1
white clover	2	1.0	31.0	32.0

Table 8-9 The number of eggs and larvae recovered from pasture plant treatments (14 male and female adult pairs seeded per treatment).

Treatment	Eggs	First instar larvae	Mean no. eggs & larvae per female ± S.E.	Life female adults at harvest
ryegrass	43	44	6.21 ± 2.6	3
white clover	26	42	4.86 ± 1.2	7
ryegrass/ white clover	24	66	6.43 ± 2.5	5

oviposition, a 63% decline in fat reserves occurred as female sexual development proceeded. The number of females ovipositing on paspalum was significantly greater ($P < 0.01$) than on ryegrass and white clover (Table 8-8). The mean time from the start of the trial to the commencement of oviposition was similar for females feeding on both grass species, 84 days, with a range of 56-108 days on paspalum and 49-119 days on ryegrass. The two surviving females feeding on white clover took 87 and 98 days to oviposit.

The number of eggs deposited in the soil in the first batch at the commencement of oviposition was similar on both the grasses. Analysis of variance shows that there was no significant difference, either in the mean number of oocytes present in the female at dissection or in the potential fecundity between females on the paspalum and ryegrass diets. Although the potential fecundity of the two females ovipositing after feeding on a white clover diet was similar to that on the grasses, dissection of the ovaries revealed they were smaller in size and less developed than in females on a grass diet. Unfortunately, due to the design of the trial, it was not possible to determine the potential fecundity of females which died before oviposition and so obtain a truer estimate of fecundity for the cohort as a whole. It is possible that the two females which oviposited on white clover were atypical of that diet.

(iv) Fecundity on plant species in the field.

Females from the subsample of the population taken at the beginning of the trial had a mean ovarian development ranking of 4.8 ± 0.4, all were mated and in 75% of the sample, 1-8 eggs were present in the oviducts. These insects had a mean fat reserve level

of 28.2 ± 6.5% (range 15.9-36.2% as shown in Appendix 8-12). In spite of the sexual maturity of the population, fat levels were still high, indicating either the very favourable nature of the paspalum dominant pasture diet or physical soil conditions at the collection site, or the absence of disease stress.

Pasture composition in the mixture treatment, as determined by point analysis at the time the adults were introduced to the cylinders, was shown to vary from the initial aim of a 50:50 mixture. The mean level of white clover was 60 ± 8% and of ryegrass, 40 ± 8%.

Analysis of variance of the eggs and larvae recovered (shown in Appendix 8-13), reveals that there was no significant difference in the number of eggs and larvae between treatments ($P > 0.1$), shown in Table 8-9. Oviposition did appear to be slightly depressed under white clover but at the conclusion of the trial, 50% of the females seeded into the cylinders in November were still alive, suggesting that the figure could further increase. Dissection of the females recovered alive from the treatments showed that a further 24-30 oocytes remained differentiated in the ovaries. Although individual females could not be related to cylinders they came from, it would appear that further oviposition by these insects was possible.

There was a very wide variation in the numbers of eggs and larvae from individual cylinders, ranging from 0-18 on ryegrass, 0-17 on the ryegrass/white clover mixture and 0-11 on white clover. This result is surprising in view of the even sexual development of the population at the start of the trial as shown by dissection. Although some mortality may have occurred between eggs and first-instar larvae during the trial and further oviposition after the arbitrary trial ending may have increased the figures, actual fecundity ranged between 4.9 and 6.4 eggs/female.

CHAPTER 9

OVIPOSITION

I INTRODUCTION

As pointed out in the literature reviewed in Chapter 3, populations of pasture inhabiting scarabaeid larvae have a clumped or aggregated type of dispersion in the field. A wide variation can occur in the physical environment of the pasture, and this can affect dispersion through a selection of oviposition sites occurring in response to the variations in physical factors.

As female black beetle adults are able to disperse in the spring, and deposit eggs singly in the soil (Cumpston, 1940), rather than in clusters, considerable potential exists for population aggregation through oviposition preference. In this chapter, the influence that both pasture height and pasture composition have in the spring on black beetle oviposition patterns is examined.

II INFLUENCE OF PASTURE HEIGHT ON OVIPOSITION

To investigate whether oviposition by black beetle adult females in spring is influenced by pasture height in spring, two trials were conducted, one as a field trial, the other in an artificial caged pot situation. The aim of these was to monitor oviposition in pasture of different height and to establish if pasture height had any influence on overwintering adults or on spring immigrants into the area.

(1) Field trial

(a) Methods

At the Otakanini Research Area, a 40 m x 20 m area of mixed ryegrass/white clover pasture was selected for the trial in August 1976. Plots each 4 m x 2 m were pegged out, arranged in blocks of eight plots, with each block surrounded by 2 m wide buffers. Four treatments, each with ten replicates, were randomised over the trial area so that each block contained two replicates of each treatment. The treatments were:

(i) No insecticide, pasture mown weekly to a height of 3 cm;

(ii) No insecticide, pasture uncut between early October - mid-November, then mown to a height of 3 cm;

(iii) Insecticide applied, mown weekly to a height of 3 cm;

(iv) Insecticide applied, pasture uncut for the same interval as treatment 2, then mown to 3 cm.

The short soil residual life insecticide, diazinon, was applied to treatment 3 and 4 at a rate of 2 kg/ha on 4 August in an attempt to remove overwintering adults. On the 7 October, mowing of treatments (ii) and (iv) ceased and the pasture was allowed to grow to simulate a silage or hay crop. The pasture was mown to a height of 3 cm and the herbage removed on 18 November. The pasture height on all plots was measured using a "Massey disc" on 11 November, by taking one measurement in the centre of each plot. On the 6 December, ten 10 cm diameter soil cores, 15 cm deep, were taken from each plot. The black beetle eggs and larvae were extracted from the soil samples and counted at Ruakura by wet sieving using a salt flotation system.

(b) Results and Discussion

Analysis of variance showed that pasture height (Table 9-1) was significantly greater ($P < 0.01$) on treatments (ii) and (iv) than on (i) and (iii). This difference had been maintained from mid-October, although initially it was much lower.

Black beetle numbers were low at sampling in all treatments (Table 9-2 , Appendix 9-1), which possibly obscured the treatment effects i.e. few black beetle were recovered even in the absence of insecticide. The population was highest in the short pasture not treated with insecticide and maintained at 3 cm. The higher number of black beetle in the short compared to the long pasture (treatments (i) and (ii)) suggests that oviposition by overwintering adults was greater in the short pasture. Although six of the ten replicates contained black beetle in treatment (i), compared with only two replicates with eggs and larvae in treatment (ii), analysis of the data revealed no significant treatment differences. It is however difficult to show statistical significance when insect numbers are so low and variable.

In this trial, pasture height has not been shown to have an effect on the oviposition behaviour of the adult females either overwintering in the area or migrating into the pasture in the spring during the dispersal period. Black beetle numbers were so low however, on all treatments, that firm conclusions concerning the effects of pasture height on oviposition preference cannot be made. A repeat of the trial using an artificial situation where high population numbers could be guaranteed by seeding adults was therefore carried out in preference to relying on erratic levels in field populations.

Table 9-1 Mean pasture height in each treatment measured on 11 November 1976 using a 'Massey disc'.

Treatments	Mean pasture height ± S.E. (cm)
No insecticide, mown to 3cm	4.0 ± 0.8
No insecticide, long pasture	32.9 ± 6.6
Insecticide, mown to 3cm	4.3 ± 0.7
Insecticide, long pasture	28.9 ± 4.8

Table 9-2 The number of black beetle recovered at sampling carried out on 6 December 1976 (Total from 100; 10cm diameter soil cores per treatment).

	Number of black beetle recovered			
Treatment	Eggs	Larvae	Total	Mean/m^2 ± S.E.
(i)	7	2	9	11.1 ± 12.3
(ii)	1	1	2	2.5 ± 5.2
(iii)	0	2	2	2.5 ± 5.2
(iv)	0	2	2	2.5 ± 7.8

(2) Caged pot trial

(a) Methods

'Ruanui' ryegrass pasture was established in 40 black plastic pots of internal dimensions 15 cm x 15 cm x 22 cm deep in August 1977. Pots were trimmed to 3 cm at regular intervals and a dressing of nitrogen fertilizer applied. At the start of October, the pots were sunk into bare soil at Ruakura Research Centre in adjacent areas enclosed by two pasture cages 3.5 m x 1.7 m in dimension. Twenty pots were placed in each cage so that the top of each pot was level with the surrounding bare soil surface. Pasture height was maintained at 2-3 cm on half of the pots, and at 12-15 cm on the remainder in each cage, with the two height treatments randomised within the cage. Asbestos sheeting, 20 cm in width was sunk 15 cm into the soil at the boundaries of the cages to prevent black beetle adult movement out of the cages.

In November, black beetle adult males and females were collected from a population free of the pathogen Adelina sp. in paspalum dominant, grass/legume pasture at Elstow near Te Aroha. Adults were maintained on a carrot diet in soil at Ruakura at 20 ^{o}C until oviposition commenced. At the commencement of oviposition, 60 male and female pairs were introduced into each cage on 10 November. In Cage A, adults were placed at random on the bare soil surface between the pasture. In Cage B, equal numbers of males and females were introduced into the long and short pasture pots by means of holes in the soil. The cages were then enclosed by a fine nylon mesh cover to prevent adult migration out of the cages.

The treatment in Cage A allowed an oviposition choice between the short and long pasture, similar to the adult spring immigrant

situation in the field, to be measured. Cage B approximated the overwintering adult, oviposition preference situation. Thermometers were placed in two pots of short and long pasture in each cage with the bulb at a depth of 4 cm. The temperature was monitored under the two pasture heights twice daily.

On the 22 December, all pots were removed from the soil and the black beetle eggs and first instar larvae present were extracted and counted by wet sieving using a salt flotation system.

(b) Results and Discussion

Pasture had no effect on soil temperature at the morning recording (Table 9-3). Analysis of the temperatures at 4 p.m. showed that under short pasture, soil temperature at 4 p.m. was significantly greater ($P < 0.01$) than under pasture maintained at a height of 12-15 cm.

The higher temperatures recorded under the short pasture, and the pasture height itself have had no apparent influence on oviposition (Table 9-4). The number of black beetle eggs and larvae recovered from each cage (Appendix 9-2) did not differ significantly between the two pasture heights. In addition, the numbers recovered from the cage where the adults were introduced at random, did not differ significantly from the cage where equal numbers of adults were placed in pots of short and long pasture. The method of seeding had an effect on the proportions of eggs and first instar larvae recovered in the two cages at sampling. Analysis of arcsin transformed data shows that a significantly greater ($P < 0.05$) proportion of the population in Cage B was in the first instar larval stage compared with Cage A. In the short pasture this was 53%

Table 9-3 Mean soil temperature over the period 11 November - 21 December 1977 under short and long pasture at two times of the day.

	Mean temperature °C ± S.E.	
	8 a.m.	4 p.m.
Long pasture	15.4 ± 1.6	20.6 ± 2.1
Short pasture	15.5 ± 1.7	22.8 ± 2.4

Table 9-4 Black beetle eggs and first instar larvae recovered from two pasture heights at sampling in December. (60 male and female adult pairs introduced per cage).

	Mean Numbers of black beetle recovered ± S.E.					
	Cage A			Cage B		
Treatment	Eggs	*L_1 Larvae	Mean/10 pots	Eggs	L_1 Larvae	Mean/10 pots
Short pasture	62	17	7.9 ± 5.7	45	51	9.7 ± 8.0
Long pasture	59	29	8.8 ± 6.3	29	56	8.5 ± 5.4

* First instar larvae

compared with 22% and in the long pasture 66% compared with 33%. This result would suggest that oviposition occurred at a faster initial rate in Cage B where the adults were seeded into the pots, than in Cage A where adults were randomly placed on the bare soil surface.

III EFFECTS OF PASTURE SPECIES ON OVIPOSITION

Trials were carried out to investigate the influence of plant species and ground cover on the behaviour of female beetles during oviposition. Two trials involved determination of plant preference in an artificial situation at the Ruakura Agricultural Research Station, and the other, assessment of oviposition preference in terms of egg distribution in relation to pasture composition in a field population near Te Aroha.

(a) Methods

(1) Pot trial 1975-76

In this trial, two preference investigations were carried out. In the first, the choices were 'Nui' ryegrass, 'G-15' paspalum and bare ground. In the second, the choices were 'G-15' paspalum, 'Pitau' white clover and bare ground. Twenty mature plants of each species were planted in black plastic pots 17 cm x 17 cm x 18 cm in dimension, each pot being 0.028 m^2 in area. In each choice system the pots were placed in bare soil in October within a 3.3 m x 1.3 m pasture cage with the pots sunk in the soil so that the top was level with the soil surface. Plant species were randomised within each cage.

The first cage contained 20 pots of paspalum and 20 pots of ryegrass and the second cage 20 each of paspalum and white clover plants. This enabled a choice between grasses and a choice between a grass and a legume to be observed. Superphosphate at 250 kg/ha was applied to the whole area at planting. Nitrolime at 125 kg/ha was applied to the grasses only.

Adult black beetle were collected from a population where the incidence of the pathogen Adelina sp. was known to be low, in a paddock of maize stubble at Ruawaro near Huntly in November. These were held in a constant environment room at 20 ^{o}C and a 14:10 light: dark hours ratio, on a diet of carrots. Some females had commenced oviposition at the time the population was introduced into the cages but dissection of a subsample showed that the majority of the females were between ovarian ranking 4 and 5 on the scale of Mercer and King (1976).

On the 11 December 50 male and 50 female adults were randomly introduced into each cage. To prevent dispersal, the borders of the cage were surrounded by 20 cm wide asbestos sheeting sunk 15 cm into the ground. In addition, the whole cage was covered by a nylon gauze cover to prevent adult flight out of the cage as shown in Plate 9-1.

The trial was harvested on 9 January. The soil in all the pots was sorted and black beetle egg and first instar larval stages were extracted using a salt flotation system and counted. The bare ground between the pots was sampled by taking 28 cores using a 10 cm diameter soil corer and the insect stages in the cores were extracted in a similar manner.



Plate 9-1 System of caging areas of pasture to prevent adult dispersal, used in the oviposition preference study and the investigation of spring dispersal.



Plate 9-2 A paspalum dominant area and a 10cm diameter soil core from the pasture plots used in the investigation of adult oviposition preference.

(2) Pot trial 1976-77

As no assessment was made of the distribution of adults within the cages at the choice treatments in Trial (1), the trial was repeated over a shorter period. The same choice treatments and layouts were used as in Trial (1). Adults were collected from the same area in November and maintained on a carrot diet as for the first trial. On the 6 December 30 female and 15 male adults were liberated at random within each caged area. Dissection of a subsample suggested that all females in the population were in the ovarian ranking level of 5. The trial was harvested on 15 December when the same sampling procedure was used except that 67 soil cores per cage were taken giving the same total area sampled for each plant species and bare ground. Adults were extracted from the soil by handsorting and eggs and larvae by a salt flotation system.

(3) Field trial 1977

Two study plots, each 20 m x 20 m were established in pasture on an Elstow humic silt loam soil type at Elstow near Te Aroha. The soil type was predominantly a drained peaty soil on alluvial pumice. The pasture contained localised areas of paspalum dominance as well as ryegrass, white clover, and varying amounts of cocksfoot, Yorkshire fog, brown top, Poa sp. and weeds. The aggregation of paspalum in the sward is shown in Plate 9-2. Both the pasture and adjacent cultivated ground supported a large population of black beetle adults.

From each plot, fifty 10 cm diameter soil cores were taken at the beginning of November using a centric systematic system of sampling (Milne, 1959). The soil cores were broken up by hand in

the Ruakura insect extraction laboratory, and plant species in the core were identified on the basis of roots present in the soil. Black beetle adults were extracted by hand sorting and eggs extracted using a salt flotation system. This enabled the relationship between plant species present in the core and black beetle adult occurrence and oviposition preference to be established.

(b) Results and Discussion

(1) Pot trial 1975-76

Non-parametric analysis was carried out on the data using the Kruskal-Wallis 1-way ANOVA by ranks (Sokal and Rohlf, 1969, Chapter 13). There was no difference in the number of eggs and larvae recovered from ryegrass and paspalum which shows that there is no oviposition preference between these species (Table 9-5). As the total bare ground area sampled was 2.5 times less than the area of 20 pots of one pasture species, the analysis of the number of black beetle recovered was not able to show significant differences between numbers from bare ground and from the grass species. In spite of the statistics, there does appear to be a real difference in oviposition preference between the plants and the bare soil.

Significantly more ($P < 0.05$) black beetle were recovered from paspalum than white clover or bare ground in cage B in the other choice system. An oviposition preference for the grass over the legume occurred in this trial. There was no significant difference between white clover and bare ground, although differences were once again obscured by the smaller bare ground area sampled relative to the pasture species.

Table 9-5 The number of black beetle eggs and first instar larvae extracted from the choice treatments in the two cages on 9 January (50 male and female adult pairs introduced to each cage on 11 December).

Choice Treatments	Total eggs and L_1 larvae* recovered	Mean number/m^2 ± S.E.
Cage A		
Paspalum	56	97 ± 28
ryegrass	62	107 ± 38
bare ground	1	5 ± 6
Cage B		
Paspalum	104	180 ± 38
white clover	37	64 ± 23
bare ground	6	28 ± 17

* First instar larvae

Table 9-6 The number of black beetle adults and eggs extracted from the choice treatments in the two cages on 15 December. (30 female and 15 male adults introduced to each cage on 6 December).

Choice Treatments	Total adults recovered	Total eggs recovered
Cage A		
paspalum	11	118
ryegrass	12	118
bare ground	1	45
Cage B		
paspalum	19	146
white clover	4	81
bare ground	1	25

(2) Pot trial 1976-77

Analysis of the data (Table 9-6), was carried out using the same non-parametric method used for trial (1). Significantly more adults ($P < 0.05$) were recovered from the two grass treatments than bare ground in the first choice system (cage A). The overall differences in the numbers of eggs recovered from the three treatments were not significant ($P > 0.1$).

Although this indicates that there was no significant difference in the degree of oviposition between bare ground and the grass species it is also of note that in relation to the next choice system, that one grass was not preferred over the other. A possible explanation of the absence of significant differences between egg numbers in the grasses and bare ground, may be that although adults preferred to aggregate under the grasses, some females oviposited in the bare ground as oviposition had commenced at the time the adults were introduced into the cages.

In the second choice system (cage B), the overall differences were significant ($P < 0.01$). Significantly more adults ($P < 0.01$) were recovered from paspalum than white clover or bare ground, with the difference between the numbers in the latter two treatments not significant ($P > 0.1$). The overall differences in the number of eggs recovered from the three choices were significant ($P < 0.05$). More eggs were recovered from paspalum ($P < 0.05$) than from white clover or bare ground, and as with the adults, the difference between bare ground and white clover was not significant ($P > 0.1$).

The results of trial (2) demonstrate a marked adult preference to aggregate under paspalum when given a choice between this species,

white clover and bare ground. This suggests that the difference in the number of eggs laid in paspalum compared with white clover and bare ground found both in this trial, and in trial (1) must be due to an adult preference to aggregate under paspalum, possibly due to a feeding preference. The net result however is an apparent preference for females to oviposit under the paspalum species, even though this may be only a secondary effect. In both trials, no preference was noted between the two grass species offered, paspalum or ryegrass.

(3) Field trial 1977

Of the 100 soil cores taken, 57 contained paspalum as a pasture component and in 18 of these, black beetle adults or eggs were found. Only two samples contained black beetle of the 43 cores without paspalum as a component. Black beetle were recovered from 20% of the total sample indicating the clumped or aggregated distribution of the population.

Both paspalum and ryegrass occurred together in 10 of the cores containing black beetle, in eight paspalum was found with no ryegrass and one core had ryegrass and no paspalum. In only one sample (containing Poa spp.) were black beetle found in the absence of paspalum or ryegrass.

These results (Table 9-7), show that black beetle were found in 32% of the cores containing paspalum as a pasture component, a significantly higher proportion ($P < 0.001$) than the cores without paspalum in which only 5% contained black beetle. In this mixed pasture species sward, ryegrass, Yorkshire fog, Poa spp., brown top, cocksfoot, white clover and weed species were present in most cores.

Table 9-7 The number of black beetle in relation to pasture composition, recovered from soil samples taken in November.

Pasture composition of sample	Number of black beetle in samples			
	Total adults	No./m^2	Total eggs	No./m^2
with paspalum	13	28.1	50	108.2
without paspalum	1	2.9	2	5.7

The presence or absence of paspalum had the major influence on black beetle occurrence.

The preference by adults to aggregate under paspalum rather than a legume shown in Trial (1) results in significantly more eggs being laid under the former species as demonstrated in both Trials (1) and (2). This preference is not however simply a behavioural choice confined to an artificial situation. The population examined in Trial (3) confirms that adults aggregate under paspalum in mixed grass/legume/weed pasture in the field, with a corresponding clumping of egg distribution under paspalum plants. Such adult and egg aggregation in the spring ensures that larval development takes place in a favourable environment as discussed in Section 2, Chapters 5 and 6.

CHAPTER 10

ADULT DISPERSAL

I INTRODUCTION

In the review of the literature on black beetle flight and dispersal in Chapter 1, the occurrence of adult dispersal in both the autumn and spring periods has been noted by many workers. The ability of the adult to disperse by flight (Johannesson, 1975; Watson, 1978), and by crawling movement across the pasture surface (King, unpublished results), is a most important aspect of adult black beetle ecology. A detailed examination of black beetle dispersal was not carried out as part of the investigations reported in this thesis as this aspect is being researched by another worker (R.N. Watson).

Studies were therefore confined to a relatively brief examination of the importance of spring and autumn dispersal to subsequent population numbers and the results are presented in this chapter.

II SPRING DISPERSAL

(a) Methods

To investigate the influence of dispersal by the adult in the spring on the subsequent black beetle summer larval population, a trial was carried out at the Otakanini Research Area. A 0.1 ha area of old pasture was renovated by undersowing at the start of

September with 'Ruanui' ryegrass/'Huia' white clover mixture at the rate of 15 kg ryegrass/3 kg white clover per ha.

Within the area of pasture, twenty 5 m x 5 m plots in two rows of 10 were pegged out with 5 m buffers between adjacent plots. Three treatments were laid down on the 16 September.

Treatment 1

Diazinon insecticide at a rate of 2.2 kg/ha was applied to five plots chosen at random in each row, in an attempt to remove any overwintering adults which were present. Around the margins of each of these 10 plots, asbestos sheeting 20 cm high sunk 15 cm into the soil with 5 cm above the soil surface was placed to prevent adult surface movement into and out of the plots. The aim of this treatment was to establish the black beetle larval population level arising from adults dispersing into the areas during spring flight, by sampling these 10 plots in January.

Treatment 2

Five of the remaining 10 plots were chosen at random from the two rows and were similarly treated with diazinon in September to remove overwintering black beetle. Within each plot a pasture cage of dimensions 3.33 m x 1.55 m, and 1.2 m high was placed immediately after insecticide treatment. Over each cage, a nylon mesh insect proof cover was placed to prevent adult movement either into or out of the caged area. In addition, an asbestos barrier was sunk into the soil to prevent insect dispersal by burrowing. These cages and covers were left in place until the end of the trial in January. The aim of this treatment was to obtain an estimate of the larval

numbers arising from the overwintering population that was not killed by the insecticide.

The population in Treatment 1, less that in Treatment 2 in January, was an estimate of the number of larvae arising from adults dispersing into the area in the spring.

Treatment 3

The remaining five plots were not treated with insecticide. Within each plot, a pasture cage was set up and covered with an insect exclusion/inclusion cover as described for Treatment 2, and shown in Plate 9-1. The margins of the cage were also surrounded by asbestos sheeting, and the cage and cover left in place until January. The overwintering population was not removed with insecticide and subsequent adult migration into the plots was prevented by the nylon mesh cover. Therefore, larval population in this treatment in January provided an estimate of that arising solely from overwintering adults.

Throughout the spring and summer until the conclusion of the trial, the areas within the cages were mown at regular intervals after temporarily removing the cages and the ten uncaged plots were grazed by sheep. Pasture was prevented from growing over the asbestos margins of the plots by regular paraquat spraying. On the 10 January, the cages and covers were removed from the ten plots that were caged. Within the remaining ten plots, 3.35 m x 1.55 m areas, equivalent to the size of a pasture cage were pegged out. From each of the treatments, ten 10 cm diameter soil cores were taken to a depth of 15 cm from the cage sized area of each plot to provide an estimate of population numbers. The soil samples were transported

to Ruakura and black beetle stages removed by wet sieving using a salt flotation system and counted.

(b) Results and Discussion

The mean number of larvae in treatment two (Table 10-1) was subtracted from the mean number recovered from treatment one to get an estimate of the population arising from adult immigrants in spring. This was then compared with the number of black beetle in treatment three by non-parametric analysis using the Wilcoxon two-sample rank test (Sokal and Rohlf, 1969, Chapter 13).

Black beetle populations per m^2 in the trial were as follows:

Larval population arising from overwintering adults = $22.2/m^2$

Larval population arising from adult immigrants in spring = 7.4

Total summer larval population = 29.6

The analysis showed that the summer population arising from overwintering adults was significantly greater ($P < 0.05$) than the population arising from adults migrating into the area in the spring. As diazinon is an insecticide with a short soil residual life against black beetle (Watson and Webber, 1976), it can be assumed that the insecticide had only a minimal influence on the numbers of the spring immigrant population. Black beetle field population data gathered over several seasons (Watson pers.comm.) would suggest that the total summer larval population of almost $30/m^2$ is typical of January population levels in mixed ryegrass/white clover pasture in all but seasons favouring very high populations which tends to validate the method. The technique used in this trial assumes that there was no adult emigration out of treatment 1, in addition to immigration.

Table 10-1 The number of black beetle larvae recovered in January from pasture treatments showing the influence of adult spring dispersal on summer population numbers.

Treatment	Number of samples	Total black beetle recovered	Mean population per m^2 ± S.E.
1. Insecticide applied	100	10	12.3 ± 4.3
2. Insecticide & caged	50	2	4.9 ± 3.5
3. No insecticide and caged	50	9	22.2 ± 11.1

In this trial, 75% of the summer larval population were the progeny of adults which successfully overwintered on the trial area up to the start of the trial in mid-September. The remainder of the summer population were the progeny of adults which migrated into the area during the spring dispersal phase of the insect.

Seasonal conditions were far more favourable for adult dispersal in the season the trial was carried out than in subsequent seasons (Watson, pers.comm.). In the trial reported here, the surface movement component of dispersal was removed by the asbestos sheet, plot margins. Adult flight did however, have a significant effect on population numbers through adults moving into the plots, although in the season the trial was carried out, adults overwintering on the site had the major influence on black beetle numbers.

III ADULT-PLANT SPECIES INTERACTION IN AUTUMN

A number of plant species were shown to have either favourable or unfavourable influences on black beetle larvae in Chapters 5 and 6. Plant species were also shown to affect adult fecundity and oviposition in Chapters 8 and 9. To investigate if plant species had any influence on adult behaviour over the autumn dispersal period, a study was made of adult survival in a series of trials carried out over the autumn period.

(a) Methods

(1) 1976 Field trial

Seedlings of the following plant treatments were individually raised in a pumice potting mixture in 8 cm diameter black polythene

bags in a glasshouse, until planting as small plants in the field at the Otakanini Research Area in October:

'Maku' lotus

'Pitau' white clover

'G-15' paspalum

'Nui' ryegrass

'Seedmaster' phalaris

Ryegrass/lotus, 50:50 mixture

Phalaris/white clover 50:50 mixture

Swards of constant species composition, spacing and plant numbers were attained by handplanting in 0.5 m^2 plots with each plot enclosed by boundaries of asbestos sheeting strips, 20 cm wide, sunk 15 cm into the soil. Each plot was planted at a total density of 36 plants per m^2. Fertiliser was applied pre-planting and plots were watered until plants were established. All treatments were trimmed to a height of 6 cm at weekly intervals by handclippers. There were five replicates of each treatment arranged in a randomised block design.

The plots were maintained over the summer until March when 30 well developed third instar larvae collected from a ryegrass/white clover pasture sward at Ruawaro near Huntly were seeded into each plot. Larvae were placed at the bases of plants in a small depression. Any larvae that did not burrow into the soil were replaced.

At the beginning of July, the area within the plots was excavated to a depth of 15 cm, the soil and plant roots were sorted by hand, and the black beetle remaining were counted and sexed.

(2) 1977 Field trial

Plots of pasture, 0.5 m^2 in area, surrounded by margins of 20 cm wide asbestos sheeting sunk 15 cm into the soil, were established in three adjacent 0.2 ha paddocks of paspalum, ryegrass and ryegrass/white clover pasture at the Otakanini Research Area. There were five replicates of each treatment placed in areas of similar pasture composition and ground coverage. Adult black beetle were collected from an area of the paspalum pasture and were seeded into the plots as follows in late March.

In the paspalum treatment, 15 males and 15 females per plot were placed to give 60/m^2 and in the ryegrass and ryegrass/white clover treatments, 8 males and 7 females to give 30/m^2. This difference in population density is similar to those found in field populations under pastures of these species in late summer-autumn.

At the time of seeding, a subsample of females was taken and fat levels determined by hot solvent extraction. The seeded adults were placed on the surface of the pasture and those which failed to burrow into the soil were replaced. Any resident black beetles in the pasture were not removed prior to seeding. The plots were left uncovered and the pastures were grazed in a normal rotational pattern. In late May the plots were excavated to a depth of 15 cm, the soil and plant roots sorted by hand, and the adults remaining extracted, sexed and counted. Fat reserve levels in females present in the plant treatments were assessed at the conclusion of the trial.

(3) 1978 Field trial

PVC cylinders, each 15 cm in diameter and 23 cm long, were sunk 15 cm into bare soil at the Otakanini Research Area in January. Forty cylinders were planted with 'Nui' ryegrass plants and the other forty with 'G 15' paspalum. Plant treatments were randomised within each of six blocks. After establishment, plants were trimmed to a height of 6 cm at two-weekly intervals with hand shears.

Newly emerged (teneral) adults were collected on 13 March from a paspalum dominant pasture containing a disease-free black beetle population. A subsample of male and female adults was taken from the population and fat reserves were determined on these individuals using hot solvent extraction. On 14 March one male/female pair was introduced into each of the cylinders. Adults which did not burrow into the soil were replaced.

All cylinders were covered with a cage of fine nylon mesh to prevent adult flight or dispersal in the first few days after seeding. On 16 March the cages were removed from half of the cylinders of each treatment. This gave 20 caged and 20 uncaged cylinders of each plant treatment.

At the end of May the cylinders and their contents were taken from the ground, and the adults present in each of the treatments extracted by hand-sorting, counted and sexed. Adults recovered were later dissected in the laboratory to determine the stage of sexual development following which reserve fat levels were assessed.

(b) Results and Discussion

(1) 1976 Field trial

The recovery of black beetle from individual replicates is shown in Appendix 10-1. Analysis of variance was carried out on transformed

means, $\log_e(1 + X)$. There were significantly more ($P < 0.05$) black beetle recovered from the paspalum treatment than from ryegrass (Table 10-2), and from these two treatments than all the others. Recovery from the two legume treatments, phalaris and from the two mixtures did not differ significantly ($P > 0.05$). Although it is probable in this trial and in trial (2) that some of the adults recovered arose from individuals resident in the plots at the time of seeding, and/or from immigrants rather than seeded specimens, this does not negate the overall treatment differences.

(2) 1977 Field trial

Data (given in Appendix 10-2), were analysed by a binomial analysis computer programme using binomial errors (Biometrics Section, Ruakura Research Centre). A significantly higher percentage of adults was recovered ($P < 0.01$) from paspalum than from the ryegrass/white clover and ryegrass treatments (Table 10-3). No significant difference was found between the percentages of adults recovered from the ryegrass and ryegrass/white clover treatments.

The subsample of 20 adult females taken from the paspalum paddock in March at the commencement of the trial had a mean dry weight of 74.0 ± 8.7 mg and mean fat content of $16.6 \pm 5.2\%$ (Appendix 10-3). A subsample of 15 females was taken from the paspalum treatment in May at the conclusion of the trial, (Appendix 10-4), had a mean dry weight of 117.4 ± 14.3 mg and a fat content (dry weight basis) of $40.0 \pm 5.2\%$, representing a significant increase ($P < 0.01$) over the March to May period. The eight females from the two treatments containing ryegrass were bulked for comparative purposes (Appendix 10-5). These

Table 10-2 The recovery of black beetle adults in July from plots seeded with third instar larvae in March. (150 larvae/plant treatment, treatments without letters in common differ significantly $P < 0.05$).

Treatment	Total adults recovered	% Recovery	
paspalum	100*	66.6	a
ryegrass	26*	17.3	b
phalaris	4	2.7	cd
white clover	1	0.66	d
lotus	1	0.66	d
ryegrass/lotus	6	6.0	cd
phalaris/white clover	2	1.3	cd
CV%		30	

* Included in the adult totals above are a pupa in the paspalum total and a third instar larva in the ryegrass total.

Table 10-3 The recovery of black beetle adults in May from plots seeded with adults in March.

Treatment	No. Adults seeded in March		No. Adults recovered in May		% Recovery
	Male	Female	Male	Female	Overall
paspalum	75	75	55	59	76
ryegrass/white clover	40	35	16	5	28
ryegrass	40	35	6	3	12

females had a mean dry weight of 70.5 ± 6.9 mg, and the mean fat level had declined to 4.0 ± 2.6%, significantly less ($P < 0.01$) than that in the paspalum treatment.

(3) 1978 Field trial

Survival of adults overall was very low in this trial, possibly due to the fact that adults used in the trial were introduced in the teneral stage soon after emergence from the pupa. Soil temperatures were high and soil moisture levels low at the time of seeding, which probably placed additional stress on the insects. Although survival was almost twice as high in the caged paspalum treatment as in the corresponding ryegrass treatment (Table 10-4), the difference was not significant ($P > 0.1$). Nevertheless, the recovery of nearly three times as many dead adults from the caged ryegrass treatment as from the same paspalum treatment suggests a higher mortality under ryegrass in the autumn. Numbers recovered in the uncaged cylinders did not differ significantly between the plant treatments ($P > 0.1$), but were less than half that recovered from the caged cylinders. This suggests that the decrease in black beetle numbers in the two plant treatments is due to both adult mortality and dispersal out of the treatment.

The dry weight of a subsample of the teneral adult females introduced into the treatments in March was 71.9 ± 10.9 mg (range 56.4-87.0) and percent fat (dry weight basis) was 18.5 ± 6.1% (range 12.2-30.0%). Those of the males were 59.9 ± 11.5 mg (range 49.6-75.7) and 14.8 ± 4.3% (range 10.3-21.4) respectively.

As the number of live adults recovered from the trial was very low, it is difficult to interpret the results of fat analysis of the survivors. The mean dry weight of the four females from paspalum

Table 10-4 The recovery of black beetle adults in May from cylinders of paspalum and ryegrass seeded with 20 male and female adult pairs / pasture treatment in March.

	Paspalum		Ryegrass	
	Caged	Uncaged	Caged	Uncaged
Females alive	3	1	2	2
Males alive	6	2	3	0
Total adults alive	9	3	5	2
Total adults dead	3	0	8	0
% recovered alive	22.5	7.5	12.5	5

was 83.5 ± 8.5 mg (range 75.6–95.6 mg), which was similar to the dry weight figure at the start of the trial. The percentage fat was 16.0 ± 5.1% (range 13.1–23.6%) again similar to the value at the start of the trial.

The mean dry weight of the eight males recovered was 74.9 ± 7.3 mg (range 64.5–87.1) and the percentage fat was 9.7 ± 4.3% (range 4.8–18.9%). Neither was significantly different from the levels at the start of the trial.

Although the mean fat level of the females from the ryegrass diet at 11.1 ± 8.0% (range 3.0–19.2%) was lower than that of those from paspalum at the conclusion of the trial, the difference was not significant. However percentage fat levels as low as 3.0% and 5.6% in females from ryegrass did not occur on the paspalum diet suggesting that the results follow the trends of lower fat levels on ryegrass recorded in the previous trial.

The trial results suggest that a strong pasture species–adult interaction operates in the autumn period with the presence of paspalum favouring the stability of adult populations. This finding is discussed further in Section 4, Chapter 14, where black beetle population trend under different pasture types in the field is examined.

CHAPTER 11

INFLUENCE OF DISEASE

I INTRODUCTION

Studies of the life cycle of the coccidian protozoan Adelina sp., the occurrence of the pathogen in black beetle populations and the possible influence it has on population mortality have been made by Longworth and Archibald (1975), Archibald et al. (1975), Archibald (1976), and are reviewed in Chapter 1. There has however been no attempt in these studies to investigate the effect of the pathogen on adult ecology, and in particular to quantify the influence of infection on the female.

Adelina sp. infects a significant proportion of the black beetle population at the Otakanini Research Area. In this chapter, the results of a series of studies carried out to determine the effect of the pathogen on adult female fat levels, potential fecundity and longevity are presented.

II EFFECT OF ADELINA ON FEMALE FAT LEVELS AND OVARIAN DEVELOPMENT

(a) Methods

Adult female black beetles were collected from the paspalum pasture at the Otakanini Research Area where Adelina was known to be present. A sample of the population was taken in the months of June, July, September and October 1977. In addition, a sample of females from a black beetle population in an adjacent paddock of maize stubble

was collected in June 1977. No further samples were taken from the maize stubble as black beetle numbers subsequently declined to very low levels making collection impossible.

The adults were brought back to Ruakura, killed using ethyl acetate and immediately dissected from the ventral surface to reveal the stage of sexual development and the presence of the protozoan. In many cases, the presence of Adelina was confirmed by the brown pigmented oocyst stage visible within the fat tissue which was termed the 'pepper-spot stage' as shown in Plate 11-1. Where this was absent, small fat samples were taken, a water mount of a smear of this material made, and then examined under a compound microscope at 400 x magnification for the presence of Adelina. This was usually found to be indicated by the presence of the sporocyst, or macrogamete stages described by Archibald (1976), which were easily visible.

After establishing the incidence of Adelina in the sample, individual females were deep frozen until fat extraction could be carried out. Determination of the level of fat reserves in females with and without the disease was done by hot solvent extraction of single females in a micro-Soxhlet using the techniques previously described in Section 2, Chapter 8.

A population of 150 female and male adults was collected from the paspalum area at the September sampling occasion. A random sub-sample of 29 females was screened for Adelina, and fat analysis was carried out on eight with and eight without the disease. The remainder of the population were retained for the trial described in the next section.

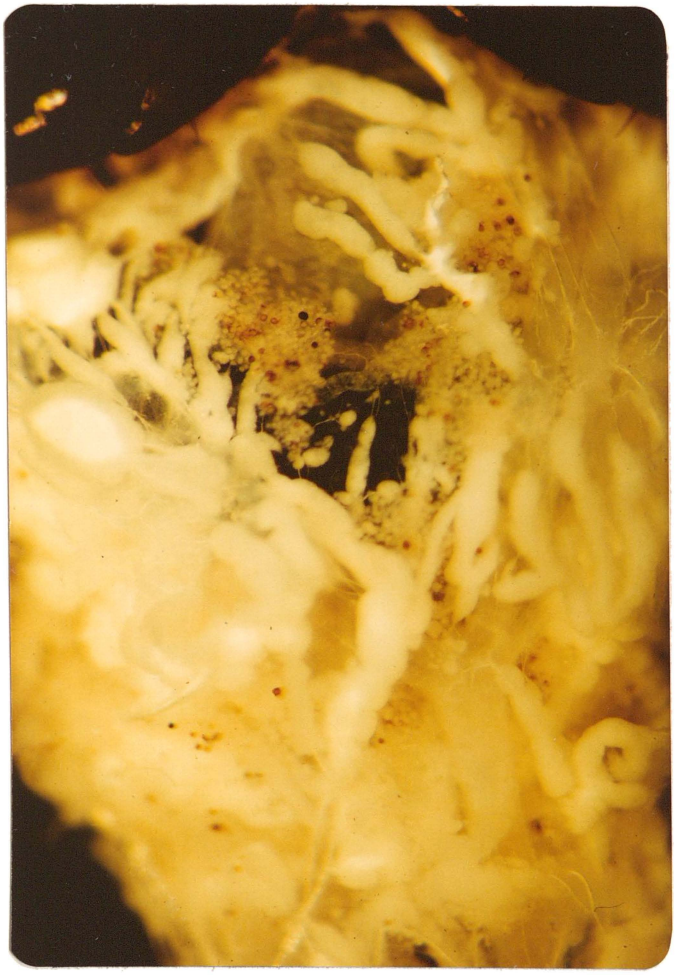


Plate 11-1 Black beetle adult female dissected to show the brown pigmented oocyst stage of Adelina sp. within the fat (20 X magnification).

(b) Results and Discussion

Apart from the June sample from the paspalum pasture, about 30% or more, of the females in the population subsample were infected with *Adelina* sp. (Table 11-1).

The effect of *Adelina* sp. infection on ovarian development is shown in Table 11-2. As there was considerable variation in the data, no significant differences were present. At each of the four sampling occasions however, the ovarian development of females infected with *Adelina* sp. was less advanced than that of females free of infection as determined visually by dissection of the adult. This result would suggest that the pathogen may retard ovarian development over the winter and spring periods.

The relationship between the level of fat in adult females and infection with the pathogen *Adelina* sp. is shown in Table 11-3. The percentage fat in individual females from the maize and paspalum sites at the various sampling times is shown in Appendix 11-1.

To investigate the relationship between oven dry weight of the adult and the weight of fat present, with and without *Adelina* (Appendix 11-2), regression analysis of the data from maize in June was carried out. This showed that the slopes of the regressions were not significantly different and that the relationship between oven dry weight and the weight of fat was not significantly influenced by the pathogen. This was primarily due to the large S.E. of the regression coefficient from the data for females without *Adelina* sp. There was however a significant relationship between oven dry weight and the weight of fat overall:

Table 11-1 The level of Adelina in adult females from the black beetle population in the paspalum area and the maize area at four times of sampling between June and October.

Time of Sampling		Number in Sample	Number with Adelina sp.	% Population with Adelina sp.
June	paspalum	20	3	15
	maize *	20	12	60
July **		17	5	29
September		29	8	28
October		13	4	31

* The maize stubble was only sampled in June

** All other samples are from the paspalum area

Table 11-2 The effect of *Adelina* sp. infection on the mean ovarian development level of adult female black beetles taken from two sites at Otakanini between June and October. (Mean level on 1-5 scale of Mercer and King, 1976).

Diet	Mean ovarian development level ± S.E. at each sampling date							
	1.6.77		27.7.77		8.9.77		13.10.77	
	A*	B**	A	B	A	B	A	B
Maize stubble	2.30 ±0.89	1.92 ±0.51	-	-	-	-	-	-
Paspalum pasture	2.19 ±0.66	2.0 ±0.1	2.58 ±0.67	2.20 ±0.45	3.0 ±0.27	2.70 ±0.75	3.78 ±0.83	3.25 ±0.29

A* = females without *Adelina* sp.

B** = females with Adelina sp.

Table 11-3 The effect of *Adelina* sp. infection on the mean % fat level of adult female black beetles taken from two sites at Otakanini between June and October.

	% Fat level ± S.E. (dry weight basis) at each sampling date							
	1.6.77		27.7.77		8.9.77		13.10.77	
Diet	A*	B**	A	B	A	B	A	B
Maize Stubble	23.5 ±13.5	6.2 ±1.2	-	-	-	-	-	-
Paspalum pasture	40.0 ±5.2	18.2 ±1.0	19.6 ±10.1	11.1 ±3.7	16.6 ±4.3	10.6 ±3.7	14.2 ±5.6	10.2 ±5.0

A* = females without *Adelina* sp.

B** = females with *Adelina* sp.

$Y = 54.94 + 1.24\ X$ where Y = oven dry weight and X = weight of fat ($r = 0.88$, $P < 0.001$).

The weight of fat in females without Adelina, from the paspalum area in June, was considerably higher than in those with, and on the basis of a 't' test (Sokal and Rohlf, 1969, Chapter 9), Adelina significantly reduced ($P < 0.01$) the weight of fat. There were however only three females in the sample screened (Table 11-1) that were found to have disease, which reduces the value of any extrapolation. Analysis of variance of arcsin transformed data showed that the fat level in Adelina infected females from the maize stubble in June was significantly lower ($P < 0.001$) than in those without the pathogen. On the basis of these results the presence of Adelina has a marked influence on the level of fat reserves in the female which appears to retard ovarian development. The influence of the pathogen on adult mortality over the winter period is unknown, although some evidence is presented in Section 4, Chapter 14, which suggests Adelina is important in overall adult mortality.

The effect of the pathogen on reducing fat reserves of females in the paspalum was not so apparent on the next three sampling occasions. Only in September were fat levels significantly reduced ($P < 0.01$) by Adelina. This may be explained by the observation that fat levels are declining in healthy females due to sexual maturation over this period whereas the fat reserves in infected females are initially low and remain low over the winter-spring period, with ovarian development retarded.

III EFFECT OF *ADELINA* ON POTENTIAL FECUNDITY

(a) Methods

From the September sample of the black beetle population from the paspalum area, 96 male and female adult pairs were maintained separately on a carrot diet in an insectary trial. Each pair was placed in a 10 cm high and 6 cm diameter white plastic pot with a snap-on lid containing Hamilton clay loam at 30% soil moisture (by weight). Males that died were replaced and fresh carrot was supplied twice a week when the soil was sieved for the presence of eggs. Fresh soil medium was provided once every two weeks.

Females that died before oviposition were screened immediately using the previously described procedure to establish any disease presence. Females that oviposited were killed with ethyl acetate as soon as the first eggs were laid, and screened for the presence of *Adelina*. All oocytes differentiated within the ovarioles and in the oviducts were counted, and this figure was added to the number of eggs in the first batch laid, recovered from the soil, to give an estimate of potential fecundity for the female. A subsample of ten females without *Adelina*, which commenced oviposition, were deep frozen after disease screening. Determination of fat reserves by solvent extraction was subsequently carried out on these females, plus all the females which oviposited with *Adelina* present.

These procedures permitted data to be obtained on the incidence of *Adelina* in the insectary trial population, the number of females with and without the disease surviving to oviposition and the potential fecundity of these individuals at oviposition.

(b) Results and Discussion

The level of Adelina in the subsample of the population screened for disease at the commencement of the trial in September was 28% as shown previously in Table 11-1. This compares favourably with the level of 29% in the trial population as determined by dissection of females dying during the trial and live females at oviposition. This result indicates that no further infection with the disease occurred during the trial period.

The pathogen had a drastic effect on the number of females surviving to commence oviposition as shown in Table 11-4. Of the females infected, 89% died before oviposition while only 16% of those without the protozoan failed to oviposit. The presence or absence of Adelina had no consistent effect on reducing the survival time of those females which died before oviposition. These individuals lived for a mean period of 85.8 $\pm$ 28.5 days (with a range of 21-143 days). Females without the pathogen and which did not oviposit survived a mean period of 55.6 $\pm$ 38.2 days (with a range of 14-119 days) between the commencement of the trial and adult death.

The three females with Adelina that oviposited took a mean of 82.3 $\pm$ 4.0 days (range 80-87) from the start of the trial to oviposition. The 57 females without Adelina which commenced oviposition took a mean interval of 83.0 $\pm$ 12.6 days (range 63-112) from September to oviposition. Due to the low number of females with Adelina which actually survived to oviposition, no comparison of the rate of sexual development with and without the disease is possible. It was not possible to rank ovarian development in females that died before oviposition except for a very small proportion, as internal structures

Table 11-4 The effect of *Adelina* on adult female black beetle potential fecundity.

	Total number	Number dying before oviposition	Number ovipositing	Mean potential fecundity (eggs in soil and oocytes in females)	
				Per ovipositing female	Per female overall
Females with *Adelina* sp.	28	25	3	35.0 ± 10.1	3.7
Females without *Adelina* sp.	68	11	57	49.6 ± 9.2	41.6

had usually deteriorated by the time dissection of the adults was carried out.

The potential fecundity of Adelina infected females was lower than that of the population free of the pathogen (Table 11-4), and although only three females in the sample with the disease oviposited, a 't-test' revealed that this difference in fecundity was significant ($P < 0.05$). The ovaries of females infected with the protozoan were however smaller and less developed in appearance at oviposition than in individuals without the disease. Although this had no apparent effect on the differentiation of oocytes within the ovarioles, the presence of the pathogen had reduced the overall ovarian development.

As pointed out in part II of this chapter, the level of fat in females with Adelina was significantly lower ($P < 0.01$) than in uninfected insects at the start of the trial. At the commencement of oviposition, the mean percentage fat levels were $19.2 \pm 8.6\%$ (infected) and $26.3 \pm 6.9\%$ (uninfected), not significantly different. In both populations however the range had increased.

Fat levels ranged from 13.6-29.2% in the three females with the pathogen and from 16.4-35.6% in the subsample of 10 females without the disease. The favourable nature of the carrot diet as a food source over the trial period is evident once again as the percentage fat in females without Adelina had increased significantly ($P < 0.01$) between the start of the trial in September and the commencement of oviposition.

The results of these trials suggest that the effect of Adelina sp. is to sterilize most females by preventing a buildup of fat reserves essential for ovarian development. The three infected females which

oviposited were presumably the least severely affected by Adelina since the other 25 did not oviposit. As the pattern of development of the pathogen in the adults is unknown, the time during the life-cycle when the individual was infected may be important in determining the ultimate fate of the female. Adelina infection resulted in an overall reduction in potential fecundity of 91%, in the population in this trial.

CHAPTER 12

DISCUSSION OF ADULT ECOLOGY SECTION

The results presented in Section 3 show that the ecology of adult black beetle is subject to the effects of many physical and biotic influences of which plant species and disease are major factors. In contrast to the Melolonthinae, black beetle (Dynastinae) has a long period in the adult relative to other stages in the life cycle. A highly variable mortality operating at the end of the life cycle can have a major influence on population trend (Morris, 1957). For these reasons, the ecology of the black beetle adult stage and indeed of other dynastids, may be of greater importance in population dynamics than it is in melolonthids. The important aspects of adult ecology will be discussed in this chapter.

I FAT LEVELS AND OVARIAN DEVELOPMENT

Lipid material, stored within the insect fat body is a source of potential energy which is utilized during the general energy consuming processes of movement, oogenesis and moulting (Gilbert, 1967). Although much remains unclear, studies reported in this thesis have shown there is a seasonal pattern in the fat level of female adults reared on paspalum, one of the most favourable pasture species for black beetle growth and survival. The evidence suggests an accumulation of fat in late autumn, with a peak being reached in early winter, followed subsequently by a decline from late winter to spring. Over the autumn to spring period, ovarian development was found to

steadily increase. These findings are similar to those of Johannesson (1975) for female black beetle adults at another site.

It is likely that the depletion of the fat reserves in the winter-spring period is partly the result of sexual development. Maelzer (1961b) found that immediately after metamorphosis, ovaries of the scarabaeid Aphodius tasmaniae were immature. He also noted that eggs were developed at the expense of the fat body, and that whether or not the first batch of eggs had been laid could be determined by the degree of depletion of the fat body. A similar pattern of ovarian development occurs in Phyllopertha horticola in which Milne (1959) found that females emerging from the soil had high visual fat body scores and were reproductively immature. These females remained in the sward and did not oviposit until the fat body was entirely consumed and all eggs matured. Studies by Fenemore (1965,1970) of grass grub ovarian development led him to conclude it was similar in pattern to P. horticola.

In spite of similar ovarian development levels, fat levels in black beetle adult females from populations at different sites were found to vary significantly at the same sampling times between July and November (Table 8-3). Diet also appears to have an effect on the body fat levels of females, as adults collected from a paspalum pasture contained more fat than those from an adjacent area of maize stubble (Table 8-4). The possible reasons for these differences are speculative but it is likely that factors such as variation in nutritional status, physical parameters such as soil moisture and temperature and possibly stress from pathogen infection may be responsible. As data were not collected on these factors, no further interpretation is possible.

II SIGNIFICANCE OF FOOD SUPPLY TO FECUNDITY

Diet in the spring pre-oviposition period may be important in affecting factors such as longevity and fecundity, although fat levels in females on different pre-oviposition diets in these studies have only been shown to differ between carrot and grasses. Actual fecundity was shown to be higher on carrot compared with grass diets over the pre-oviposition period. In contrast to black beetle adults, grass grub females lay their first cluster of eggs before feeding (Farrell, 1973; Kain, 1975). Consequently the first oviposition is not influenced by adult diet.

This study has shown that food over the period from early spring to oviposition also has an important influence on potential female fecundity. Potential fecundity on a carrot diet was 51 eggs/female whereas mean potential fecundity on a grass diet such as paspalum was 35 eggs/female. Fewer adults laid on a pasture plant diet compared with a carrot diet. In addition 0.58 eggs/day were produced on a carrot diet compared with 0.40 eggs/day on a paspalum diet. Actual fecundity was 45 eggs/female on a carrot diet and 10 eggs/female for those feeding on paspalum plant roots. It is apparent that the lower oviposition rate and earlier adult senescence of black beetles reared on grass diets such as paspalum, reduces the fecundity of females relative to those fed on carrot, and prevents the potential being realized. The favourable influence of the carrot diet on the number of females ovipositing and on actual fecundity, may explain the large difference found in fecundity reported by other workers, reviewed in Chapter 1. The figures of Cumpston (1940), Taylor (1951) and Wright (1958) were possibly derived from females feeding on more favourable diets than plant roots.

There is a large variation also in the fecundities of other scarabaeid species, e.g. in the sub-families Melolonthinae and Rutelinae, fecundities per female in the laboratory have been recorded of 50 eggs for Aphodius tasmaniae (Carne, 1956), 22-59 eggs for the European chafer Amphimallon majalis (Gyrisco et al. 1954), 14-18 eggs for the Garden chafer Phyllopertha horticola (Milne and Laughlin, 1956), 27 eggs for Sericesthis geminata (Wensler, 1971), 28-41 eggs for Rhopaea magnicornis (Chadwick, 1970) and estimates for grass grub of 18 eggs (Farrell, 1973) and 18-30 eggs (Kain, 1975).

Fecundity in the Dynastinae, tends to be higher than amongst the Melolonthinae. Heteronychus licas has a fecundity of 60-75 eggs (Taylor, 1966) and Heteroligus meles, 10-42 eggs (Taylor, 1964). Fecundities of 100 eggs per female have been reported for Aliscnotum impressicolle (Wilson, 1969) and a range of 14-132 eggs per female for Xylotrupes gideon ulysses (Bedford, 1975). Dale (1963) found a fecundity of 12-16 eggs for Pericoptus truncatus, the New Zealand sand scarab. This is uncharacteristically low for a dynastid, especially one with a three year life cycle, although it may reflect a lack of natural enemies in its habitat and marked variation in its physical environment.

The continued access to carrot by ovipositing black beetle females was shown to have a dramatic effect on actual fecundity (Appendices 8-8 and 8-9). Female longevity and fecundity were significantly reduced when the carrot food source was removed from adults as soon as oviposition commenced. Feeding by the adult has been shown to have an influence on the fecundity of other scarabaeid insects, dependent generally on the length of adult life. Both Raw

(1951) and Milne and Laughlin (1956) found no difference in the mean fecundity of Phyllopertha horticola between starved females and those fed over oviposition, and concluded this was because of the relatively short adult life. However, the fecundity of females of A. tasmaniae (Maelzer, 1961b), S. geminata (Wensler, 1971) and grass grub (Farrell, 1973) were significantly increased when feeding was allowed during oviposition. In all cases this increased fecundity appeared to be due to an increase in female longevity.

As shown in Tables 8-6 and 8-7, the pasture plant species diet from early spring to oviposition also had a major influence on black beetle fecundity. On the basis of the number of eggs laid per female, pasture species can be separated into two groups. Grass species such as paspalum and ryegrass, but excluding phalaris, are relatively favourable diets giving relatively high fecundities, while phalaris and legume species could be termed unfavourable. This division follows that of the influence of these groups of pasture species on larval feeding, growth and survival as presented in Chapters 5 and 6. The feeding deterrents and toxins characteristic of the legumes and phalaris, may influence both larvae and adults.

The type of diet, shown to be important for black beetle, also has an influence on grass grub fecundity. Farrell (1975) found that grass grub adult females fed on 'Maku' lotus foliage had a lower weight loss and greater survival and fecundity than females on a diet of other legumes or grasses. It is of interest in comparison with the black beetle results, where pasture species favourable for larval growth and survival also favour fecundity, that the effect of lotus foliage on grass grub adults is in direct contrast to the poor feeding,

growth and survival characteristics of grass grub larvae feeding on 'Maku' lotus roots (Farrell and Sweney, 1974b; Kain et al., 1975; Kain and Atkinson, 1977).

Although there was some variation in the actual fecundity of females feeding on white clover between September and oviposition, considerable reduction in female longevity undoubtedly occurred (Tables 8-7 and 8-8). This would have an adverse effect on the fecundity of a population in a white clover pasture. There is also a suggestion from the results that the white clover component in a ryegrass/white clover mixture, reduces fecundity (Table 8-6).

The effect of an unfavourable plant species on fecundity appears to be a function of the length of the period the female feeds on the species in the spring. The adverse effect of a white clover diet, between September and oviposition, on the fecundity of females was not evident when adults were not placed on the legume diet until the commencement of oviposition (Table 8-9). This suggests that the type of diet is less important in the field once oviposition starts, as the eggs to be laid are already developed by the female. The food source is critical however over the spring pre-oviposition period when final ovarian development and egg differentiation take place.

III OVIPOSITION BEHAVIOUR

The studies carried out on the oviposition behaviour of female black beetle adults demonstrated that population aggregation could be influenced by oviposition in the spring. In both a small plot caged situation and in field plots, pasture height was not shown to have any influence on the oviposition pattern. This is similar to the situation

with grass grub (Kelsey, 1957,1968). Both Phyllophaga spp. and Melolontha melolontha have been noted to prefer tall pasture for oviposition (Anon, 1933).

Pasture species were however shown to have a major influence on oviposition. In caged pot trials, greater numbers of eggs, first-instar larvae and adults were recovered from under plant species than bare ground. Aggregation was found to be greater under a grass species (paspalum) than under a legume (white clover). The unfavourable nature of white clover, previously shown to influence both larval growth and survival and adult fecundity, was also apparent in the oviposition studies. This aggregation difference may be due to a feeding preference, but the net result is an apparent preference for females to oviposit under grass species, even though this may only be a secondary effect.

Wallace (1946) reported the avoidance of legumes by black beetle adults although the observation may be the result of a feeding preference rather than an oviposition preference. Phyllophaga spp. female adults are also considered to be repelled by legume crops (Anon, 1933) and so eggs are not deposited in fields planted with these crops.

The sampling of a black beetle field population during oviposition revealed a very clumped distribution with only 20% of the samples containing black beetle. There were significantly more adults and eggs recovered from sample cores containing paspalum than without paspalum. Although no difference was apparent between paspalum and ryegrass in the caged situation, paspalum appeared to be preferred in the field with a clumping of the egg distribution under

paspalum plants. Where paspalum comprises a significant proportion of the sward, but with a clumped distribution, the plant species-oviposition interaction involving the selection of oviposition sites will undoubtedly influence population distribution.

The selection of oviposition sites has been shown to occur in other scarabaeids with both soil moisture and plant cover being shown to exert an influence. When given a choice of soil moistures, adults of Sericesthis nigrolineata, Anoplognathus porosus and A. hirsutus preferred to oviposit in soil near field capacity (Hilditch et al.,1974). Watson (pers.comm.) found that black beetle adults also preferred moist, rather than dry soil for oviposition. Hilditch et al. also found a plant cover effect on oviposition by these Australian species, with fewer larvae recovered from white clover and bare ground treatments compared with ryegrass. Maelzer (1961b) considered that adults of Aphodius tasmaniae aggregated in preferred areas and laid most eggs in moist soils. Soil moisture levels were also shown to influence the oviposition of Amphimallon majalis (Tashiro et al.,1969) and grass grub (Galbreath, 1970).

In contrast to the apparent preference of black beetle adults and of the Scarabaeidae studied by Hilditch et al., to oviposit under grass species rather than legumes, Kain (1975) noted that various studies of grass grub oviposition behaviour had failed to establish that plant species influenced the choice of oviposition sites. Kelsey (1957,1968) found that oviposition was greater under growing pasture cover than in bare ground, similar to the situation with black beetle. Radcliffe and Payne (1969) and Radcliffe and Kain (1971) were however unable to demonstrate any marked plant preference by adult grass grubs for feeding or oviposition.

IV DISPERSAL

The literature reviewed in Chapter 1 provides evidence that the most striking differences in the flight behaviour between most species of Melolonthinae and those of Dynastinae, are in the abilities of the latter sub-family to undertake flight both before and after a winter inactive period. In the investigation of the importance of spring dispersal, it was found that in the seasonal conditions operating, 75% of the black beetle summer larval population were the progeny of adults which overwintered on the trial area up to the start of the trial in mid-September. The remainder of the summer population were the progeny of adults which migrated into the area during the spring dispersal phase of the insect.

Spring flight is known to be variable and dependent on the seasonal climatic conditions (Watson, 1978). In the season the trial was carried out, conditions were considered to be favourable for dispersal. The results suggest that in some years, adult dispersal by flight into an area could have a significant influence on summer larval population levels.

Over the autumn period when dispersal occurs, plant species were found to have a significant effect on the numbers of adults entering the overwintering phase of the life cycle (Chapter 10). Higher numbers of adults were recovered from paspalum swards after the autumn period, than from ryegrass, phalaris, legumes, and mixtures of ryegrass or phalaris with a legume. No study was made however of the effect of a paspalum/legume mixture on black beetle rates of development. Adults recovered from paspalum were also heavier and

contained more fat, which may indicate a higher plane of nutrition on this species.

The differences between plant species discussed above may be due to either differential survival and/or dispersal by the adult. Unfortunately, due to very low survival of beetles in the trial designed to separate the contribution of the two components (Table 10-4), the relative influence of survival and dispersal is unknown. There does appear however, to be a strong pasture species-adult interaction operating in the autumn, with the favourable nature of the species studied, closely following that previously shown in Chapter 8 for the fecundity-plant species interactions. Paspalum would appear to favour greater population stability between autumn and winter. This aspect is discussed further in Section 4 dealing with population ecology.

V EFFECTS OF ADELINA

The investigation of the effect of Adelina sp. on female fat levels, ovarian development and fecundity demonstrated the very important influence the pathogen has on these aspects of adult ecology. Infection with Adelina appeared to retard ovarian development over the winter and spring periods and reduced female fat levels at two sites in June by from 55% to 74%.

Adelina sp. infection has a most dramatic effect on fecundity with 89% of the females with the pathogen failing to oviposit in contrast to only 16% of those without the disease. The potential fecundity of infected females which did oviposit was reduced and infection with the pathogen resulted in a 91% overall reduction of

potential fecundity in the trial population. This was a major reduction in fecundity in population terms.

The pathogen appears to have a sterilization effect with most infected females being unable to build up fat reserves essential for ovarian development, with a resultant reduction in the numbers of females ovipositing and of population fecundity. A factor such as this, operating late in the generation life cycle has the potential to be of considerable importance in influencing population trend. This aspect will be examined further in the population ecology section.

VI SUMMARY

1. The level of fat in adult females increases after emergence in the autumn, and reaches a peak in early winter before declining over the late winter to oviposition stage. Ovarian development steadily increases over the autumn to spring period.
2. Diet was found to cause differences in female fat levels and adults from different sites showed variation in fat reserves, even though the level of ovarian development was similar.
3. Diet also had an influence on fecundity, which was higher on carrot than on pasture plant species. Females on the latter diets laid eggs at a lower rate and senescence occurred earlier than on a carrot diet.
4. Continued access to a favourable diet once oviposition commenced was shown to increase female longevity and fecundity.
5. Fecundities were highest amongst the pasture plants on grass species with the exception of phalaris, and lowest on legumes and phalaris.

6. The longevity and hence fecundity of adult females feeding on a white clover diet from early spring to oviposition were considerably reduced relative to the favourable grass species. The presence of white clover in a mixture with a grass species also appeared to reduce fecundity.

7. Although pasture height in the spring had no apparent effect on oviposition, adult aggregation and oviposition were found to be greater under paspalum, than white clover or bare ground. In a grass/legume mixed pasture sward, the black beetle adult and egg stages were found to be aggregated under paspalum concentrations in the pasture.

8. In a season considered favourable for adult spring dispersal, 75% of the summer larval population in an area was found to have arisen from adults which overwintered in the pasture.

9. Trials carried out over several seasons showed that adult mortality and/or dispersal were lower from paspalum pasture than from ryegrass, legumes or mixed ryegrass/legume pastures.

10. The infection of adult females with the pathogen Adelina sp. appeared to sterilize the females by preventing the build up of fat reserves necessary for ovarian development. This resulted in a reduction of the number of females ovipositing and a 91% overall reduction of potential fecundity in the trial population.

SECTION 4

POPULATION ECOLOGY

CHAPTER 13

SAMPLING METHODS AND STATISTICS

I. INTRODUCTION

The objective of these population studies was to investigate seasonal changes in black beetle numbers in the field, and any interaction with pasture type that occurred. The importance of this objective was confirmed when laboratory and field studies of the interactions between black beetle and plants showed the growth and survival of both larvae and adults appeared to be influenced by the type of plant diet. To meet this objective, several population estimates per season were obtained from a number of non-replicated plots of different pasture composition, over three generations.

This resulted in the population studies being carried out with compromise levels of precision and times of sampling in order that all experimental work could be handled. As is discussed in the next chapter, this has resulted in omissions in the data which can explain the sources of population mortality within plots and variation between generations and between plots. This approach is in direct contrast to the much more detailed studies made by East (1972) and Kain (1975), of the population dynamics of grass grub where in life table studies, much of the variance in generation mortality was accounted for.

In addition to yielding data on black beetle generation survival and mortality, the studies reported here gave information on the vital aspects of any sampling plan such as the sample unit, sample timing and pattern, the spatial distribution of the population, the sample size required for given levels of precision, and the extraction of black beetle life stages from samples. These aspects will be discussed in this chapter.

II SAMPLE UNIT

(1) Methods

In a preliminary investigation of the efficiency and cost of the type of sampling unit, black beetle population estimates were made at two sites using a 10 cm diameter soil core and a 17.8 cm wide spade square. The 10 cm soil core was chosen as this sample unit had been used by both East (1972) and Kain (1975) in their investigation of grass grub population dynamics, which meant that equipment for taking this size sample was readily available. A spade square has been widely used in ecological studies of soil inhabiting invertebrates, although it has the disadvantage of giving a large volume of soil to be sorted which can pose problems when extraction of the soil fauna takes place remote from the sampling site.

The comparison was carried out on black beetle populations at two sites: the properties of Mr M. Mead near Te Uku, Raglan County, and Mr C. Mikkelson, Patetonga, on the Hauraki Plains.

At Mead's property, 10 plots each 20 m x 20 m in size were laid down in a 5 x 2 block. Black beetle population numbers were estimated from simple random samples taken on 13 and 14 March, at a time when the population was in the third larval instar or a later developmental stage. Sampling points in each plot were chosen on a random basis by measuring intersects from two adjacent sides of each plot, the distances used being derived from a table of random numbers.

In each plot, 10 spade squares, 17.8 cm wide, were taken, as well as 20 soil cores, each 10 cm in diameter. The spade square samples were carefully dug to a depth of 15 cm, ensuring parallel sides and walls as vertical as possible. Soil from each sample was placed on a galvanised tin sampling tray, and then carefully sifted to extract all black beetle stages, which were sexed, counted and then stored for further study. Although great care was taken with sampling, the major problem of using a spade square sampling unit remained: the problem of accurately delineating the square, compared to the soil corer. East (1972) used this method of sampling on soil types too stony to permit the use of a soil corer, and overcame the problem by using a metal guiding frame.

Soil cores were taken using the soil corer of Kain and Young (1975) to a depth of 15 cm. These were then placed singly in plastic bags which were labelled with the plot number, packed in wire crates and returned to Ruakura where they were cool-stored at 9 ^{o}C until sorted. Black beetles were extracted from the soil cores by breaking the core and carefully sifting the soil to expose the insects which were then treated as for the spade square samples. Comparative estimates of the time taken for each sampling method were made.

Ten plots of the same size as those at Mead's were laid down at the property of Mr C. Mikkelson and sampled in an identical manner on 19 and 20 March, to obtain population estimates. The soil type at this site was peat. Once again, spade square samples were sorted on the site, and cores returned to Ruakura and cool-stored. Cores from both sites were assessed on 2 April, at which time it was noted that live adults were present on the floor of the cool store. It was concluded that due to indifferent temperature control, the temperature was probably higher than 9 ^{o}C at times over the storage period, and this had permitted some black beetle adults to burrow through the plastic bags containing the soil cores.

In view of this it was decided to carry out a further comparison of core and spade square sample statistics. This was made at Mikkelson's property in a paddock adjacent to the first sample area, where samples were taken from two plots each 20 m x 20 m in dimension on 3 and 4 April. From each plot, 10 spade squares were taken as well as two lots of 10 cm diameter soil cores, one of 20 cores/plot and the other of 50 cores/plot. Sampling technique was the same as used in the March samples. Spade square samples were again sorted in the field, while cores were stored at 5 ^{o}C at Ruakura and then sorted on 6 April. No adult movement out of the soil cores occurred over this storage period.

(2) Results and Discussion

(a) Cost of sampling

All sampling and extraction in the field was carried out by two people as it was found that the physically demanding operation of taking samples using a corer and hammer became impractical for a person working alone.

The time taken on a person-minute basis to locate the sampling position, take a 17.8 cm spade square sample to a depth of 15 cm, place the sample on a sorting tray, break up and sort through the soil, extract, count and record the insects and then return the soil to the sampling hole was 10.4 minutes per sample.
When the sample unit was the soil core, it took 3.8 minutes per sample to locate the sample position, take the sample and place it in a plastic bag, number the bag, place it in the wire crate and then fill in the hole with soil. Loading and unloading of the samples, placement in the cool store and then removal for sorting took a further 0.5 minute per sample. Breaking up the soil core, sorting through the soil, extraction of the insects present, recording them and disposal of the soil took a further 1.5 minutes per sample. This gave a total time for the whole operation of obtaining a population estimate using a 10 cm diameter soil core of 5.8 person minutes per sample.

The cost ($\underline{C}_u$) can be computed on the basis of the smallest sample unit (Southwood, 1966). The relative cost of the spade square when expressed on the basis of the 10 cm diameter core is:

$$\underline{C}_u \text{ (17.8 cm spade square)} = 2.7 \text{ minutes.}$$

(b) Sample statistics

(i) Mead's property

The variances ($\underline{S}^2$) of the sampling units calculated from the sampling should also be compared on the basis of the smallest unit (Finney, 1946). The variance per unit on a common basis (the core) is $\underline{S}_u^2$. Then the relative net cost for the same precision for each unit will be proportional to $\underline{C}_u \underline{S}_u^2$.

On the basis of relative net cost, sampling using the soil core as the sample unit is cheaper for the same level of precision (Table 13-1). The mean population density estimate per m^2 as determined by the spade square method was almost double that obtained using the 10 cm core as the sample unit. As pointed out previously, this may have been partly due to the loss of adults from the cores during storage, so tending to give an underestimate. This will be discussed further in the light of the results from Mikkelson's.

(ii) Mikkelson's property

The same criteria can be used in calculating relative net cost for each unit. As with the sampling at Meads, the relative net cost for the same level of precision is less using the 10 cm soil core (Table 13-2). Once again the population estimate on a m^2 basis is higher using the spade square sample unit.

To check on the degree to which the core unit samples had provided an underestimate of the black beetle population, the sample unit comparison was carried out again at Mikkelson's as previously detailed. This time, the much shorter storage period and the lower storage temperature prevented any adult movement out of the cores.

Table 13-1 The population statistics and the cost of sampling using the two sample units at Mead's property.

Sample Method	Mean/ Sample	S^2	S_u^2	$C_u S_u^2$	Mean/m^2
10cm dia. core	0.07	0.07	0.07	0.406	8.63
17.8cm spade square	0.52	0.81	0.21	0.567	16.46

Table 13-2 The population statistics and the cost of sampling using the two sample units at Mikkelson's property.

Sample Method	Mean/ Sample	S^2	S_u^2	$C_u S_u^2$	Mean/m^2
10 cm dia. core	0.19	0.19	0.19	1.10	23.44
17.8 cm spade square	2.85	3.60	0.92	2.49	90.90

Table 13-3 The population statistics and the cost of sampling using the two sample units when insect movement from the soil cores during storage was prevented.

Sample Method	Mean/ Sample	S^2	S_u^2	$C_u S_u^2$	Mean/m^2
10 cm dia. core 20/plot	0.38	0.34	0.34	1.97	46.9
50/plot	0.41	0.35	0.35	2.03	50.6
17.8 cm spade square	3.35	4.69	1.20	3.24	106.0

Once again, the soil core was the cheaper sample unit on the basis of relative net cost, when this is computed on the smallest sample unit size (Table 13-3). A similar finding was made by Kain (1975) when sampling grass grub populations with different sample units. The population estimate from the spade square was over double that derived from the soil core. Increasing the number of sample units from 20 cores to 50 cores/plot has no significant effect on mean population estimate or variance. It is of interest that at 50 cores/plot the area actually sampled was 0.41 m^2 compared with 0.32 m^2, using 10, 17.8 cm spade squares. Comparison of Tables 13-2 and 13-3 suggests that in fact there was little or no significant movement of adults out of bags in the cool store in the first sampling study at Mikkelson's.

It is apparent from these studies that the larger sample unit has consistently overestimated population density. This is likely to be primarily due to difficulties in accurately delineating sample unit size. Black beetle larval feeding results in a fine layer of dusty soil in the plant root zone just beneath the soil surface. This is the result of the large quantities of soil passing through the insect gut, so destroying the soil texture. During sampling with the spade square, it was impossible to prevent insect stages from this zone from falling into the sample hole, while the sample was being removed for sorting. This has obviously contributed to the overestimate of population density.

This problem has occurred on both the peat soil type at Mikkelson's and on the ash soil type at Te Uku. As much of the black beetle distribution is confined to light sandy and peat soil

types, the overestimation is likely to be experienced in most populations.

No comparison of sample unit sizes was made at other stages of the insect life cycle. This was because of the need to transport samples to Ruakura to extract the eggs and small larval instars using a salt flotation system. It was found that the whole operation was much easier when the weight and volume of soil in each sample was kept to a minimum. In view of the advantages in cost and precision discussed in this section, the 10 cm diameter soil core was adopted as the sample unit in all studies of black beetle population ecology.

III EXTRACTION SYSTEM

Extraction was carried out in the extraction laboratory of the Insect Control Group at Ruakura, described by Pottinger and Oliver (1978) using the flotation and wet sieving technique of Kain and Atkinson (1976). Soil cores from the population study sites were transported to Ruakura, and held in a cool store at 5 ^{o}C until processing. Usually this storage time was not longer than a week. Experience showed that all black beetle life stages could be held at this temperature with no adverse effect on survival, or the ability to recover the insect from the soil.

The extraction system enabled relatively rapid extraction of the small black beetle stages from the soil samples and the time taken is shown in Table 13-4. The whole operation involved three persons, one carrying out operations 1 and 2, and the other two, operations 3 and 4. As was found by Kain and Atkinson (1976) the

Table 13-4 Time taken by three operators to process one sample and extract black beetle eggs and small larvae.

Operation	Time (minutes/sample) Mean/sample	Range
1. Removing sample from bag, crumbling sample on tray and removing large debris:	0.45	0.30 - 0.52
2. Filling bucket with solution and emptying sample into bucket:	0.21	0.18 - 0.24
3. Decanting sample into sieves, emptying soil from bucket and washing sieves with solution:	0.72	0.52 - 0.97
4. Examining sieves in inspection tray, removing insects, counting and recording:	1.32	0.30* - 1.91**
Total extraction operation:	2.70	1.30 - 3.64

* zero eggs per sample

** 12 eggs per sample

extraction rate was governed by the time for the slowest operation which was usually the inspection process when the sample contained several eggs and small larvae which had to be separated from other fine buoyant debris. Kain achieved extraction times for grass grub eggs and first instar larvae of just over 2 minutes/sample, using a similar system, with three operators.

Black beetle eggs and first instar larvae were seeded into crumbled soil cores known to contain no black beetle, and the recovery of insects from these cores was recorded when the operators were not aware of the presence of these life stages in the sample. These tests were regularly carried out at various times during extraction to ensure efficiency was being maintained, and gave recovery efficiencies of between 95% and 97%, similar to those recorded by Kain and Atkinson for grass grub eggs and first instar larvae.

As the larger larvae, pupal and adult stages of black beetle were readily observed when crumbling the soil core, the flotation procedure was not used when these stages were present, unless it was known that due to the degree of overlap within the population, eggs and small larvae could be expected to be present. Samples containing the larger life stages were carefully crumbled on the sorting tray, the soil sifted to expose the insects, which were then sexed (in the case of adults), counted and recorded. Recovery efficiencies when tested for these stages were never below 98%.

IV POPULATION STUDY SITES

As mentioned in the introduction to this chapter, the primary objective of the population studies was to investigate seasonal changes in black beetle numbers in the field and any interaction with pasture type that occurred. To facilitate this, two study areas were set up, one at the Otakanini Research Area, and the other on the property of Mr S. Phillips, Wharepapa, near Helensville.

(1) Otakanini Research Area

This research area of approximately 10 hectares is situated on the South Kaipara peninsula adjacent to the harbour, some 7 km north of Helensville (Appendix 13-1). The area has been leased by the Research Division of the Ministry of Agriculture and Fisheries since 1963, and was used for animal and pasture production research until 1973. At the end of this period, severe pasture damage caused principally by high populations of black beetle, forced the closure of the animal stocking rate trial. The leased area was then converted to a research area for the study of the ecology and control of black beetle, and the other insect pest present, white fringed weevil (*Graphognathus leucoloma* (Boheman)).

To investigate the interaction of various pasture species with the dynamics of black beetle and white-fringed weevil populations, six adjacent plots, 0.2 ha in area, each of different pasture species composition were established. In 1974, pure swards of lucerne ('Wairau') white clover ('Grasslands Pitau'), ryegrass ('Grasslands Ruanui') and paspalum were established. Similar sized plots of mixed stands of ryegrass-white clover and phalaris

('Grasslands G14') - white clover were established in 1975. The pastures were rotationally grazed with sheep (250 to 750 s.u./ha/day) for 2 to 4 days, with each pasture type being managed according to its requirements for maximum growth. The desired pasture composition was maintained by the following herbicide treatments each year. Paspalum plot: 0.5 kg paraquat and 1.5 kg simazine applied in the spring before the start of paspalum growth. Ryegrass plot: 4 kg ethofumesate in May and 3 kg M.C.P.P. in the spring. Ryegrass/white clover plot: 2 kg M.C.P.B. in the spring. White clover plot: 1 kg carbetamide in late winter. Lucerne plot: 1 kg each of pronamide and 2,4-DB or 1 kg paraquat in the winter. Phalaris/white clover plot: 1 kg 2,4-DB in the spring. The layout of the study plots is shown in Appendix 13-2 and Plate 13-1.

The interaction of black beetle with changes in pasture composition induced by insect feeding damage was investigated. Pasture production was monitored in each of the plots from twelve, 5 m x 3 m sub-plots, half of which were treated with insecticides in the spring (2 kg/ha fensulfothion and 20 kg/ha chlordane) to remove both black beetle and white fringed weevil, and the other six sub-plots were untreated. Before each grazing, the herbage from two 5 m x 0.45 m strips in each sub-plot was harvested using a rotary mower, and the dry matter calculated gravimetrically from oven-dried subsamples of the herbage at Ruakura. The pasture composition in each of the subplots was assessed seasonally by herbage dissection.

Soil moisture was monitored in each of the six pasture plots at regular intervals. Five, 2.5 cm diameter soil cores were taken



Plate 13-1 Overview of the Otakanini Research Area showing the six pasture plots used in the population dynamics studies. Pegged areas in plots mark pasture production and damage assessment areas.

from each plot around a fixed point on both a flat area and a slope area. The soil cores were taken to a depth of 9 cm, the core was subdivided into 3 cm gradations and the percentage soil moisture was determined gravimetrically on oven dried sub-samples. Rainfall at the research area was monitored using an 'Ota Keiki' tipping-bucket, automatic recording rain gauge. Soil temperature was recorded continuously at a depth of 2.5 cm in the soil in each of the six pasture plots, using remote sensing 'Ota Keiki' automatic recording, soil thermographs. The soil type on the area was a Redhill sandy loam.

(2) Wharepapa plot

This site was five kilometres from Otakanini and the soil type was also Redhill sandy loam. The pasture composition was kikuyu dominant mixed with other grasses and with legumes (Plate 13-2). The roots of the kikuyu formed a dense layer in the top 8 cm of the soil profile. In spite of this, considerable pasture damage occurred in the January/March 1974 period at which time the farmer first noted the damage and monitoring commenced.

Preliminary sampling showed high black beetle populations in an area of about 0.2 ha, adjacent to the Woodhill State Forest. Within this area, four adjacent plots, each 20 m x 20 m in dimension, were marked out and population estimates were confined to these plots (Plate 13-3). Sampling commenced in March 1974 when the population was in the late larval instar, pupal and teneral adult stage, and data from the 1973/74 and 1974/75 generations are presented in the next chapter to contrast with population data collected after spring 1975, during the thesis study period.



Plate 13-2 Kikuyu dominance in mixed grass/legume pasture in the study plots at Wharepapa in March 1977.



Plate 13-3 View of the four study plots at Mr S. Phillips, Wharepapa, adjacent to the Woodhill Forest.

The site was irregularly grazed by stock (usually a mixture of young steers and sheep). Until 1977, these were set-stocked, but more recently a rotational grazing pattern has been adopted by the farmer. Lax grazing over the summer-autumn periods when the kikuyu rate of growth was very high usually resulted in rank pasture (15 - 25 cm in length) over this period. This would have an insulating and cooling effect on the soil when soil temperatures would be highest.

Due to problems with access to the site, particularly following rain, and a shortage of automatic climate monitoring recorders, it was not possible to monitor rainfall, soil temperature and moisture, as was done at Otakanini. However, climatic data are available from a meteorological station maintained by the N.Z. Forest Service at the Woodhill Forest, about 1 km from the Wharepapa site. As weather patterns are likely to be similar over such a short distance and the modifying effects of topography and aspect were not significant, Woodhill climatic data are presented to illustrate conditions in the Wharepapa plot.

Black beetle populations at Wharepapa were infected with high levels of pathogens and a study of the interactions of these pathogens with black beetle populations was carried out by Entomology Division, DSIR, on an adjacent site 200 m from the study site described in this thesis. Data from these DSIR studies have been presented by Archibald (1976), Archibald *et al.* (1975) and Longworth and Archibald (1975).

V DISTRIBUTION WITHIN THE SOIL PROFILE

The physical environment of black beetle populations is influenced greatly by factors such as soil moisture and soil temperature, the levels of which will vary with depth. For this reason, the depth at which the various life stages feed and live in the soil will moderate the influence these physical factors have on growth and survival. The effect of these factors was examined in Section 2. In addition, any sampling designed to monitor the influence of the various life processes on population stability must make allowance for the depth of population occurrence in the soil.

Samples taken to provide population estimates in the paspalum and ryegrass plots at several stages in a generation were carefully handled to keep the soil core intact, and at the time of insect extraction were sectioned with a knife into four portions. These were 0–3 cm in depth, 3–6 cm, 6–9 cm, and 9 cm to the end of the core, usually to a depth of 12–15 cm. Each section was handled as a separate sample and the insects extracted, counted and recorded.

In order to establish population distribution in the soil profile three sampling times were chosen to give data on eggs, larvae, pupae and adults. The distributions at the various sampling times in the paspalum and ryegrass plots are shown in Tables 13–5 and 13–6 respectively.

No individuals were found at a depth greater than 9 cm and few at 6–9 cm. This confirms observations made during the collection of all insect stages from pasture for use in laboratory trials, that the upper levels of the profile are preferred by black beetle.

Table 13-5 The distribution of black beetle at three depths in the soil profile in December, February and June in the paspalum plot.

	% of total black beetle population at each of three depths		
	7 December 1976	17 February 1977	9 June 1977
Stage of Development	eggs, 1st instar larvae	larvae, pupae	larvae, pupae, adults
Total numbers/m^2	62.9	56.7	26.5
Soil Depth			
0 - 3cm	70.2	77.2	59.5
3 - 6cm	24.5	16.3	19.0
6 - 9cm	5.3	1.1	14.3
Unknown*	0	5.4	7.2

Table 13-6 The distribution of black beetle at three depths in the soil profile in February and June in the ryegrass plot.

	% of total black beetle population at each of three depths	
	17 February 1977	9 June 1977
Stage of Development	larvae, pupae, teneral adults	larvae, adults
Total numbers/m^2	21.0	2.5
Soil Depth		
0 - 3cm	54.8	75
3 - 6cm	24.8	25
6 - 9cm	10.2	0
Unknown*	10.2	0

* Unknown: Those individuals found in the loose soil at the bottom of the bag which probably moved out of the soil core before cool storage prevented any further locomotor activity.

Significantly more insects were recovered in the top 3 cm of soil at all stages of the life cycle. In this region, the soil temperatures and organic matter levels, shown to be of importance to larval growth and development in Section 2, will be higher, and soil moistures usually lower.

All pupae and pre-pupae recovered from both plots were found at either 0-3 or 3-6 cm. None were noted at a depth greater than 6 cm. This finding contrasts with the situation with grass grub where larvae and pupae can be found at depths as great as 25 cm (Kelsey, 1970; cited in East, 1972), so compounding the problems associated with sampling.

VI SAMPLING TECHNIQUE

At the Otakanini Research Area, estimates of black beetle population numbers commenced in spring 1974 in the paspalum, lucerne and white clover plots, and these data are presented in the next chapter to contrast with that obtained during the thesis study period. Population monitoring in the ryegrass, ryegrass/white clover and phalaris/white clover plots commenced in spring 1975.

The sampling pattern followed at Otakanini was a combination of stratified random sampling with proportional allocation (Yates and Finney, 1942; Healy, 1962; Sampford, 1962; Cochran, 1963) and the centric systematic area-sample which Milne (1959) showed could be treated as a random sample. Each plot was subdivided into 10 equal sized strata or sub-plots of approximately 200 m^2, which were permanently identified. These were arranged in a 5 x 2 layout in each plot with two strata across the plot and five strata down the plots as shown in Appendix 13-2.

Following the pattern of stratified sampling with proportional allocation, equal numbers of sample units were taken from each of the strata. At the commencement of the population studies, it was decided to compromise precision by taking a fixed number of samples from each plot, regardless of population density, population dispersion pattern and the stage of the life cycle. This approach was considered as being validated by the need to consider the physical resources available for sampling and extracting the insect before the level of precision of the population estimates were known. It was decided that 200 sample units per plot, giving 1200 sample units from Otakanini at any one sampling occasion was the maximum sample size that could be handled. In view of this, 20 sample units were taken from each stratum, giving 200 units per plot.

In contrast to the studies of East (1972) and Kain (1975) the samples were not taken randomly within each stratum, but following the system detailed by Milne (1959) were taken at regularly spaced intervals in a systematic manner. All distances were determined by pacing, and four rows of five samples were taken in each sub-plot. As reviewed earlier, the main danger from systematic sampling is the occurrence of unexpected periodicity in the universe. Soil type was relatively constant over the whole plot area and uniform pasture composition was maintained by herbicide treatment. Possibly because of this, no regular periodicity was noted in the course of the population studies.

Samples were taken using the 10 cm diameter soil corer described by Kain and Young (1975), driven into the soil by a 20 kg hammer to a depth of 15 cm to ensure all insects present in the

10 cm diameter of the core were recovered. Two operators hammered the corer into the ground, one of these chose the next sampling position and carried the hammer to this point while the other pulled up the corer and emptied the sample into a plastic bag held by a third person. The sample holes were filled in at each sampling occasion. After 200 samples had been taken from a plot, the cores from each stratum were collected and packed into permanently labelled wire milk crates, which enabled samples from individual strata to be subsequently identified. Crates of samples were picked up by a tractor with a tray, placed on a truck and trailer, and taken to Ruakura where they were cool stored until extraction of the insects commenced.

By rotating the sampling jobs, it was found that three operators could choose 200 sample sites, take the samples, bag them, collect them, pack them into crates and transport the crates to the vehicle in 2 hours. The cost per sample when expressed in person minutes is 1.8 minutes per sample. This time is less than the 3.8 minutes per sample for two people to take a 10 cm core discussed previously in II(2) of this chapter. The difference is due to the greater efficiency when three people carry out the sampling operation as was done at Otakanini, and also to the much faster method of choosing the sample site.

At Wharepapa, 50 sample units (10 cm diameter soil core) were taken from each of the four adjacent plots following a centric-systematic sampling method. Samples were taken and handled in the same way as at Otakanini.

In spite of the increased precision that stratifying sampling on damage was shown to have in grass grub populations by East (1972) and Kain (1975), this approach was not possible with black beetle. The pasture damage caused by the second and third larval instars coincides with the occurrence of summer drought which results in a senescence and browning off of the pasture. The presence of black beetle damage cannot be readily distinguished from the influence of drought except in cases where pulling of pasture by grazing animals indicates where severe damage has occurred, often resulting in the loss of the plant root system.

A crucial factor in the success of stratifying grass grub sampling on damage is the close relationship between pasture damage and grass grub distribution in successive seasons. Kain (1975) found that by adding a 1.2 m margin to the area of grass grub pasture damage from the previous season, at the egg sampling occasion had a dramatic effect on reducing sample variance. The fact that 80% of grass grub eggs are laid by the female in or near the pupation area results in this situation. In contrast, black beetle have an ability to disperse large distances as an adult in both autumn and spring before oviposition occurs. No relationship of specific area of occurrence from one season to the next was noted in these studies which would permit the stratification of sampling, with the exception of pasture composition discussed in Chapter 9.

Also a factor in the problem of stratifying black beetle sampling on damage is the very short larval life stage, relative to grass grub. Often by the time black beetle larval damage is visible, the insect has developed to the more mobile adult stage. Grass grub

in contrast, remain in the larval stage until the end of the winter, so enabling a correlation of larval occurrence with pasture damage.

VII TIMING OF SAMPLING

A major and often insurmountable problem, when sampling soil-inhabiting insect populations to obtain estimates of age specific mortality, is posed by overlap of individual life stages, or extended oviposition. Such a problem is encountered in black beetle populations, where because oviposition occurs over a relatively long period, most developmental stages can be found in the soil in the later part of the summer period.

To investigate the period of egg laying and the problems which might be encountered in sampling black beetle populations to provide age specific population estimates, a series of successive samples were taken over the period from October 1975 to February 1976 from the paspalum plot at Otakanini.

As shown in Table 13-7, black beetle oviposition was found to extend from the end of September until at least the middle of November when the egg density per m^2 was still increasing. On the evidence of the presence of old generation females in the population in December, and egg hatching taking some 20 days at 20 ^{o}C in the laboratory it is concluded that some further oviposition occurred after the December sample. First instar larvae were present in the population from mid November to the early January sample, and peaked both as a proportion and in density in December. In view of this overlap, it was decided that unless intensive close interval sampling was carried out over the egg and larval development period, it would be

Table 13-7 The black beetle population density in the paspalum plot and the proportion of the population in the various development stages between September 1975 and October 1976.

Sampling Date	Black Beetle per m^2	% of Total Population in each Life Stage			
		Egg	First Instar	Second Instar	Third Instar
30/9/75	25.3	100	0	0	0
23/10/75	117.2	100	0	0	0
18/11/75	146.2	88	12	0	0
1/12/75	112.9	56	44	0	0
6/1/76	78.3	11	36	44	9
12/2/76	59.8*	0	10	13	70

* includes 7% of the total population as pre-pupae and pupae.

impossible to derive age specific estimates of mortality for life table work. As the cost of such a programme was outside the resources of this study, it was decided to compromise on sampling times.

Black beetle population sampling at Otakanini was carried out in December to provide an estimate of egg and first instar larval numbers as well as adults of the previous generation. Further samples were taken in February for the late larval stages, pre-pupae, pupae and adults, in March for pupae and teneral adults before any influence of adult dispersal had taken place, in June for overwintering adults after autumn dispersal, and again in September at the commencement of adult spring activity, but before any spring dispersal, to obtain an estimate of winter mortality. Other samples were made at irregular times as discussed in the next chapter to provide further information on pathogen incidence.

Population sampling at Wharepapa was carried out in December, February, March, May and September. No sample was made in June as access was impossible due to wetness of the soil preventing any movement of transport to the site. A sample in May was taken while conditions permitted. In addition to these sampling occasions, further population estimates were made on an irregular basis to provide more detailed information on the influence of pathogens on the population.

VIII SPATIAL DISTRIBUTION

The spatial distribution or dispersion of each of the black beetle populations sampled in this study is of considerable ecological

interest for the insight it provides on patterns of oviposition, and changes due to insect movement and mortality during the life-cycle as well as the suitability of the sampling programme used to estimate population numbers. The distributions of black beetle populations at various stages of the life cycle in the paspalum, ryegrass and ryegrass/white clover plots at Otakanini and in the kikuyu pasture at Wharepapa will be presented in this section. As population numbers were very low in the lucerne, white clover and phalaris/white clover plots, the dispersion was not examined.

(1) Frequency distributions

The frequency distributions of black beetle populations at different times of sampling over the generation are shown in Figs. 13-1, 13-2, 13-3 and 13-4. No estimate of population numbers was made in February 1978 in the paspalum and Wharepapa plots. At Wharepapa, the pre-winter sample was carried out in May, owing to problems with access in June, and an extra sample was taken in March.

All frequency distributions show marked positive skewness where this is a measure of the departure of the data from a normal distribution and is assessed by Fisher's measure of skewness (G_1), values of which are given in the figures. Over the three generations for which data are presented, a wide range of population densities was found in the three pasture plots at Otakanini, and at Wharepapa. Generally, two main trends are apparent from the figures: firstly, within a developmental stage the lower the population mean, the more skewed the frequency distribution, and secondly, the skewness of the distribution is very marked in the egg and first larval instar, decreases considerably by February, increases

Figure 13-1 Frequency distributions of black beetle populations in the paspalum plot at Otakanini at five sampling times per generation. The dominant development stages present are: December - eggs and first instar larvae, February - third instar larvae, March - pupae and adults, June and September - adults. ($\bar{x}$ = mean number of black beetle/m^2, G_1 = Fisher's measure of skewness, the frequency classes are shown on the x-axis and the number of individuals in each class on the y-axis.)

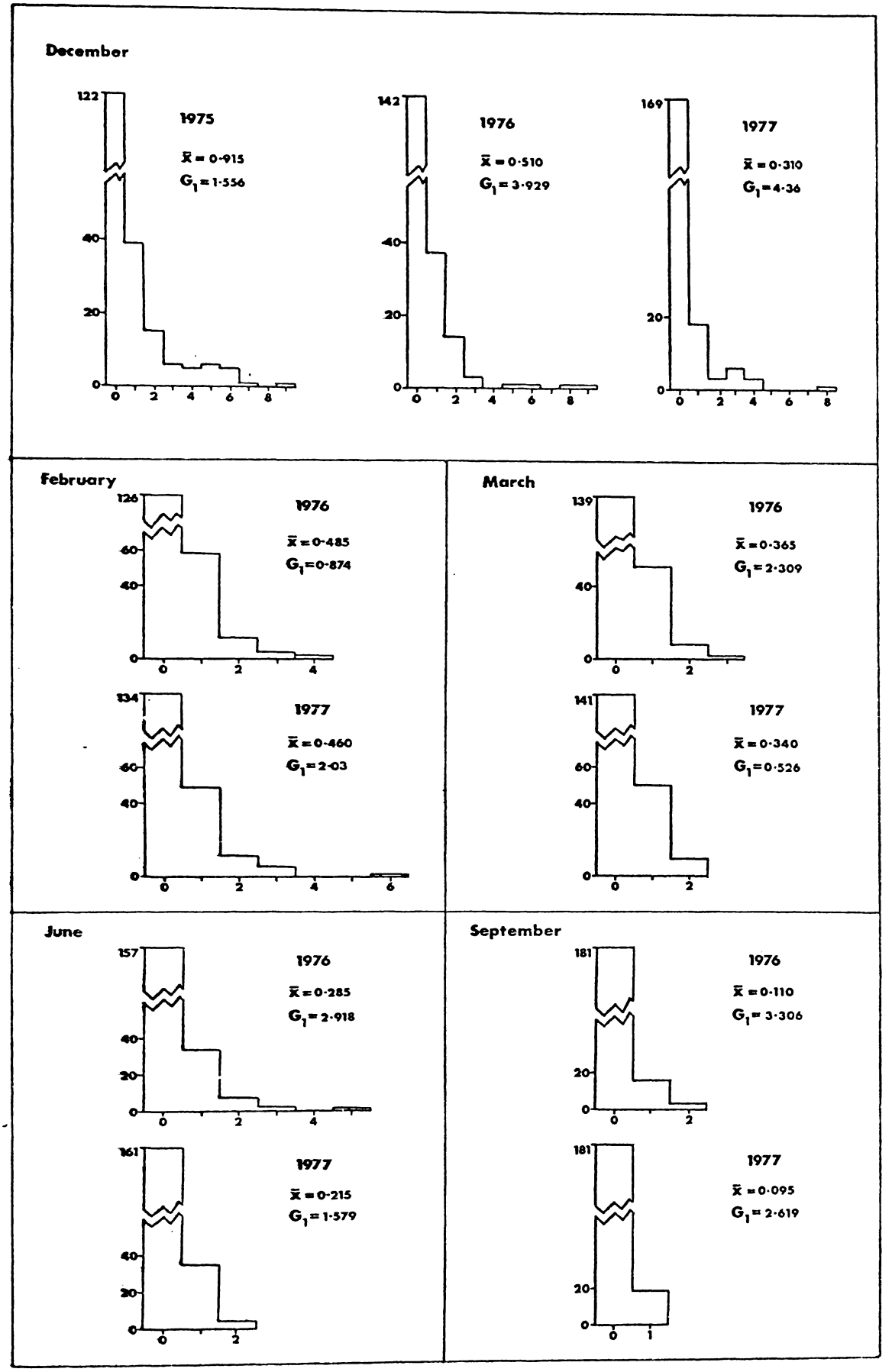

December
1975
x̄ = 0·915
G1 = 1·556
1976
x̄ = 0·510
G1 = 3·929
1977
x̄ = 0·310
G1 = 4·36
February
1976
x̄ = 0·485
G1 = 0·874
1977
x̄ = 0·460
G1 = 2·03
March
1976
x̄ = 0·365
G1 = 2·309
1977
x̄ = 0·340
G1 = 0·526
June
1976
x̄ = 0·285
G1 = 2·918
1977
x̄ = 0·215
G1 = 1·579
September
1976
x̄ = 0·110
G1 = 3·306
1977
x̄ = 0·095
G1 = 2·619

Figure 13-1

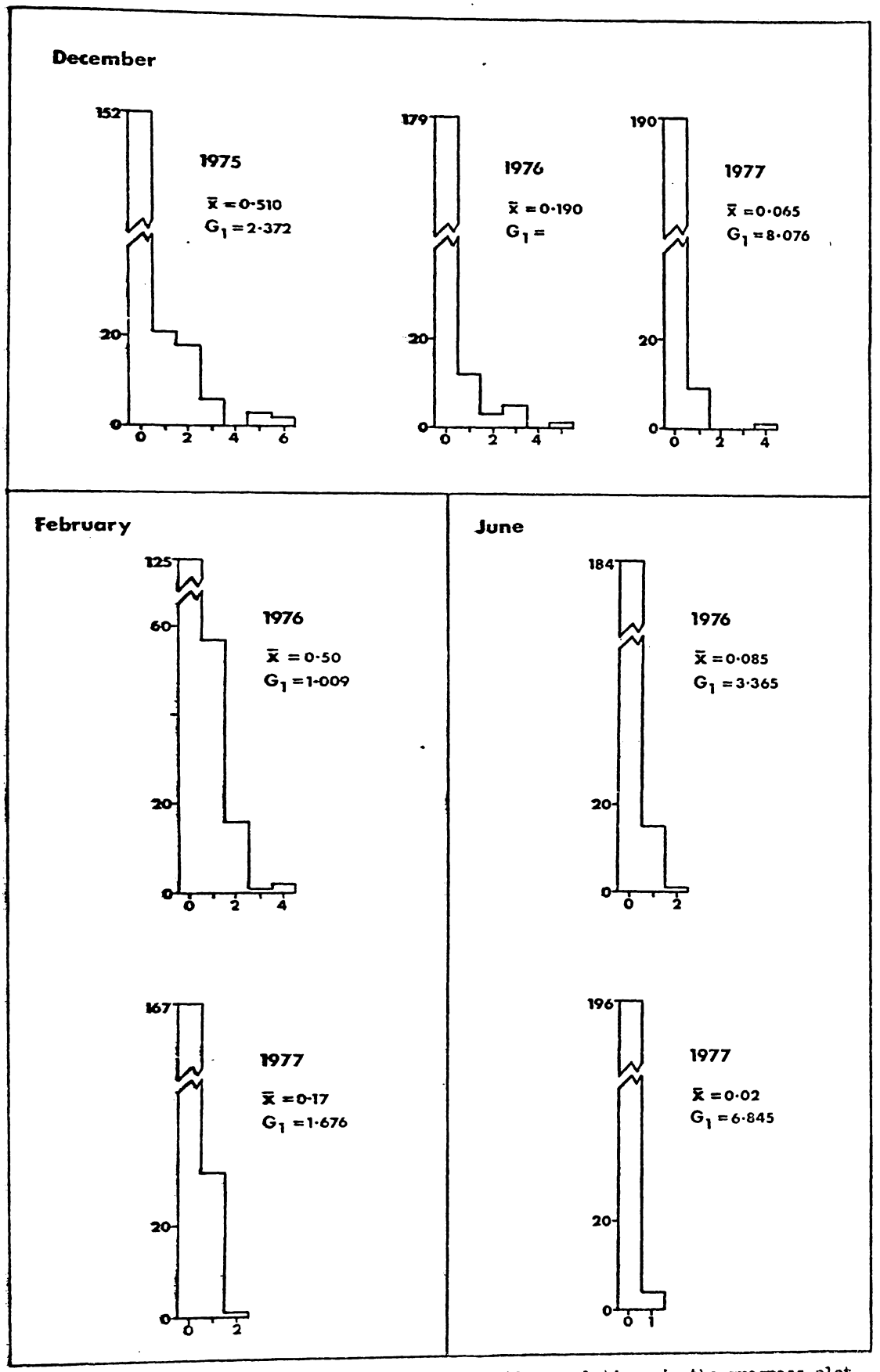


Figure 13-2 Frequency distributions of black beetle populations in the ryegrass plot at Otakanini at three sampling times per generation (dominant development stages present and symbols as in Figure 13-1.)

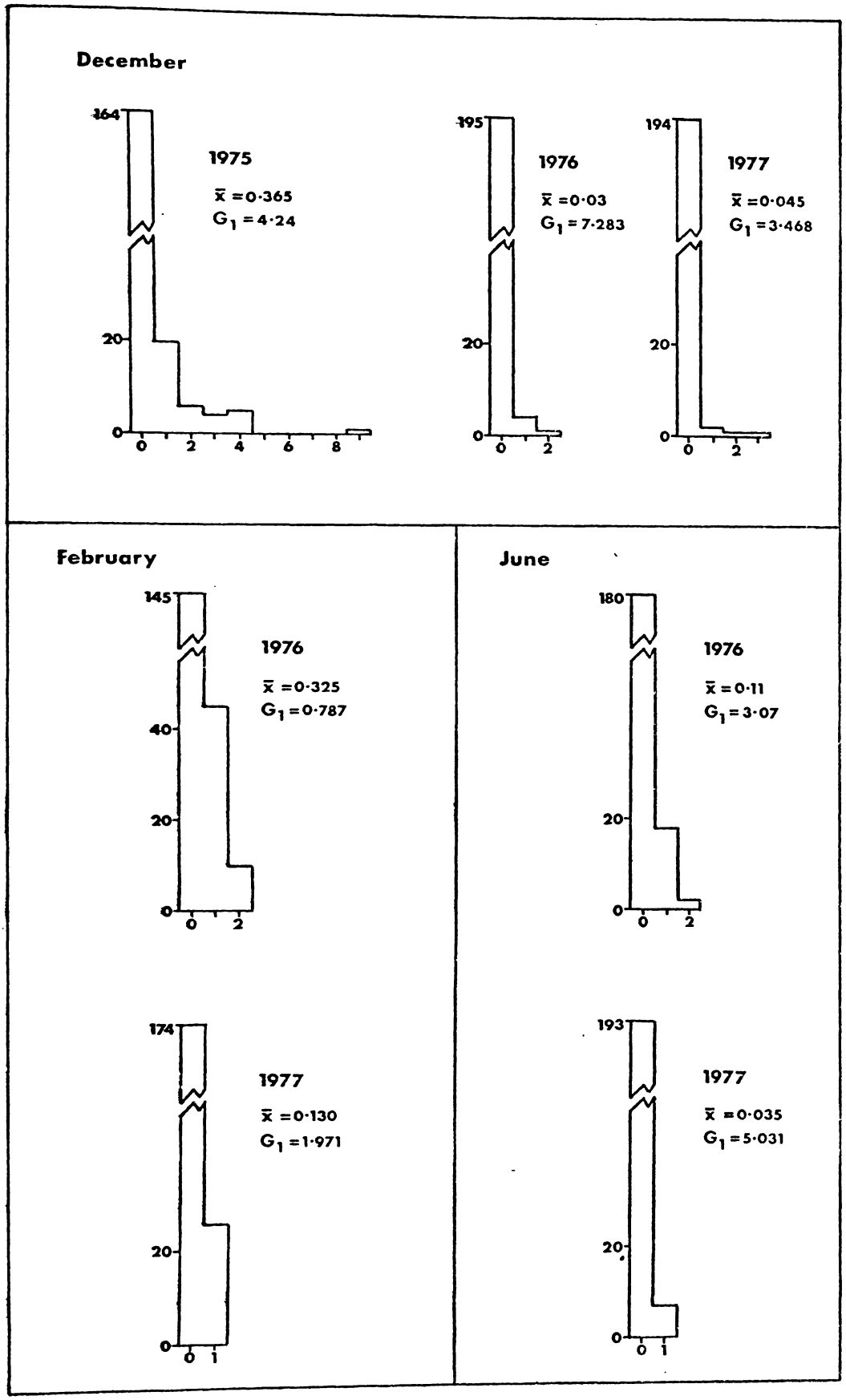


Figure 13-3 Frequency distributions of black beetle populations in the ryegrass/white clover plot at Otakanini at three sampling times per generation (dominant development stages present and symbols as in Figure 13-1.)

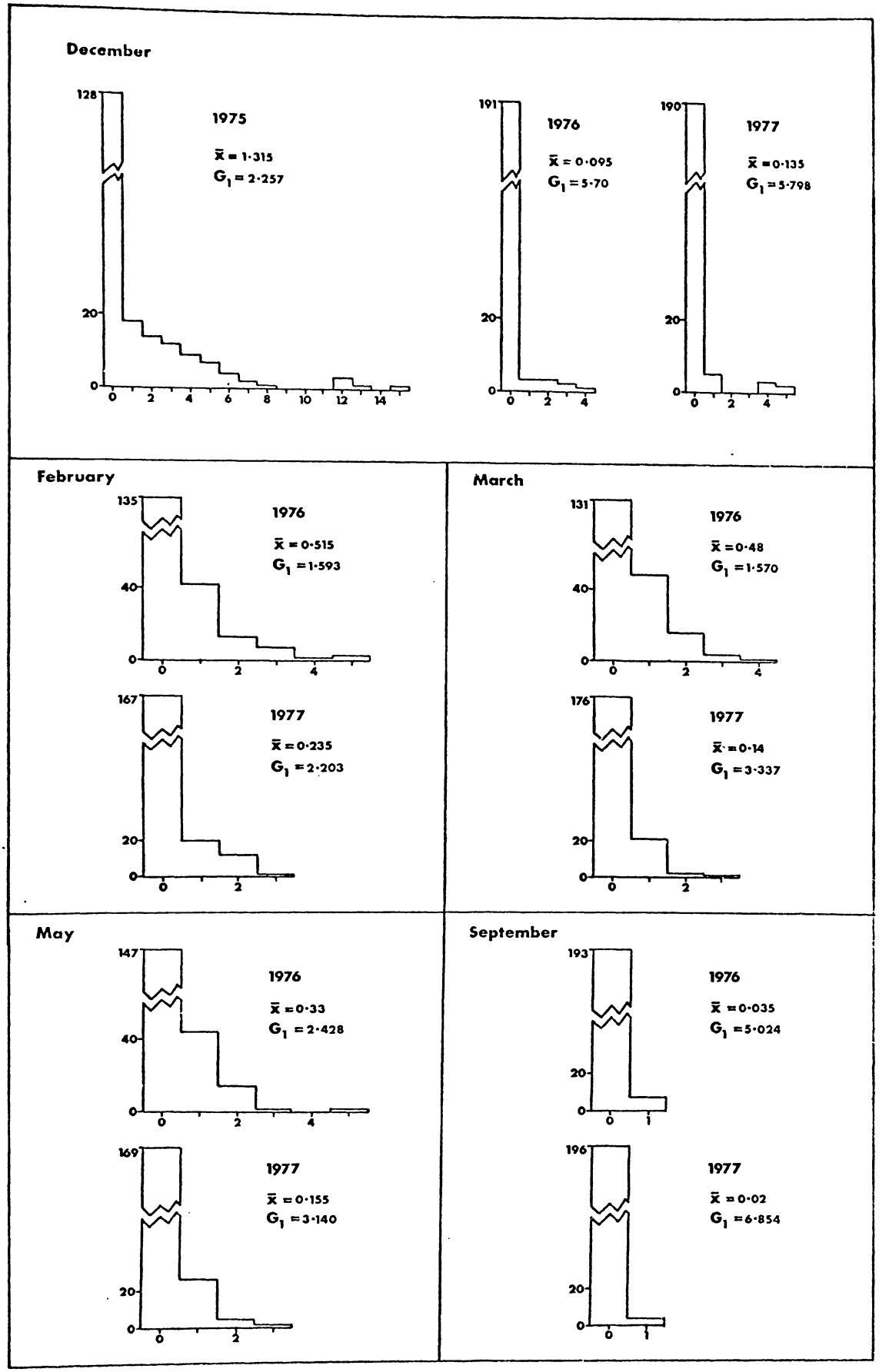


Figure 13-4 Frequency distributions of black beetle populations in the Wharepapa plot at five sampling times per generation (dominant development stages present and symbols as in Figure 13-1).

again by the beginning of the winter and reaches a high level in September when over 90% of the sample units were zeros.

For all stages and for all populations, the zero class of the frequency distribution was always considerably greater than any of the other class intervals. The very marked skewness exhibited at the egg stage due to the female oviposition pattern of depositing aggregates of eggs in the soil, decreased by February as larval movement during feeding occurred.

These results show some marked similarities to the results of Kain (1975) with grass grub. He found that the positive skewness at the egg stage tended to decrease up until the May third instar larval sampling. Thereafter, skewness increased slightly up to the beetle stage in the spring. Skewness was less marked at high than at low populations. If the sample comes from a normal population, G_1 is approximately normally distributed with a mean of zero (Snedecor and Cochran, 1967). The figures show that at no stage of development or population density does G_1 approach zero and only in February 1976 and March 1977 in the paspalum and in February 1976 in the ryegrass/white clover plots is the value of G_1 less than unity.

(2) Population dispersion

In the previous section, the frequency distribution data revealed that the population samples did not come from black beetle populations with a normal distribution, where the variance was independent of the mean. The marked skewness and the tendency for the variance to be either greater than or approximately equal to the mean (Tables 13-8, 13-9, 13-10), suggested that the dispersion of the populations tended toward an aggregated or over-dispersed

distribution described by the negative binomial model, or alternatively, a random distribution described by the Poisson series. The characteristics of these two distributions were reviewed in the literature review in Chapter 3. In this section, the results of testing the frequency distributions of populations at all sampling times at both Otakanini and Wharepapa against the negative binomial and Poisson models are presented.

The dispersion parameter $\underline{k}$ was calculated by the iterative method of Bliss and Calhoun (1954) using a "Genstat" programme written by N.R. Cox, Biometrics Section, Ruakura Research Centre, run by the Computer Services Section, MAF, Wellington. The goodness of fit of the negative binomial model with the observed frequency was tested with a X^2 by the methods of Bliss and Fisher (1953), using the same "Genstat" programme. Where the frequency distribution revealed little skewness of the population, the observed distribution was tested against a Poisson computed as shown in Sokal and Rohlf (1969, Chapter 5) and the goodness of fit was assessed using a "G-test" (Sokal and Rohlf, 1969, Chapter 16). If the distribution did not differ significantly from that described by the Poisson series, the fit of the negative binomial was not investigated.

The results of the analyses of the distributions for the paspalum plot, ryegrass and ryegrass/white clover plots and the Wharepapa plot are shown in Tables 13-8, 13-9 and 13-10 respectively. The X^2-test showed that for all plots, the observed distribution did not depart significantly from that described by the negative binomial model for the December sampling occasions with the following exceptions. At the low population density in the ryegrass/white

Table 13-8 The type of frequency distribution model which most adequately fits the population counts of black beetle taken from the paspalum plot between 1975 and 1978.

Generation and Sampling Time		$\bar{x}$	s^2	k	SE_k	Distribution model
1975/76	December	0.915	3.696	0.434	0.090	Negative binomial
	February	0.485	0.573	-	-	Poisson
	March	0.365	0.373	-	-	Poisson
	June	0.285	0.370	0.655	0.311	Negative binomial
	September	0.110	0.115	-	-	Poisson
1976/77	December	0.510	1.449	0.421	0.117	Negative binomial
	February	0.460	0.662	1.289	0.616	Negative binomial
	March	0.340	0.273	-	-	Poisson
	June	0.215	0.197	-	-	Poisson
	September	0.095	0.085	-	-	Poisson
1977/78	December	0.310	0.859	0.151	0.047	Negative binomial
	March	0.135	0.127	-	-	Poisson

$\bar{x}$ = mean no./sample

s^2 = variance

k = dispersion parameter of the negative binomial

SE_k = standard error of k

Table 13-9 The type of frequency distribution model which most adequately fits the population counts of black beetle from the ryegrass and ryegrass/white clover plots between 1975 and 1977.

Plot	Generation and Sampling Time	$\bar{x}$	S^2	k	SE_k	Distribution model
Ryegrass	1975/76 December	0.510	1.100	0.285	0.073	Negative binomial
	February	0.500	0.569	-	-	Poisson
	June	0.085	0.085	-	-	Poisson
	1976/77 December	0.190	0.436	0.113	0.043	Negative binomial
	February	0.170	0.157	-	-	Poisson
	June	0.020	0.019	-	-	Poisson
Ryegrass/ white clover	1975/76 December	0.365	1.039	0.178	0.051	Negative binomial
	February	0.325	0.313	-	-	Poisson
	June	0.110	0.122	-	-	Poisson
	1976/77 December	0.030	0.039	-	-	Poisson
	February	0.030	0.115	-	-	Poisson
	June	0.035	0.035	-	-	Poisson

$\bar{x}$ = mean no./sample

S^2 = variance

k = dispersion parameter of the negative binomial

SE_k = standard error of k

Table 13-10 The type of frequency distribution model which most adequately fits the population counts of black beetle from the Wharepapa plot between 1975 and 1977.

Generation and Sampling Time	$\bar{x}$	S^2	k	SE_k	Distribution model
1975/76 December	1.315	3.815	0.254	0.466	Negative binomial
February	0.515	0.854	0.757	0.254	Negative binomial
March	0.480	0.244	-	-	Poisson
May	0.330	0.155	-	-	Poisson
September	0.035	0.032	-	-	Poisson
1976/77 December*	0.095	0.220	-	-	-
February	0.235	0.331	0.392	0.174	Negative binomial
March	0.140	0.139	-	-	Poisson
May	0.155	0.184	-	-	Poisson
September	0.020	0.016	-	-	Poisson

$\bar{x}$ = mean no./sample

S^2 = variance

k = dispersion parameter of the negative binomial

SE_k = standard error of k

* = observed distribution differed significantly ($P < 0.001$) from both the negative binomial and Poisson.

clover plot in December 1976, the distribution was best described by the Poisson series. In the Wharepapa plot, the distribution in December 1976 could not be described by either the negative binomial or the Poisson. Although the distribution was skewed (Fig. 13-4), with a G_1 value of 5.70, the high frequency in the zero class prevented the fitting of the negative binomial model.

In June 1976 and February 1977 in the paspalum plot and at the February sampling occasions of both generations in the Wharepapa plot, the black beetle distribution was also over-dispersed and could best be described by the negative binomial. At all other sampling occasions at both Otakanini and Wharepapa, the distribution was random and fitted the Poisson series.

These analyses indicate that although the female black beetle adult deposits eggs singly in the soil, the pattern of oviposition is such that the distribution of the populations is aggregated or clumped. This gives rise to problems with sampling and increases the sample size necessary to achieve a given level of precision, which is discussed in the next section. As larval development proceeds, the data suggest that the population dispersion becomes less aggregated and eventually becomes random. Southwood (1966) noted that this change in distribution with the age of the population from an aggregated pattern of eggs and young larvae to random in later instars has been observed by a number of workers.

In addition however, changes in population density often lead to changes, or at least apparent changes in distribution (Southwood, 1966). The random distribution of low population densities and the aggregated distributions of higher densities have been noted for several insect species by Finney (1941), Iwao (1956) and Harcourt (19[illegible].

The black beetle population density changes between the December and February sampling occasions showed considerable variation in all plots ranging from insignificant change to significant decrease. Over this period, development from eggs to third instar larvae and pupae takes place. The large population decrease in the paspalum plot recorded between December 1975 and February 1976 was accompanied by a change in distribution from that described by the negative binomial to that of the Poisson. However, the significant decrease over the same period in the Wharepapa plot saw an increase in $\underline{k}$ suggesting increasing randomness. In view of this ambiguity in the data, it is not possible to state definitely if population development between December and February results in an actual change in population dispersion within the plots. As considerable movement by black beetle larvae feeding within the soil has been observed, it is likely that some movement away from the clumped oviposition sites will take place however, resulting in a more random distribution.

The very mobile adult stage comprises the greatest proportion of the life stages present in black beetle populations from March onwards. It would be expected that population dispersion over this period would tend towards the random in the absence of an adult preference for feeding or overwintering sites. This random distribution late in the generation is evident in the data from all plots, although this could be an artifact of low densities rather than a lack of adult preference.

(3) Precision of the data

As a fixed number of sample units were taken in all study plots for all life stages of black beetle, it is important to establish the relative precision of the population estimates. The frequency distributions have revealed the highly skewed distributions of black beetle populations. The calculation of confidence intervals for estimated population means is based on the central limit theorem which was described previously. The number of samples that must be taken from a population for the central limit theorem to be safely applied increases with skewness and can be estimated for all the sampling times and developmental stages of black beetle, using the formula of Cochran (1963), where the number of samples equals $25\ G_1^2$, with G_1 being Fisher's measure of skewness.

For each sampling occasion a pooled estimate of within stratum variance ($\underline{s}^2_{\underline{w}}$) was calculated from an analysis of variance of the data. Yates (1965) pointed out that it is safe to use the pooled variance estimate in stratified sampling with proportional allocation even when the stratum variances differ widely. Knowing the mean and the variance, and using the formula of Cochran (1963), the number of sample units necessary for a given level of precision can be calculated.

The mean, variance, number of samples required for the central limit theorem to apply ($25\ G_1^2$), the number of samples required for a 10% relative standard error of the mean ($10\%\ \underline{s}\ \underline{\bar{x}}$) and the level of precision achieved at each of the sampling occasions are shown for the paspalum plot, the ryegrass plot, the ryegrass/white clover plot, and the Wharepapa plot in Tables 13-11, 13-12, 13-13 and 13-14 respectively.

Table 13-11 The number of samples required for the central limit theorem to apply ($25\ G_1^2$), the sample size required to provide an estimate of the mean population of black beetle in the paspalum plot with a relative standard error of 10% (10% S.E.) and the level of precision attained when estimating population numbers at each sampling occasion.

Sampling Time*	($\bar{x}$) Mean no./sample	Variance ($S_{\bar{x}}^2$)	$25\ G_1^2$	10% S.E.	% S.E. of $\bar{x}$ attained
December 1975	0.915	3.696	61	440	14.9
February 1976	0.485	0.500	19	208	10.3
March 1976	0.365	0.373	133	287	11.9
June 1976	0.285	0.370	213	463	15.0
September 1976	0.110	0.115	273	870	21.0
December 1976	0.510	1.449	386	500	15.7
February 1977	0.460	0.605	103	286	11.9
March 1977	0.340	0.273	7	236	10.9
June 1977	0.215	0.197	62	425	14.6
September 1977	0.095	0.085	171	941	21.7
December 1977	0.310	0.859	476	813	20.2

* The predominant black beetle life stages present at each sampling time are shown in Appendices 14-3, 14-4, 14-5.

Table 13-12 The number of samples required for the central limit theorem to apply ($25\ C_1^2$), the sample size required to provide an estimate of the mean population of black beetle in the ryegrass plot with a relative standard error of 10% (10% S.E.) and the level of precision attained when estimating population numbers at each sampling occasion.

Sampling time*	$(\bar{x})$ Mean no./sample	Variance (S^2_w)	$25\ C_1^2$	10% S.E.	% S.E. of $\bar{x}$ attained
December 1975	0.510	1.099	141	425	14.5
February 1976	0.50	0.569	26	228	10.7
June 1976	0.085	0.085	283	1180	24.3
December 1976	0.190	0.436	439	1207	24.6
February 1977	0.17	0.157	70	342	16.3
June 1977	0.02	0.02	1174	4875	49.4
December 1978	0.065	0.123	1630	2905	38.0

* The predominant black beetle life stages present at each sampling time are shown in Appendices 14-7 and 14-8.

Table 13-13 The number of samples required for the central limit theorem to apply ($25\ G_1^2$), the sample size required to provide an estimate of the mean population of black beetle in the ryegrass/white clover plot with a relative standard error of 10%, (10% S.E.) and the level of precision attained when estimating population numbers at each sampling occasion.

Sampling Time	$(\bar{x})$ Mean no./sample	Variance $(\underline{S}^2_{\underline{w}})$	$25\ G_1^2$	10% S.E.	% S.E. of $\bar{x}$ attained
December 1975	0.365	1.039	450	780	19.7
February 1976	0.325	0.313	16	296	12.2
June 1976	0.11	0.122	236	1005	22.4
December 1976	0.03	0.039	1326	4389	46.8
February 1977	0.13	0.115	97	679	18.4
June 1977	0.035	0.035	633	2846	37.8
December 1977	0.045	0.147	304	4108	45.4

Table 13-14 The number of samples required for the central limit theorem to apply ($25\ C_1^2$), the sample size required to provide an estimate of the mean population of black beetle in the Wharepapa plot with a relative standard error of 10% (10% S.E.), and the level of precision attained when estimating population numbers at each sampling occasion.

Sampling Time *	($\bar{x}$) Mean no./sample	Variance (S_w^2)	$25\ C_1^2$	10% S.E.	% S.E. of $\bar{x}$ attained
December 1975	1.315	3.815	127	220	10.5
February 1976	0.515	0.854	64	147	8.5
March 1976	0.480	0.244	62	106	7.3
May 1976	0.330	0.155	147	142	8.4
September 1976	0.035	0.032	631	2593	36.0
December 1976	0.095	0.222	812	2458	35.0
February 1977	0.235	0.331	122	409	14.3
March 1977	0.140	0.139	278	709	18.8
May 1977	0.155	0.184	246	679	18.5
September 1977	0.020	0.016	1174	4075	44.5
December 1977	0.135	0.349	840	1914	31.0

* The predominant black beetle life stages present at each sampling time are shown in Appendices 14-9, 14-10, 14-11.

Considering firstly the number of samples required for the central limit theorem to apply and the sample size for a population estimate of 10% $\frac{S}{\bar{x}}$, in all cases the latter is considerably higher than 25 G_1^2 with the exception of the May 1976 sample at Wharepapa. This anomalous result at Wharepapa appears to be due to the high number of insects recovered from one stratum. Both East (1972) and Kain (1975) found that 10% $\frac{S}{\bar{x}}$ required two to three times more samples than 25 G_1^2 for grass grub populations.

Generally, the higher the population density of eggs and first instar larvae at the start of the generation, the lower the values of 25 G_1^2 and 10% $\frac{S}{\bar{x}}$. However, as the skewness of the population distribution decreases from December, through to late stage larvae, pupae and teneral adults, the sample size necessary to satisfy the two conditions also declines, but increases again for September, partly reflecting low population numbers late in the life cycle. When the data are interpreted in relation to the constant sample size of 200 sample units per plot, it can be seen in the paspalum plot that apart from the December samples in 1976 and 1977 and the adult sample in September 1976, the number of samples actually taken satisfies the requirement for the central limit theorem reasonably well. The level of precision is less satisfactory and this will be considered below.

Considering the ryegrass and ryegrass/white clover plots, low population densities, high variances and very skewed distributions at most sampling occasions have resulted in a large sample size necessary to satisfy the two criteria, particularly in the 1976/77 generation, and the egg and larval population in December 1977. Accordingly,

care must be taken in interpreting population trends from these two plots.

In the Wharepapa plot, the number of samples taken for the 1975/76 black beetle generation is close to or greater than the numbers necessary for 25 G_1^2 and a 10% relative standard error at all sampling times with the exception of adults in September. At the much lower population densities of the 1976/77 generation and at the December 1977 sample of the 1977/78 generation, much larger sample sizes are necessary.

Data collected for grass grub populations by East (1972) and Kain (1975) showed that the grass grub adult population in spring always required a smaller sample size than was necessary for the egg stage. In contrast, with the low black beetle adult populations in the spring compared with adult grass grub populations, the very skewed distribution nearly always required considerably more samples than for black beetle eggs.

Considering the level of precision actually attained, it can be seen that only in the 1975/76 generation in the Wharepapa plot, excluding the September sample (Table 13-12), was the relative standard error less than 10%. It should be stressed however, that this criterion of Morris (1955) is only a guide for population studies. Life tables have been constructed where the percentage error of the population means actually attained was considerably higher, even greater than a 20% relative standard error (East, pers.comm.).

The level of precision actually reached is reasonable in the paspalum plot and the Wharepapa plot, and in most instances the relative standard error is less than 20%. The relative standard

error in the ryegrass and ryegrass/white clover plots is unacceptably high, particularly in the 1976/77 generation when population numbers were low. Examination of the 25 G_1^2 values in Tables 14-9 to 14-12 shows that at most sampling occasions in the paspalum plot, in the Wharepapa plot, and the February sampling times in the ryegrass and ryegrass white clover plots, the central limit theorem can be safely applied.

CHAPTER 14

POPULATION STUDIES

I INTRODUCTION

The influence that some of the factors in the ecosystem, such as temperature, moisture, diet and disease have on larval and adult black beetle ecology was examined in small scale studies carried out in the laboratory and in field plots. These were described in sections 2 and 3. The results of studies on the dynamics of black beetle populations over several seasons in the 0.2 ha pasture plots at Otakanini and Wharepapa which were described in Chapter 13, are presented in this chapter.

Population numbers in February are presented to contrast the population dynamics in white clover, lucerne and phalaris/white clover with the other pasture species. A series of life tables for paspalum, ryegrass and Wharepapa plots are presented and the key factors determining population trend and the density relationships of the various mortalities are examined. The magnitude, variability and density relationships of each mortality in the life tables are discussed to investigate the possible role of the mortalities in population change and regulation. An examination is made of the factors which are likely to be important components of each mortality in an attempt to provide an explanation for the observations on population dynamics. Finally, models of the dynamics of black beetle populations in the paspalum, ryegrass and Wharepapa plots are presented and predicted densities obtained through simulation are compared with observed densities.

II POPULATIONS UNDER LEGUMES AND GRASSES

The population estimates from December 1974 for the six pasture plots at the Otakanini Research Area and the Wharepapa plot described in Chapter 13, are shown in Appendices 14-1 and 14-2 respectively. Population monitoring commenced in all plots, with the exception of the phalaris/white clover plot, in the 1974/75 generation. The population numbers in February between 1975 and 1977 in each of the six plots are shown in Fig. 14-1.

As the phalaris/white clover pasture plot was not established until autumn 1975, no population estimate was possible for February 1975. It is apparent that there are major differences in black beetle numbers both between pasture plots and between generations. The populations in the plots can be divided into two groups. Those in paspalum, ryegrass and ryegrass/white clover, and the other three plots (white clover, lucerne and phalaris/white clover). Population levels were lower in the latter group at each sampling time, and became so low by February 1977, that monitoring of black beetle was discontinued due to the large sample size required to give estimates of population densities with acceptable standard errors.

In sections 2 and 3 of this thesis, studies of the interaction of pasture plant species with black beetle larval and adult ecology revealed that species could be grouped into either favourable or unfavourable categories. Lucerne, white clover and phalaris were all shown to be unfavourable for growth and development. The adverse

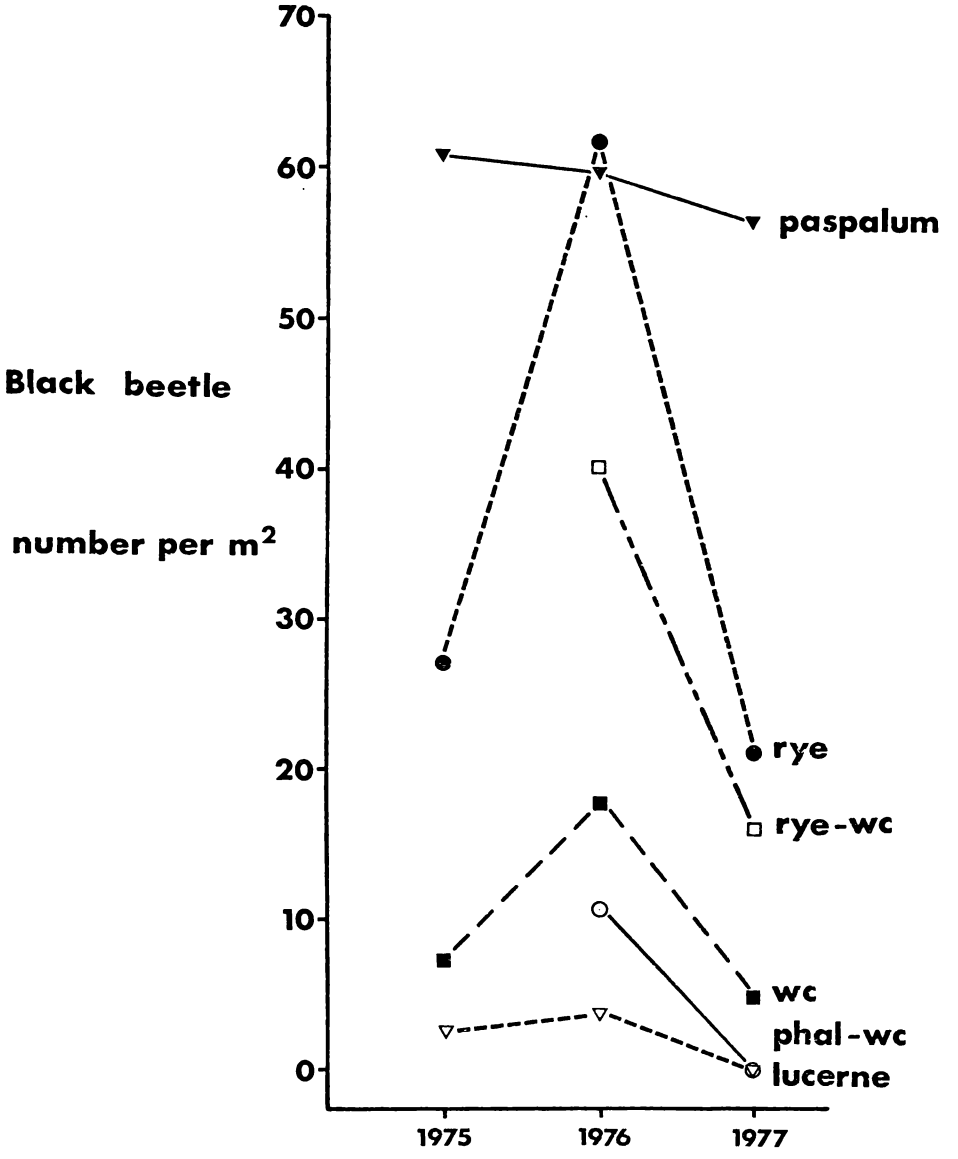


Figure 14-1 Black beetle population estimates (no. per m^2) in February in the paspalum, ryegrass, ryegrass/white clover, white clover, phalaris/white clover and lucerne plots at the Otakanini Research Area between 1975 and 1977. (Sampling in the ryegrass/white clover and phalaris/white clover plots commenced in December 1975).

effects of these species on adult longevity, fecundity, oviposition preference, and on larval root consumption, growth and survival noted in these small scale studies, apparently operated collectively in the large paddock size plots to give low population numbers relative to the other three plots. The estimated black beetle populations were zero in the lucerne and phalaris/white clover plots in February 1977. Although black beetle monitoring was discontinued after this sample, these two plots and the white clover plot have been regularly sampled since this time for white fringed weevil populations, and black beetle numbers have remained consistently low at a level of $0-5/m^2$ (East, pers.comm.).

III LIFE TABLES

In this section, the life tables, presented in Appendices 14-3 to 14-6 for the paspalum plot at Otakanini, Appendices 14-7 and 14-8 for the ryegrass plot at Otakanini and Appendices 14-9 to 14-11 for the Wharepapa plot are discussed. The method of presentation of the life table data is in the form required for the analysis of successive life tables using the methods developed by Varley and Gradwell (1960,1963,1965,1968), to recognise the key factor for the index of population trend.

It is customary to base the initial stage in the life table on egg numbers as was done by East (1972) and Kain (1975) for grass grub, or on potential natality as was done by Varley and Gradwell for the winter moth (Operophtera brumata L.). In view of the problems encountered in obtaining an estimate of black beetle egg numbers at the start of a generation, discussed in the previous

chapter, and the relatively inaccurate estimate of adults in spring on which to base potential natality, the black beetle life tables are based on a February to February generation. As shown in Chapter 13, estimates of the black beetle populations in February were usually obtained with a standard error of the mean of less than 10%. Taking the initial stage of the life table as the February sample is therefore likely to provide a more accurate basis for calculating population trend than on a December to December or potential natality basis. In addition, the February sample also represents the economically important stage of the life cycle in pasture, the root-feeding larvae.

The life tables show that at most sampling times, more than one black beetle life stage was present, thus preventing the calculation of age-specific mortalities. Instead, individual mortalities (k-values) are related to population changes over discrete time-periods, although as sampling was not always carried out at the same time of the month in different generations, these time periods are themselves variable. The index of population trend I is calculated as:

$$I = \frac{\text{population density in February in generation } n+1}{\text{population density in February in generation } n} \times 100$$

For comparative purposes, life-table data collected from February 1975 onwards (prior to the main study period) are included for the paspalum plot at Otakanini and the Wharepapa plot. No life table can be derived for the 1978/79 generation at Wharepapa as the population was not sampled in June and September 1978. Only two life tables are possible from the ryegrass plot as no sampling was

possible between February 1975 and December 1975, when the pasture was being re-established, and sampling ceased in February 1978 due to the input into other work. Life tables are not presented for the ryegrass/white clover plot for two reasons. The very low December population estimates in 1976 and 1977 (Appendix 14-1) which may be due to very large errors in sampling (the standard error attained was over 46% of the mean), or possibly to a delay in adult oviposition resulting in a mistiming of sampling, give rise to an apparent population increase between December and February in each generation. In addition, the general population trends between February and June for ryegrass/white clover show marked similarity to those for ryegrass (Appendix 14-1). As population numbers were so low in the lucerne, white clover and phalaris/white clover plots, no attempt has been made to construct life tables for these plots.

(1) Indices of population trend

The indices of population trend from the paspalum, ryegrass and Wharepapa plot life tables (Appendices 14-3 to 14-11) are presented in Table 14-1. The index of population trend approached 100% in the paspalum plot in the 1975/76 and 1976/77 February to February generations, indicating the relative stability of the population. This was followed by a population decrease and then an increase as evidenced by the indices of population trend for the 1977/78 and 1978/79 generations.

The two life tables for the population in the ryegrass plot reveal a decreasing black beetle population with relatively low indices of population trend (Table 14-1). Possible reasons for this decrease are examined later in the chapter.

Table 14-1 Indices of population trend (February to February basis) in the life table plots.

Plot	Initial population density (no./m^2)	Index of population trend (%)			
		1975-76	1976-77	1977-78	1978-79
Paspalum	61.1	98.0	94.8	37.7	172.9
Ryegrass	61.7	-	34.0	58.6	-
Wharepapa	108.5	58.5	45.7	158.6	227.0*

* based on February 1979 population estimate of 104.4/m^2.

Table 14-2 Average magnitude of individual mortalities (expressed as k-values) in the life table plots.

Mortality	Paspalum	Ryegrass	Wharepapa
k_0 (variation in natality)	-0.09	-0.66	0.06
k_1 (summer mortality)	0.18	-0.07	-0.14
k_2 (late summer mortality)	0.13	0.85**	0.13
k_3 (autumn-winter disappearance)	0.17		0.12
k_4 (winter-spring disappearance)	0.30	0.78	0.82
k_5 (delayed development)	0.12	0.00	0.03
k_6 (proportion females)*	0.22	0.30	0.16

* k_6 = 0.30 for a 1:1 sex ratio

** $k_2 + k_3$

The indices of population trend for the Wharepapa plot (Table 14-1) show a declining population in the 1975/76 and 1976/77 generations. This has been followed by a population increase in 1977/78 which is in marked contrast to the low index for the same generation in the paspalum plot. Although no life table can be constructed for the 1978/79 generation, the index of population trend based on the February 1979 estimate shown in Appendix 14-2, shows that a further population increase has occurred. The possible reasons for these population increases will be discussed later in this chapter.

(2) Average mortalities

For the purposes of constructing the life tables, the black beetle life cycle was divided into a number of successive periods (see for example Appendix 14-3). The individual mortalities (or k-values) operating within these periods, which together make up the total generation mortality, are shown in Table 14-2. Possible factors involved in these k-values are:

k_o : adult dispersal, disease, variation in the timing of sampling;

k_1 : variation in the timing of sampling, the influence of soil temperature and moisture, rainfall and predators;

k_2 : larval combat, disease;

k_3 : adult dispersal, disease, pasture composition;

k_4 : disease, pasture composition, high soil moistures;

k_5 : the rate of population development;

k_6 : variation in the sex ratio and adult female longevity.

The components of these k-values will be discussed in more detail later in this chapter.

The average magnitude of the individual mortalities calculated from the life table values (Appendices 14-3 to 14-11) are also shown in Table 14-2. The paspalum plot is characterised by a relatively small variation in the average values between mortalities when compared with the other two plots, with no individual k on average being greater than 0.30. As the black beetle population in the ryegrass plot was not sampled in March, values for k_2 and k_3 are considered together. The most striking contrasts with the paspalum plot are the relatively high $k_2 + k_3$ values and the high negative value of k_o which may indicate marked adult spring immigration into the ryegrass plot during oviposition. The Wharepapa plot has a high value for k_4, although as in the paspalum plot, the other mortalities tend to be on average, fairly low. The identification of the key factors influencing population change, and consideration of the intergeneration variation in these mortalities are discussed below.

IV ANALYSIS OF LIFE TABLES

(1) Key factor identification

The series of individual mortalities (k-values) as presented in the life tables determine the total generation mortality (K) such that

$$K = k_o + k_1 + k_2 + k_3 \ldots\ldots\ldots k_i$$

Following the methods of Varley and Gradwell, graphical correlation was used to determine which k is most closely correlated with K. This mortality is then the key factor causing population change. Although total generation mortality will vary, depending on the initial starting point of the life table, the calculation of K based on the mortalities operating in a February to February generation appears to be a valid approach for the reasons previously discussed. Due to the problems associated with the timing of the December sample to obtain an estimate of egg numbers there are considerable inaccuracies in the relative levels of k_o and k_1 between generations, i.e., as measured k_1 may include some of the k_o mortality and vice versa. To overcome this problem and to strengthen the graphical correlation, k_o and k_1 have been added together.

The correlation of individual mortalities with total generation mortality by plotting k-values against K for each generation is shown for the paspalum and ryegrass plots at Otakanini and for the Wharepapa plot in Figs. 14-2, 14-3 and 14-4 respectively.

In addition to the graphical correlation carried out to identify the key factor, the test of Podoler and Rodgers (1975) was undertaken to verify the visual test and to further investigate the relative importance of changes in each mortality to changes in the total mortality. Individual mortalities were plotted as k-values on the y-axis against total mortality to calculate the linear regression coefficient (b), with the key factor being the mortality which gives the greatest value for the slope, b. In the paspalum plot, values of each k and K were pooled from groups of three sub-

Figure 14-4 Visual correlation of k-values with K for the black beetle population in the Wharepapa plot between 1975 and 1978.

Figure 14-3 Visual correlation of k-values with K for the black beetle population in the ryegrass plot at Otakanini between 1976 and 1978.

Figure 14-2 Visual correlation of k-values with K for the black beetle population in the paspalum plot at Otakanini between 1975 and 1979.

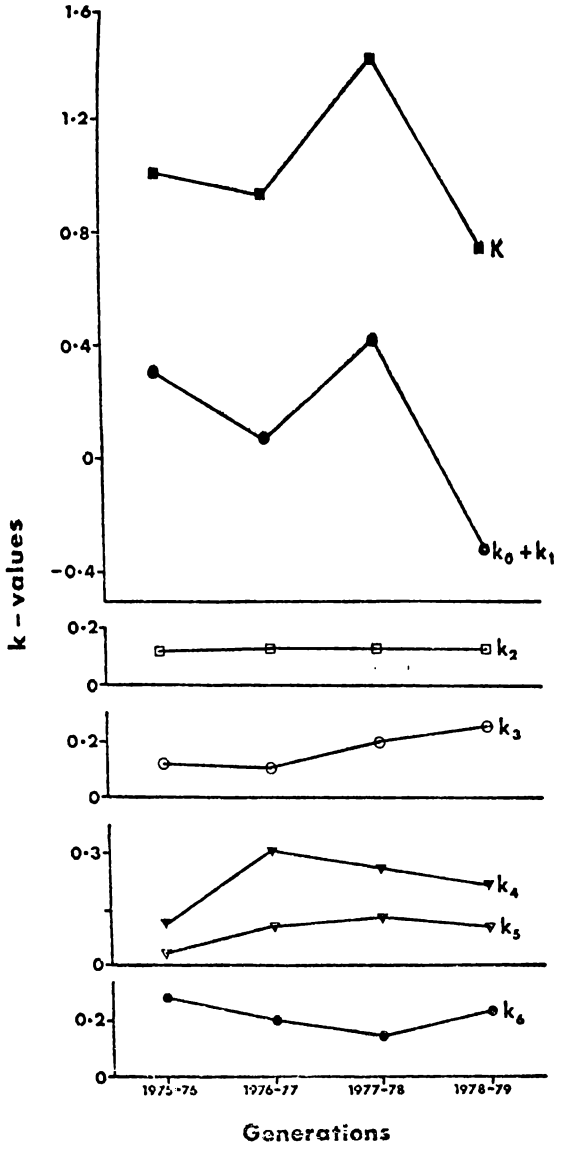


Figure 14-2

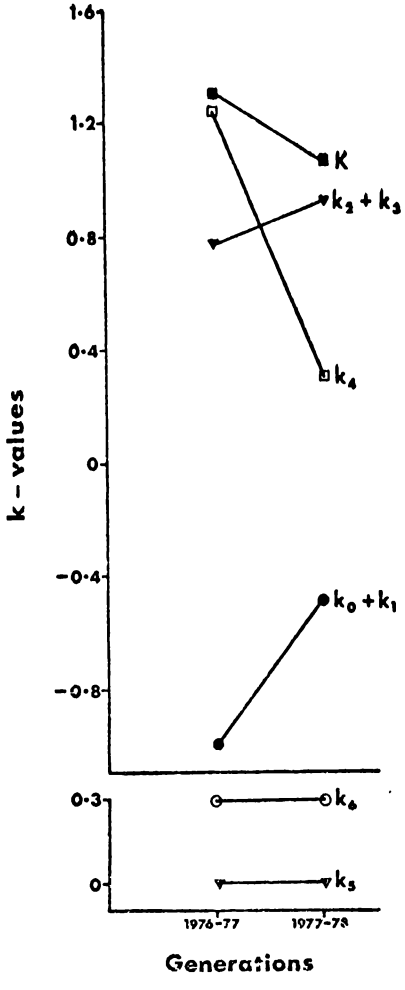


Figure 14-3

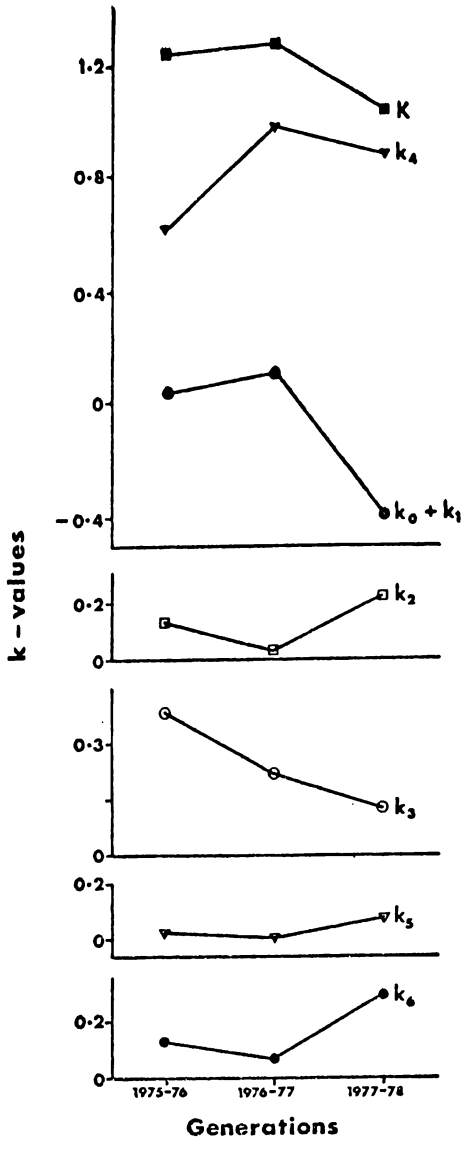


Figure 14-4

plots in each generation for the 1975/76, 1976/77 and 1977/78 generations on a February to February basis with the value for sub-plot 10 in each generation being excluded. Due to the number of zero sub-plot values in the 1976/77 and 1977/78 generations this pooling of data was necessary to strengthen the regression analysis. The data for the paspalum plot are shown in Appendix 14-12. As individual sub-plot values were lacking for some sampling occasions of the 1978/79 generation, regression analysis was only carried out on the data from the February 1975 to February 1978 period.

The large number of zero values for both log-density and k-values in sub-plots in the ryegrass plot prevented any meaningful calculation of K and slope values for the regression of individual mortalities on total mortality. In the Wharepapa plot, data from the four sub-plots sampled were pooled from each of the 1975/76, 1976/77 and 1977/78 generations (shown in Appendix 14-13), to calculate the slope values of the regressions. The pooling of k_o and k_1 was carried out for both the paspalum and Wharepapa plots for the reasons already detailed in the graphical correlation tests.

The results of the regressions of mortalities (k-values) on total generation mortality (K) for the paspalum plot and the Wharepapa plot are shown in Tables 14-3 and 14-4 respectively.

In the paspalum plot, the results of the graphical correlation (Fig. 14-2) show that changes in $k_o + k_1$ are most closely associated with changes in total generation mortality (K). This correlation is confirmed by slope values for the regressions in Table 14-3, with $k_o + k_1$ having the highest b, and following Podoler and Rodgers, changes in variation in natality and/or summer mortality are the key factors causing population change.

Table 14-3 The regression of individual mortalities (k-values) on total generation mortality (K) to identify the key factor for black beetle population change in the paspalum plot in the 1975/76, 1976/77 and 1977/78 generations.

k's	slope (b)	correlation coefficient (r)
$k_o + k_1$	0.874	0.824
k_2	0.230	0.615
k_3	-0.033	-0.075
k_4	-0.027	-0.068
k_5	-0.116	-0.381
k_6	0.073	0.412

Table 14-4 The regression of individual mortalities (k-values) on total generation mortality (K) to identify the key factor for black beetle population change in the Wharepapa plot in the 1975/76, 1976/77 and 1977/78 generations.

k's	slope (b)	correlation coefficient (r)
$k_o + k_1$	0.521	0.504
k_2	0.149	0.262
k_3	-0.115	-0.147
k_4	0.489	0.436
k_5	-0.045	-0.217
k_6	-0.001	-0.007

In the ryegrass plot there appears to be no one mortality closely associated with changes in K (Fig. 14-3), possibly due to the inherent variability of the data, the low black beetle population numbers and the fact that the correlation was only possible over two generations. The change in k_4, the winter-spring disappearance does however appear to have the greatest influence on total K.

The results of the graphical correlation of the data from the Wharepapa plot (Fig. 14-4) suggest that variation in two mortalities, $k_o + k_1$ and k_4 follow closely the changes in K. The slope values shown in Table 14-4 confirm that the test of Podoler and Rodgers suggests that there are two key factors at Wharepapa with $k_o + k_1$ only slightly more important than k_4. It is concluded that the key factors causing changes in black beetle populations appear to be $k_o + k_1$ (paspalum and Wharepapa plots) and k_4 (ryegrass and Wharepapa plots).

(2) Density relationships of mortalities

The density relationships of the black beetle mortalities in the paspalum and Wharepapa plots were investigated by plotting the k-values of the mortalities against the logarithms of the densities on which they acted following the methods of Varley and Gradwell (1960,1970). Where the slope of the regression differs significantly from b = 0, density dependence was investigated using the methods of Varley and Gradwell (1970), Luck (1971) and Benson (1973) previously detailed in Chapter 1.

To increase the number of points in the regressions, the values of k and log density from groups of three sub-plots were pooled per generation in the paspalum plot and from each of the four sub-plots per generation in the Wharepapa plot. These sub-plot values, shown in Appendices 14-12 and 14-13 were pooled from the 1975/76, 1976/77

Figure 14-5 Plots of k-values from the paspalum plot against the log densities of black beetle on which they acted for (i) k_o variation in natality; (ii) k_1 summer mortality; (iii) $k_o + k_1$ combined; (iv) k_2 late summer mortality; (v) k_3 autumn-winter disappearance; (vi) k_4 winter-spring disappearance, (vii) k_5 delayed development; (viii) k_6 proportion of females; (ix) test for density dependence of k_6, N_1 and N_2 the initial and final numbers of black beetle per m^2 respectively. Significant relationships ($P < 0.01$) are shown for k_o, $k_o + k_1$, k_2 and k_6. Black beetle numbers per m^2 from groups of 3 sub-plots were pooled per generation with sub-plot 10 excluded, for February to February generations, 1975/76, 1976/77 and 1977/78.

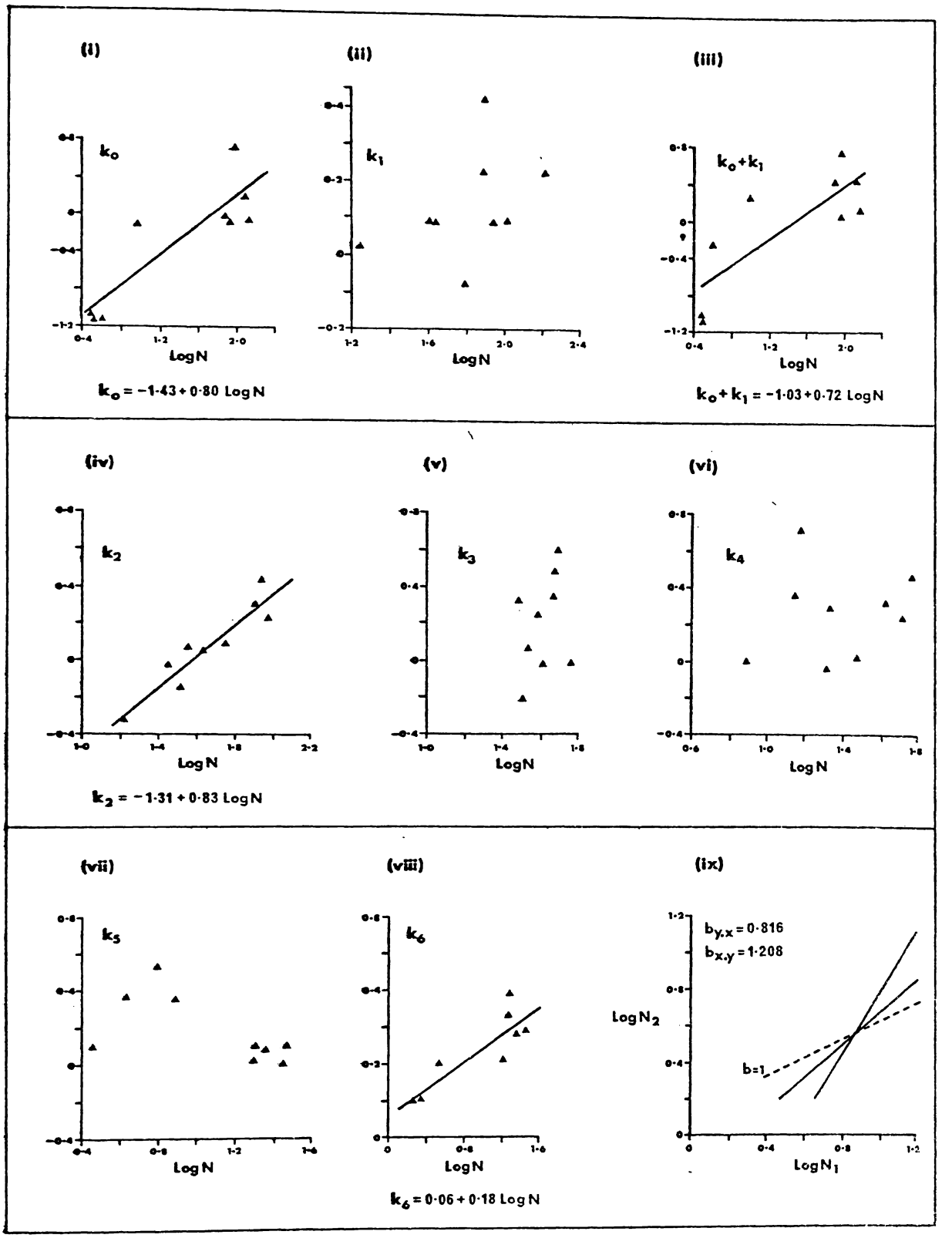

(i)
k_o
Log N
$k_o = -1{\cdot}43 + 0{\cdot}80$ Log N
(ii)
k_1
Log N
(iii)
$k_o + k_1$
Log N
$k_o + k_1 = -1{\cdot}03 + 0{\cdot}72$ Log N
(iv)
k_2
Log N
$k_2 = -1{\cdot}31 + 0{\cdot}83$ Log N
(v)
k_3
Log N
(vi)
k_4
Log N
(vii)
k_5
Log N
(viii)
k_6
Log N
$k_6 = 0{\cdot}06 + 0{\cdot}18$ Log N
(ix)
$b_{y.x} = 0{\cdot}816$
$b_{x.y} = 1{\cdot}208$
b=1
Log N_2
Log N_1

Figure 14–5

and 1977/78 generations to give 9 and 12 points for the paspalum and Wharepapa plots respectively. As no individual sub-plot values were available from the February and September 1978 sampling times in the paspalum plot, data from the 1978-79 generation paspalum life table could not be included in the regression analysis.

(a) Paspalum plot

The results of the regression of the various k_i-values on log initial number of black beetle (log N_1) and of log N_2 on log N_1 and vice versa for the paspalum plot are shown in Appendix 14-14. The slope of the regression line for $k_o + k_1$ (Fig. 14-5) differed significantly from b = 0 ($P < 0.01$) suggesting that the combined mortalities were density dependent. However, as the regression of log N February (N_2) on log Potential Natality (N_1) did not differ significantly from b = 0 ($P > 0.1$), density dependence cannot be proved. It will be shown when the possible components of the mortalities are discussed later in this chapter that one factor influencing summer mortalities (k_1) is the level of soil moisture. This influence of weather affects insects as individuals and so acts as a density independent mortality, which may suggest that at least the k_1 component of the combined $k_o + k_1$ mortality is density independent. Due however to variations in the timing of sampling in December and in the timing of peak oviposition in the spring, it would be dangerous to extrapolate too much from the December to February summer mortality data (k_1).

It is of interest that the slope of the regression of k_1 as a separate mortality against the logarithm of the December density does not differ significantly from zero ($P > 0.1$), whereas that of k_o on

potential natality differs significantly from b = 0 ($P < 0.01$) (Fig. 14-5), which suggests that k_1 may be acting in a density independent and k_o in a density dependent manner. The regression of log Potential Natality on log N December was not significant however ($P > 0.1$) and so density dependence in k_o could not be proved. The variation in natality (k_o) does not represent a mortality in the strict sense but comprises the death of reproducing females before the end of the reproductive life, variations in the fertility of the females, and the net product of migration of the female, either into or out of the plot. Further discussion of the parameters influencing k_o will be made later in the chapter.

The slope of the regression line for k_2 (Fig. 14-5) differed significantly from zero ($P < 0.001$) which suggests that the late-summer mortality was density dependent, but since both $b_{x.y}$ and $b_{y.x}$ in the test for density dependence (Appendix 14-14) did not differ significantly from b = 0 ($P > 0.2$), this cannot be proved. Examination of the life tables (Appendices 14-3 to 14-6) and of Fig. 14-2 shows that k_2 values for the entire paspalum plot were relatively constant between generations, and apparently independent of changes in population density. The density relationship of k_2 within generations was examined by plotting the data from the 10 sub-plots for each generation separately. Although no density dependence could be proved, the regression coefficient was significantly different ($P < 0.01$) from b = 0 for the 1976/77 and 1977/78 generations suggesting some degree of intra-generation density dependence in k_2 may be present.

The slopes of the regression lines for k_3, k_4 and k_5 (Fig. 14-5) did not differ significantly from b = 0 ($P > 0.2$, $P > 0.5$ and $P > 0.5$) for the three slope values respectively. It is therefore concluded from the data available that no strong density dependence of k_3, k_4 or k_5 was evident.

When the logarithm of the proportion of females (k_6) was plotted against the logarithm of numbers of spring adults (Fig. 14-5), the slope was significantly different from b = 0 ($P < 0.01$) suggesting density dependence. In the test for density dependence (Appendix 14-14), both $b_{x.y}$ and $b_{y.x}$ were found to differ significantly from b = 0 and b = 1 ($P < 0.01$) and the two lines lie on the same side of b = 1 (Fig. 14-5) proving the density dependence of k_6. To further examine the density dependence of k_6 in the paspalum plot, the values of k_6 from the 10 sub-plots sampled at each sampling occasion were plotted against log. September adults for each separate generation. In 1975/76, the slope of k_6 did not differ significantly from b = o ($P > 0.05$), although in 1976/77 and in 1977/78 the slopes did differ significantly from zero ($P < 0.01$). For each of the 1976/77 and 1977/78 generations, both $b_{x.y}$ and $b_{y.x}$ differed significantly from b = 0 and b = 1 ($P < 0.001$) and for each generation, both lines were found to lie on the same side of b = 1, thus proving density dependence in two of the three generations. In the 1976/77 and 1977/78 generations however, 50% and 30% of the sub-plots respectively had no apparent population at sampling in September which gave rise to zero values for k_6. The pooling of data from groups of three sub-plots in each generation removed the zeros, but their influence on the density relationship persists. In view of

this, the density dependence of k_6 may be a spurious result and as such should be interpreted with caution.

(b) Wharepapa plot

The slope of the regression line for $k_o + k_1$ (Fig. 14-6) did not differ significantly from b = 0 ($P > 0.1$) showing that variations in natality and summer mortality combined were not density dependent. The slopes of the regression lines for k_2 and k_4 (Fig. 14-6) were also found not to differ significantly from b = 0 ($P > 0.5$, $P > 0.1$, respectively) and so late-summer mortality and winter-spring disappearance were apparently density independent. Although the slope of k_3 (Fig. 14-6) differed significantly from b = 0 ($P < 0.05$) in the test for density dependence (Appendix 14-15), $b_{y.x}$ was not significantly different from b = 1 ($P > 0.5$) and so the density dependence of autumn-winter disappearance was not proved. The data does suggest that some density relationship is present, with higher k_3-values and hence disappearance over the autumn-winter period occurring at higher densities. This may reflect greater autumn dispersal of adults in seasons when climatic conditions favour high population numbers. This factor will be examined further later in this chapter.

As most of the sub-plot values of k_5 in each of the three generations were zero (Appendix 14-13), no analyses of this mortality were carried out. It is apparent that in contrast to the paspalum plot, virtually no pre-adult stages survived the winter-spring period, which may be the result of the very wet winter soil conditions noted at Wharepapa, with water frequently lying on the soil surface due to the effect of poor drainage on the site.

Figure 14–6 Plots of k-values from the Wharepapa plot against the log densities of black beetle on which they acted for (i) $k_o + k_1$ combined, variation in natality + summer mortality; (ii) k_2 late summer mortality; (iii) k_3 autumn-winter disappearance; (iv) k_4 winter-spring disappearance; (v) k_6 proportion of females; (vi) test for density dependence of k_6, N_1 and N_2 are the initial and final numbers of black beetle per m^2 respectively. Significant relationships ($P < 0.01$) are shown for k_3 and k_6. Black beetle numbers per m^2 from 4 sub-plots per generation for February to February generations 1975/76, 1976/77, and 1977/78.

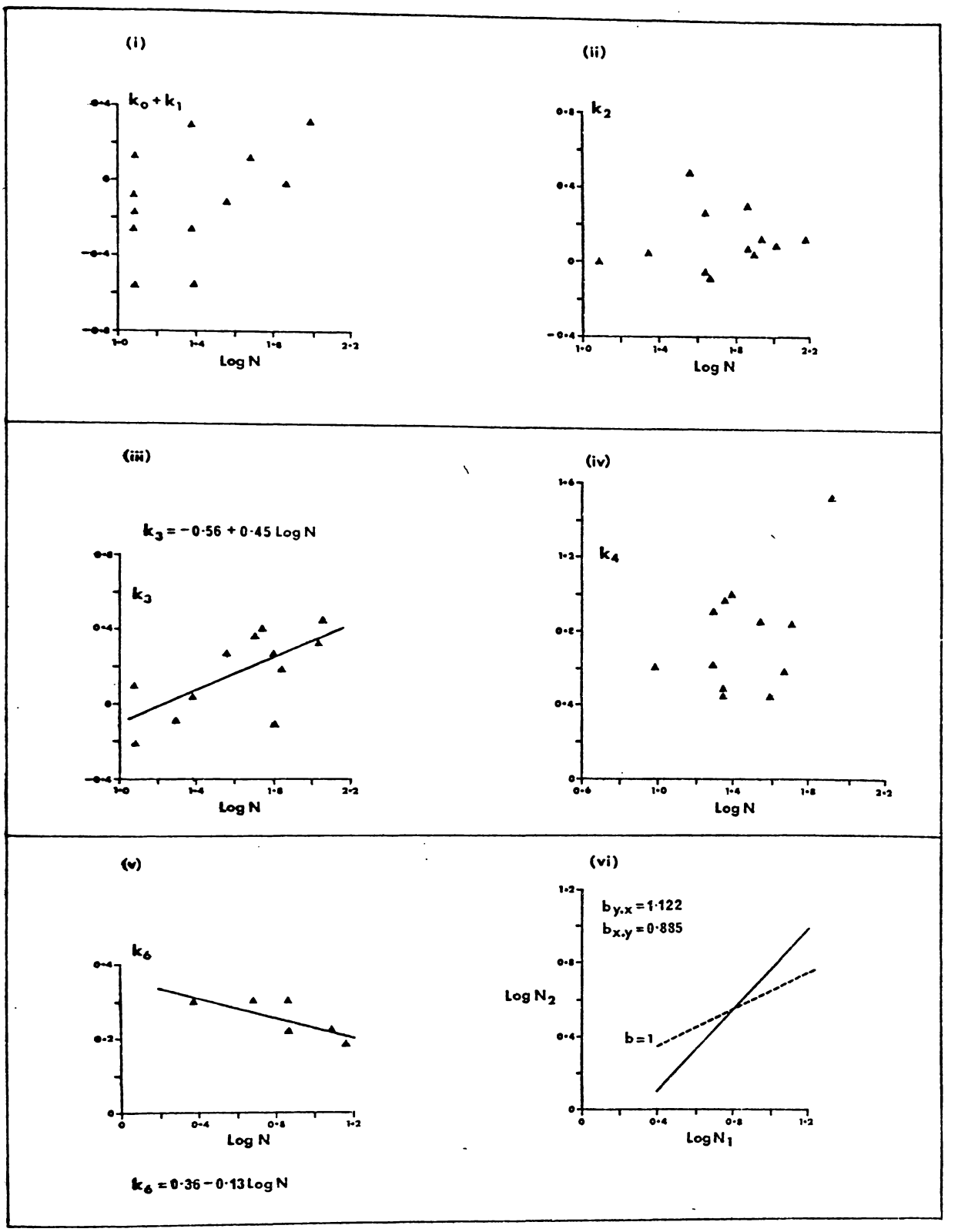

(i)
$k_0 + k_1$
Log N
(ii)
k_2
Log N
(iii)
$k_3 = -0.56 + 0.45 \log N$
k_3
Log N
(iv)
k_4
Log N
(v)
k_6
Log N
$k_6 = 0.36 - 0.13 \log N$
(vi)
$b_{y.x} = 1.122$
$b_{x.y} = 0.885$
b = 1
$\log N_2$
$\log N_1$

Figure 14-6

The slope of the regression line for k_6 (Fig. 14-6) was significantly different from b = 0 ($P < 0.001$) and had a negative value suggesting an inverse density dependence. In the test for density dependence (Appendix 14-15), both $b_{x.y}$ and $b_{y.x}$ differed significantly from b = 0 and b = 1 ($P < 0.01$), and as $b_{x.y}$ and $b_{y.x}$ were the same line, so lying on the same side of b = 1 (Fig. 14-6), inverse density dependence is proved. As k_6 provides a measure on a log scale of the proportion of females in the population, a low value of k_6 indicates a greater ratio of females to males than a high k_6-value.

The inversely density dependent relationship shown for k_6 means that as adult population density decreases, the proportion of females increases. This relationship is not shown in the data in Appendix 14-13 largely due to the need to obtain an estimated value for the proportion of females at low sub-plot densities. In the 1976/77 and 1977/78 generations where the individual sub-plots contained only one or two adults of the same sex, the sex ratio was estimated as 1:1 for the purposes of providing data for the regression analysis. Due to this, Appendix 14-13 suggests that at low adult densities in September, the proportion of females decreases.

Examination of the 1975/76 and 1976/77 Wharepapa life tables (Appendices 14-9 and 14-10) shows that as the adult population in September decreased from around $9/m^2$ to $4/m^2$, the male to female sex ratio changed from 1:3 to 1:6 which supports the hypothesis of inverse density dependence of k_6. However, in the 1977/78 generation no adult females were recovered in the September population sample,

necessitating an estimated sex ratio of 1:1 for the purposes of the regression calculations. No definite conclusions are therefore able to be drawn from available data on the density relationship of k_6.

(3) Influence of mortalities on populations

Considerable care must be exercised in interpreting the contribution of the various mortalities to the generation mortality in these population studies. Problems associated with sampling were discussed in the previous chapter. These, coupled with the significant differences apparent in the rates of population development between generations and plots discussed in the next section of this chapter, to some extent prevent accurate estimates of the mortalities operating over discrete time periods, and create problems in the comparison of these mortalities between generations and between pasture plots. In addition only a small number of generations were studied at each site. In spite of these deficiencies in the data, it is possible to make some general conclusions on the interpretation of the mortality data.

The important aspects of each mortality to consider are the magnitude, variability and density relationships. The first two are of importance in determining population trend with a highly variable mortality being potentially important in influencing population change and a relatively stable one being unlikely to be a key factor. A density dependent mortality may be potentially important in population regulation.

(a) Paspalum plot

Both variation in natality (k_0) and summer mortality (k_1) were highly variable over the four generations presented in the life tables and showed considerable fluctuation of magnitude. These two mortalities combined were the key factor determining population trend and so influencing population change from generation to generation. Analysis of the density relationships of k_0 and k_1 separately (Fig. 14-5 and Appendix 14-14), suggests that k_1 acted in a density independent manner and so is unlikely to have been important in population regulation.

In contrast, k_0 may have been density dependent (Fig. 14-5 and Appendix 14-14), and therefore potentially important in population regulation. This mortality, which possibly represents the effects of adult dispersal in spring and the influence of factors such as disease or adult female fecundity and longevity, has the potential to be a major determinant of population change. This apparently occurred in the 1978/79 generation when k_0 was -0.44 (presumably reflecting either spring immigration of adults or increased fecundity, and the index of population trend was 173%. It is not known whether either k_0 acting on its own or in concert with k_1 as a combined mortality can regulate populations in the sense of returning them to an equilibrium density following any departure from this level. As the slope of k_0 against log density did not closely approach b = 1, during the study period, it was not perfectly regulatory. The actual role of k_0 could only be determined from further life table studies plus detailed knowledge of the components involved in this mortality.

The mortalities, k_o and k_1 are of major importance in the February to February population budget, as their action occurs at the end of the generation. They therefore have a major influence in determining the number of larvae in late summer which is the period when economic damage to pastures takes place and so any insight into their magnitude, variability and density dependence will have considerable predictive value.

Late summer mortality between February and March (k_2) was very constant over the four generations and had a relatively low magnitude which explains its lack of influence on population change. This mortality may have been density dependent and so could be potentially significant in regulating population numbers.

Both k_3, autumn-winter disappearance and k_4, winter-spring disappearance were variable in the 1976/77, 1977/78 and 1978/79 generations and their magnitude made one or both, major mortalities (Fig. 14-2, Appendices 14-4, 14-5, 14-6). Both of these mortalities operate relatively early in the generation, and during a period when the major proportion of the population is in the mobile adult stage which is readily able to avoid localised (i.e. within plot) unfavourable conditions of soil moistures or diet. Disappearance over this period is therefore unlikely to have been of major importance in influencing population trend in the paspalum plot where mass dispersal of adults out of the plot, which has been shown to occur in other areas (Watson, pers.comm.) does not appear to have taken place, or alternatively, has been masked by migration into the plot. The apparent density independence of k_3 and k_4 also suggests that these mortalities were not important in population

regulation in the paspalum plot.

For the purposes of presenting the population budgets, it has been assumed that the pre-adult stages remaining in the population in September will die before reaching the ovipositing adult stage. This appears a reasonable assumption as contrary to the evidence in South Africa where adults arising from these stages may oviposit (Watson, pers.comm.), a similar situation has not been noted under New Zealand conditions. The measure of delayed development (k_5) which is the mortality due to the death of these pre-adult stages in the spring, was relatively constant over the four generations, with the exception of the 1975/76 generation, had a low order of magnitude, and appeared to be density independent. For these reasons, k_5 had little effect on either population change or population regulation in the paspalum plot.

The proportion of females (k_6) appeared to be density dependent in the paspalum plot, suggesting that the proportion of females in the adult population increased as density decreased. Further examination of the density relationship of k_6 in individual generations suggested however, that this was a spurious result largely arising from the large number of sub-plot zero population values in the 1976/77 and 1977/78 generations. The individual life tables do show that there was a higher proportion of females at the lower adult densities of the 1976/77 and 1977/78 generations relative to the 1975/76 generation, although the proportion declined again in the 1978/79 generation. k_6 has a relatively high magnitude and is a significant contributor to total generation mortality, although it should be noted that a 1:1 sex ratio has a 'base-line' level of

$k_6 = 0.30$. However, the lack of variability suggests that this mortality, considered on its own, is not of major importance in determining population change or in regulating populations relative to k_o or k_1.

The population studies in the paspalum plot are unable to identify conclusively the factors responsible for population regulation (if any), but they suggest possible density dependence in k_o, k_2 and k_6 which therefore could be potentially significant in population regulation. Further life tables compiled over a greater range of densities and seasonal conditions would be necessary to elucidate this, but it can be concluded that variation in k_o and k_1 combined was the key factor observed in this study.

(b) Ryegrass plot

As it was possible to only compile two life tables for the black beetle population in the ryegrass plot, it is difficult to draw many definite conclusions on the importance of the mortalities to population change and regulation. Also, the relative importance of k_2 and k_3 is obscured by the need to combine the two mortalities due to the absence of a March population estimate. In contrast to the paspalum plot, the mortality over the February to September period comprising the combined effects of k_2, k_3 and k_4 was extremely high, and the major contributor to generation mortality. Fig. 14-3 shows that k_4 was more closely correlated with K than $k_2 + k_3$ which acts in the opposite direction. If these three mortalities are combined there is a good visual correlation with K over the two generations.

The much greater population decrease over the February to June period in the ryegrass plot compared with the paspalum was demonstrated

in Chapter 10. This showed remarkably good correlation with the percentage population decrease recorded between February and June in 1976 and 1977 for the paspalum and ryegrass plots shown in Table 14-5. The decrease over this period is apparently of major importance in determining population trend in the ryegrass plot. All three mortalities were high and exhibited considerable variation over the two generations. The high negative value of k_o in the 1976/77 generation compensated to some extent for the action of these mortalities. In spite of the very low level of precision in the September population estimate, the data suggest that a significant level of adult migration into the ryegrass plot may have taken place over the spring oviposition period.

The mortalities represented by k_5, k_6 and k_1 were not highly variable in nature, and on the basis of this limited evidence do not appear to have been of importance in determining population changes. On the basis of only two life tables there can be no conclusions drawn on likely causes of population regulation, but it does appear that mortality and disappearance during the autumn and winter-spring periods (k_2, k_3 and k_4) were important in population change. Possible components of these mortalities will be discussed in the next section of this chapter.

(c) Wharepapa plot

The mortalities represented by k_o and k_1 were both large and highly variable over the three generations in the Wharepapa plot. As has been shown already, these plus k_4 were the key factors most closely associated with total generation mortality and so determine population change.

Table 14-5 Black beetle population decreases in the paspalum and ryegrass pasture plots at Otakanini between February and June.

	% decrease in black beetle population numbers between February and June	
Year	Paspalum	Ryegrass
1976	41	83
1977	53	88

The negative values for k_1 (Appendices 14-9 to 14-11) are evidence that the timing of the December sample was apparently too far astray to permit any meaningful analysis of k_o and k_1 separately. Analysis of the combined data however, shows $k_o + k_1$ to be a key factor, and also density independent. In view of this apparent density independence, the potential for $k_o + k_1$ regulating populations in the Wharepapa plot is low.

The greatest mortality over the three generations was k_4, disappearance over the winter-spring period. This is similar to the situation in the ryegrass plot, but in marked contrast to the paspalum plot where k_4 was much lower and relatively unimportant in determination of population trend. High winter soil moisture levels may have contributed to this mortality at Wharepapa. Although it was important in determining population change, this winter-spring disappearance appeared to be density independent over the density range found in the three generations monitored at Wharepapa, and so had no influence on population regulation.

Apart from the autumn-winter period in the 1975/76 generation, k_3 had a low order of magnitude and had little effect on population trend. There was a suggestion of density dependence in k_3 which may therefore have importance in population regulation. The population in the Wharepapa plot contained an insignificant proportion in the pre-adult stage in the early spring period. Delayed development (k_5) was therefore low and showed little variability, and so had no significant influence on population trend. In contrast, the proportion of the population in pre-adult stages in the paspalum plot in September was considerably greater.

Table 14-6 Summary of the influence of mortalities on black beetle populations in the paspalum, ryegrass and Wharepapa plots.

Mortality	Paspalum	Ryegrass	Wharepapa
$k_0 + k_1$	Density dependent?* (key factor)		Density independent (key factor)
k_2	Density dependent?		Density independent
k_3	Density independent		Density dependent?
k_4	Density independent	(key factor)	Density independent (key factor)
k_5	Density independent		Density independent
k_6	Density dependent?		Inversely density dependent?

* Density dependence appears to have arisen from k_0 with k_1 density independent.

The mortality due to the proportion of females in the population (k_6) was shown to be related to density in the Wharepapa plot, but doubt surrounds the reality of this finding as discussed in the previous section. It is apparent that the variability and magnitude of k_6 were not great in the three generations and consequently this mortality was of minor significance relative to $k_o + k_1$ and k_4 in determining population trend.

The conclusions which can be drawn from these studies concerning the influence of the various mortalities on black beetle populations are summarised in Table 14-6.

V COMPONENTS OF POPULATION MORTALITIES

In this section a number of factors which are considered to influence population numbers will be examined in an attempt to provide some explanation for the mortalities discussed in the previous part of this chapter. Emphasis will be given to those mortalities which were shown to be key factors influencing population change. Factors examined include the influence of soil temperature and moisture, rainfall, the rate of population development and dispersal, pathogens, predators and parasites, the influence of changes in pasture composition, and larval combat.

(1) Soil temperature and moisture

(a) Otakanini

Soil temperatures were monitored in the paspalum, ryegrass and ryegrass/white clover plots as described in Chapter 13. As no temperature recorders were available to monitor soil temperature in the ryegrass plots in the 1975/76 season, a comparison is only possible between the three plots in the 1976/77 season. It is likely however that the relative temperature patterns of this season can be extrapolated to cover the situation in the 1975/76 season, and other seasons, given the same pasture composition and system of pasture management.

The temperature patterns in Table 14-7 show higher soil temperatures in the ryegrass and ryegrass/white clover plots than in the paspalum over the critical period of oviposition, and egg to larval development between October and February. As was shown in the previous chapter, oviposition can commence in September. The importance of temperature on egg hatching and viability and on larval feeding and growth was demonstrated in Section 2, and showed that little development and activity occurred below 15 ^{o}C. The much greater daily periods when soil temperature was above 20 ^{o}C in the ryegrass and ryegrass/white clover pasture plots suggests that the rate of population development will be much faster in these plots. As the major proportion of the population has been shown to be present in the top 3 cm of the soil profile, then these temperature measurements taken at a depth of 2 cm accurately represent the temperature pattern the black beetle populations experienced over the 1976/77 season.

Table 14-7 Temperatures recorded at a depth of 2cm in the soil, in the paspalum, ryegrass and ryegrass/white clover plots at the Otakanini Research Area between October 1976 and February 1977.

Month	Plot	Hrs/day > 15 °C	Hrs/day > 20 °C	Mean Max. Temp. °C	Mean Min. Temp. °C	Monthly Mean Temperature °C
October 1976	pasp.	1.5	0	15.0	8.6	11.8
	rye	11.6	0.9	18.3	12.2	15.3
	rye/wc	7.7	0	15.7	12.7	14.2
November 1976	pasp.	4.2	0.3	15.6	9.9	12.8
	rye	17.2	2.8	19.7	13.9	16.8
	rye/wc	18.2	3.9	20.6	13.9	17.3
December 1976	pasp.	11.6	1.4	18.5	13.0	15.7
	rye	23.6	7.9	22.0	16.3	19.2
	rye/wc	23.6	6.9	21.8	16.6	19.2
January 1977	pasp.	21.0	4.3	21.6	15.1	18.3
	rye	24.0	15.3	25.1	17.7	21.4
	rye/wc	24.0	15.0	26.3	17.3	21.8
February 1977	pasp.	22.4	7.3	22.4	15.4	18.9
	rye	24.0	14.8	25.7	18.2	22.0
	rye/wc	24.0	10.2	31.1	18.2	24.6

Due to the distance of the research sites from Hamilton, soil moisture measurements were taken too infrequently to permit correlations between soil moisture and rainfall. Nevertheless, comparisons of monthly mean moisture levels in the paspalum, ryegrass and ryegrass/white clover plots can be made, and are shown in Table 14-8.

Soil moisture levels were consistently higher in the paspalum plot in both the 1975/76 and 1976/77 seasons. This is probably due to the much greater degree of herbage cover over the soil surface, which prevented evaporation of moisture. Reduced evaporation from the soil surface was apparently of greater significance than higher levels of transpiration from the dense cover of foliage in the paspalum plot. These temperature and moisture differences between adjacent plots were recorded on identical aspects and soil type.

The 1976/77 results show good correlation with the soil temperature data. Conditions were cooler and moister in the paspalum plot compared with the ryegrass pastures. The influence of this on population rate of development will be shown later.

These data provide information on the influence of soil moisture and temperature on summer mortality (k_1) and late summer mortality (k_2). The temperature patterns over the October 1976 to February 1977 period indicate that soil temperatures were lower in the paspalum plot over the oviposition period relative to the ryegrass and ryegrass/white clover plots. This may have resulted in a later commencement of oviposition, a longer period between oviposition and egg hatching and so a greater chance of egg mortality in the paspalum plot. In addition, the chances of under-estimating the black beetle

Table 14-8 Mean monthly soil moisture levels between October and March in the paspalum, ryegrass and ryegrass/white clover plots at Otakanini.

	% Soil Moisture (0 - 9cm depth) in each plot					
	Paspalum		Ryegrass		Ryegrass/White clover	
Month	1975/76	1976/77	1975/76	1976/77	1975/76	1976/77
October	43	53	37	43	37	44
November	49	51	36	32	36	41
December	38	46	20	33	22	32
January	38	39	25	19	27	18
February	36	26	25	22	24	20
March	28	31	18	20	19	21

population in December when using an arbitrary sampling date may have been greater in the ryegrass and ryegrass/white clover plots and so would tend to cause an under-estimate of the magnitude of k_1 in comparison with the paspalum plot.

Soil moisture determinations were made too infrequently to determine the relationship between soil moisture and egg and early instar larval mortality (k_1) in separate generations except by inference. The results of soil moisture investigations reported in Chapter 4 suggest that while the black beetle egg stage is relatively tolerant of high soil moistures, first instar larvae are much more susceptible. By inference from rainfall data it is possible to suggest the contribution of soil moisture to summer mortality in the paspalum plot.

Reliable rainfall records are available from Otakanini commencing in November 1975, with the installation of a tipping bucket, automatic rainfall recorder. Rainfall over the December, January and February periods from 1975 to 1979 are shown in Table 14-9.

Rainfall in January was abnormally high in 1976 relative to the other three years for which rainfall records are available. Almost all of this January 1976 total was recorded over seven days with the pattern shown in Table 14-10.

Between 9 and 15 January inclusive, 204.5 mm of the total January rainfall of 211.5 mm was recorded. Soil moisture levels were likely to be saturated over this period, so providing unfavourable conditions for the survival of small black beetle larvae. It is interesting to note that summer mortality was high in the paspalum plot in this generation ($k_1 = 0.27$). As shown previously in

Table 14-9 Monthly rainfall in mm during December, January and February, 1975 to 1979, at the Otakanini Research Area

	Rainfall in mm in each Period			
Month	1975/76	1976/77	1977/78	1978/79
December	32	81	102	67
January	212	48	35	6
February	20	35	17	123

Table 14-10 Pattern of rainfall in January 1976, recorded at the Otakanini Research Area.

Date	Rainfall ≥ 1.0mm
9 January	13.5
10 January	16.0
11 January	5.5
12 January	51.5
13 January	101.5
14 January	4.5
15 January	12.0
16 January	2.5
24 January	1.0
28 January	1.5
31 January	2.0

Table 14-8, soil moisture levels also tended to be highest in the paspalum plot. This coupled with the lower soil temperatures in the paspalum (Table 14-7) may explain why the value for k_1 between December 1975 and February 1976 was only 0.01 in the ryegrass plot* compared with 0.27 in the paspalum plot. However, variation between the plots in stage of development at sampling in December could also influence this comparison. The absence of a January sample prevents further clarification of this point.

In contrast, k_1 had values of 0.07 and 0.13 in the paspalum plot in the 1976/77 and 1978/79 generations when rainfall was considerably lower over the December to February period. In 1977/78 k_1 was again 0.27, although this was calculated from a February population estimate based on the March sample assuming a mean value of k_2. Considerable rainfall was recorded in December 1977, but as much of this fell before the December population estimate was made, rainfall and associated high soil moisture levels are not likely to have had a major influence on the magnitude of k_1. Some other unknown mortality, present in the overall summer mortality, must have been present, or alternatively, the estimated value of the February 1978 population is lower than it actually was. In view of this anomaly in the k_1-value for 1977/78, no definite conclusions can be drawn on the influence of soil moisture on k_1 in the paspalum plot.

High summer soil temperatures, sufficient to cause larval mortality could contribute to both k_1 (between December and February) and k_2 (between February and March). Laboratory studies of the

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* Population monitoring commenced in the ryegrass plot in December 1975 although the life tables for this plot commence from February 1976.

effect of high soil temperatures on larval survival described in Section 2, showed that although some second instar larval mortality occurred at temperatures of 35 ^{o}C and above when larvae were exposed for periods of four hours duration on four successive days, no third instar mortality occurred below 40 ^{o}C. In three seasons from 1975–1978 in the paspalum plot and two seasons from 1976–1978 in the ryegrass and ryegrass/white clover plots, summer soil temperatures were observed to peak in February. The typical temperature pattern between October and February is illustrated by Table 14–7. The automatic temperature recorders showed the temperature never exceeded 30 ^{o}C in the paspalum plot, but frequently did in the ryegrass plots, particularly when summer drought had caused pasture senescence.

During a drought period in February 1978, soil temperatures were recorded, using a standard mercury column thermometer, from the paspalum and ryegrass plots at three depths, at 3.00 pm when peak temperatures occurred. The results are shown in Table 14–11. Soil moisture levels were determined gravimetrically from samples taken at the same time and the results are shown in Table 14–12.

As shown previously (Table 14–7), soil temperatures were lower and soil moistures higher in the paspalum plot, than the ryegrass plot. Temperatures did not exceed 30 ^{o}C in the paspalum, but even under the dry ryegrass plants where soil was covered to some extent, temperatures reached 38 ^{o}C in the top 2 cm. Under bare soil in the ryegrass paddock, the temperature of over 40 ^{o}C near the soil surface is unlikely to influence population survival as feeding larvae are commonly found under the crowns. It was shown in Chapter 13 that a lower proportion of black beetle larvae, pupae and teneral adults was found in the top 3 cm of the soil profile in the ryegrass plot i-

Table 14-11 Soil temperatures ($^{\circ}C$) at three depths at 3.00 pm on 9 February 1978 in the paspalum and ryegrass plots at the Otakanini Research Area.

	Soil Temperature, $^{\circ}C$		
	Paspalum	Ryegrass	
Depth		Bare Soil	Under stubble cover
2 cm	26.8	41.5	38.5
4 cm	25.5	35.0	33.0
6 cm	24.5	31.5	29.0

Table 14-12 % Soil Moisture (0 - 9cm depth) on 9 February 1978 in the paspalum and ryegrass plots at the Otakanini Research Area.

	% Soil Moisture	
Depth	Paspalum	Ryegrass
0 - 3 cm	20.4	7.1
3 - 6 cm	26.8	13.2
6 - 9 cm	27.1	14.8

February compared with the paspalum (Tables 13-5,13-6). It is possible that this could be induced by the much higher soil temperatures encountered in the ryegrass.

No occasion was found in the temperature measurement data where temperatures of over 40 ^{o}C were maintained for several hours over consecutive days at 2 cm depth in the ryegrass and ryegrass/white clover plots. The overlap of developmental stages in these two plots was not as apparent as in the paspalum, and virtually no larvae other than the third instar stage were found in February in contrast to the situation in paspalum where first and second instar larvae were common in February. Accordingly, it is unlikely that mortality caused by high soil temperatures would be of any significance to the k_1 and k_2 mortalities in the ryegrass and ryegrass/white clover plots as larvae in these plots would be in the late second and third instars which are more tolerant of high soil temperatures. Although the early larval instars comprised a greater proportion of the population in the paspalum plot, the much lower soil temperatures recorded suggest that little of the k_1 and k_2 mortality in this plot could be ascribed to high soil temperatures over the study period. It would be dangerous to extrapolate this conclusion outside the study area where a different situation may exist.

(b) Wharepapa

The role of soil temperatures in the k_1 and k_2 mortalities at Wharepapa is unknown as no measurements were carried out in this plot. As a dense foliage cover was maintained throughout the summer period it is likely that soil temperatures would follow the same general pattern as in the paspalum plot, with temperature being lower than in

ryegrass and ryegrass/white clover pasture on a comparable site. Mortality due to high summer soil temperatures would therefore not be a major contributor to k_1 and k_2.

Although no soil moisture measurements were made at Wharepapa, the rainfall data and water balance analysis from the nearby Woodhill forest permit some extrapolation of soil moisture levels at Wharepapa. There is therefore justification for examining rainfall patterns and drawing speculative conclusions on the influence of soil moisture on k_1.

Estimates of the black beetle populations monitored at the various sampling times in this study from 1975 onwards were presented for the Wharepapa site in Appendix 14-2. It is necessary in the discussion of rainfall and population trend to examine the 1974/75 and 1975/76 survivorship curves between December and February. These are presented in Fig. 14-7.

Population numbers did not differ significantly between December and January in the 1974/75 generation, in contrast to a 60% decrease over the same period in the 1975/76 generation. Almost 70% of the black beetle population was in the egg stage at the December 1975 sampling occasion compared with only 29% the previous year. For this reason, much of the black beetle population is likely to have been in the first instar larval stage (sensitive to high soil moisture levels), over the period December 1975 to January 1976.

Monthly rainfall in January 1976 was exceptionally high as shown in Table 14-13. The December and January sampling times in the two generations were virtually identical. Rainfall over the two sampling intervals is compared with the 1973/74 and 1976/77 periods in Table 14-14.

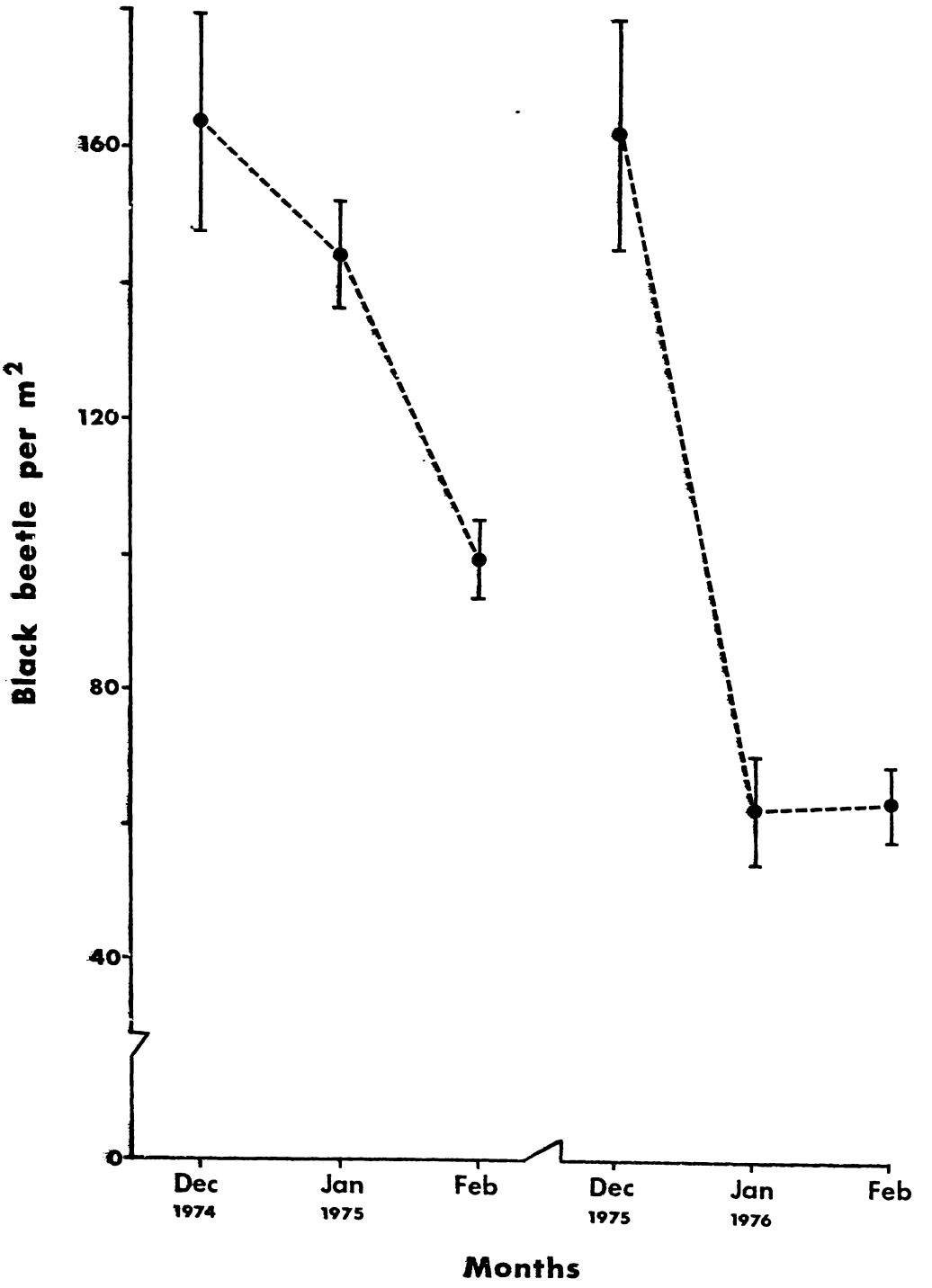


Figure 14-7 Survivorship curves of the black beetle population in the Wharepapa plot between December and February in two generations. (Mean number of black beetle per m^2 $\pm$ standard error of the mean).

Table 14-13 The monthly rainfall over December, January and February 1975/76 compared with that of six other years and the 1941 - 1970, 30 year average at Woodhill State Forest.

Month	Rainfall in mm in each Period								
	1941-70 (average)	1970-71	1971-72	1972-73	1973-74	1974-75	1975-76	1976-77	1977-78
December	86	47	149	44	72	52	33	104	112.3
January	71	47	34	49	8	28	175	64	47.2
February	91	119	37	5	23	32	26	44	48.1

Table 14-14 Rainfall at Woodhill State Forest between the December and January black beetle population sampling times in 1974/75 and 1975/76 compared with that over the same period in 1973/74 and 1976/77

Period	Rainfall in mm
18/12/73 - 22/1/74	64.6
*18/12/74 - *22/1/75	30.0
*17/12/75 - *20/1/76	195.7
18/12/76 - 20/1/77	119.4

* The sampling times of the December and January population estimates shown in the generation survival curves in Figure 14-7.

Table 14-15 Maximum daily rainfall and number of days with > 1.0 mm of rain in January at Woodhill State Forest between 1970 and 1976.

	Year						
	1970	1971	1972	1973	1974	1975	1976
Maximum daily rainfall in January (mm)	36	19	11	18	8	7	76
Number of rain-days > 1.0 mm	7	5	6	7	1	7	11

Table 14-16 Water balance for the month of January at the Woodhill State Forest.

Year	RO	NR	DE	ND
1948-70 avg.	2.5	0.2	67.5	16.6
1971	0	0	92	22
1972	9	2	40	10
1973	0	0	90	22
1974	0	0	111	26
1975	0	0	111	28
1976	58	4	31	7

RO = Runoff in mm

DE = Water deficit

NR = number of days in which runoff occurred

ND = number of days of deficit

The data reveal the much higher rainfall over the population sampling interval in 1975/76 compared with the other periods, and as shown in Table 14-13, most of this fell during January 1976. Data are available from the Woodhill forest showing the pattern of precipitation in January. The maximum daily rainfall in January 1976 compared with that between 1970 and 1975 and the number of rain days are shown in Table 14-15.

The very high rainfall of 76 mm over the 24 hour period commencing 9 am, 13 January, and the large number of rain days in January 1976, suggest that the soil at Wharepapa may have been saturated for a considerable period. Coulter (1973) suggested a simple method of water balance analysis based on daily rainfall data, actual evapotranspiration and an arbitrary soil moisture capacity, which has had widespread adoption. The amount that available water (soil moisture plus rainfall) is unable to meet the average monthly potential evapotranspiration rate (PE), is calculated as water deficiency (DE) in mm. The period when soil moisture is exhausted, i.e., when there is a water deficiency, is termed days of soil dryness (ND). Each day's rainfall is allocated to the day's water need (PE) and any remainder will replace soil moisture and then provide a surplus for runoff (RO). The number of days in which runoff occurred is NR.

The monthly water balance data for Woodhill Forest using a soil moisture capacity of 75 mm was provided by the N.Z. Meteorological Service and is shown in Table 14-16.

Table 14-16 reveals the abnormally high runoff and the low number of days with a water deficit in January 1976, revealing that the soil moisture would have been at or greater than field capacity

on at least four days, and very wet the rest of the month. The only other years in which runoff occurred in January between 1948 and 1976, were 1961 (RO = 49 mm), 1965 (RO = 8 mm) and 1972 (RO = 9 mm).

This evidence shows clearly that soil moisture levels were abnormally high in the Wharepapa plot in January 1976. The values of k_1 in the 1974/75 and 1975/76 generations were 0.01 and 0.41 respectively. It is possible that first instar larval mortality induced by high soil moisture levels is responsible for a major portion of the 1975/76 summer mortality. This shows close similarities with the pattern of k_1 mortality in the paspalum plot. It is therefore reasonable to conclude that high rainfall and soil moisture made a significant contribution to k_1 and hence to population change in the paspalum and Wharepapa plots in the 1975-76 generation. As the December population estimates in the 1976/77 and 1977/78 generations at Wharepapa appear to have under-estimated the actual egg and early larval populations it is not possible to determine the influence of soil moisture on k_1 for these generations.

(2) Rate of population development

The differences in the physical soil environment shown to exist between pasture plots would be expected to have an influence on the rates of population development. Any variation in population development could affect the magnitude of individual mortalities. A comparison of the proportion of the total population in the various insect developmental stages at any sampling time, can be made between the pasture plots. It is

convenient to express the level of population development as a ranking index (R_i). Calculation of R_i was made using the formula:

$$R_i = \frac{\sum(N_E + N_{L1} \times 2 + N_{L2} \times 3 + N_{L3} \times 4 + N_{pp} \times 5 + N_{pu} \times 6 + N_{TA} \times 7 + N_A \times 8}{N}$$

where N_E = number of eggs, NL_1 = number of first instar larvae, N_{L2} = number of second instar larvae, N_{L3} = number of third instar larvae, N_{pp} = number of prepupae, N_{pu} = number of pupae, N_{TA} = number of teneral adults, N_A = number of adults.

N = total number of individuals = $N_E + N_{L1} + N_{L2} + \ldots + N_A$.

The ranking of population development (R_i) in each of the paspalum, ryegrass, ryegrass/white clover and Wharepapa plots where population sampling was carried out is shown in Appendix 14-16. The population development data indicate that development is faster in ryegrass pasture than in paspalum as shown in Table 14-17.

In December 1975 the population was less advanced in the paspalum plot than in the other two plots. Numbers in the egg stage comprised 52% of the total population in the paspalum compared with 29% and 31% in the ryegrass and ryegrass/white clover plots respectively.

Summer mortality (k_1) between December 1975 and February 1976 had a value of 0.27 in the paspalum plot compared with 0.05 in the ryegrass plot. This could be explained if further mortality between eggs and early instar larvae occurred in the paspalum plot after the December sample, whereas much of the egg to early larval

Table 14-17 The level of population development expressed as the mean ranking index (R_i) for the paspalum, ryegrass and ryegrass/white clover plots at Otakanini.

Month	Year	Mean R_i* ± standard error in each plot		
		Paspalum	Ryegrass/white clover	Ryegrass
December	1975	1.47 ± 0.05	1.72 ± 0.05	1.71 ± 0.08
	1976	1.61 ± 0.20	1.33 ± 0.31	1.49 ± 0.14
February	1976	3.90 ± 0.29	3.93 ± 0.32	4.61 ± 0.29
	1977	3.70 ± 0.12	3.92 ± 0.32	5.38 ± 0.50
June	1976	6.98 ± 0.35	7.37 ± 0.24	7.29 ± 0.52
	1977	6.39 ± 0.36	6.29 ± 0.80	6.75 ± 0.23

* Mean R_i calculated from R_i values for each of the 10 sub-plots sampled in each pasture plot.

instar mortality had already taken place in the other two plots. In view of the higher soil temperatures prevailing in the latter two plots, cessation of oviposition and adult senescence would be likely to occur earlier than in the paspalum plot.

In contrast, in December 1976, the R_i was greater in the paspalum plot with only 39% of the population in the egg stage compared with over 50% in the other two plots. It is of interest that with the population development more advanced in 1976 in the paspalum, k_1 had a low value of 0.07.

In spite of this variation in R_i in December in the paspalum and ryegrass plots in 1975 and 1976, in February 1976 and 1977, population development was more advanced in the ryegrass plot. This may be expected in an environment where soil temperatures have been shown to be higher. In February R_i in the ryegrass/white clover plot was not significantly different from paspalum in spite of higher soil temperatures. A possible explanation for this may be given in the result from the small plot trial discussed in Chapter 6 where the rate of development of black beetle larvae was slower in cylinders of ryegrass/white clover than in pure ryegrass. The presence of the unfavourable white clover in the pasture mixture may have negated the enhancing influence of higher soil temperature on growth.

To investigate whether the level of population development was related to the magnitude of individual mortalities, the relationships between the initial R_i and individual k-values were established. The k-values for the plots are given in Appendices 14-12 and 14-13.

The linear relationships between k_1 for the pooled data from the paspalum, ryegrass and ryegrass/white clover plots and for the paspalum plot alone, and the R_i in December were both significant ($P < 0.01$). These are shown in Fig. 14-8(a). The data from the 1976/77 generation in the ryegrass/white clover plot were omitted from the regression as the large negative value of k_1 indicates mistiming of the December sample. Due to the large negative values of k_1 for the 1976/77 and 1977/78 generations in the Wharepapa plot when problems with mistiming of sampling occurred, no relationship could be established for this plot.

The inverse relationship for the other three plots shows that the greater the level of population development in December, the lower the level of the summer mortality (k_1). This result suggests that when oviposition or the rate of egg development is delayed in the spring, the population is more susceptible to the mortality factors operating over the December-February period. Fig. 14-8(a) suggests that when the R_i in December is greater than 1.7, then $k_1 = 0$. At this level of population development in December, much of the population will have developed to the late first instar and second instar larval stages, more tolerant of high soil moisture levels. This would reduce the effect on larval mortality of adverse soil moisture levels in the late December-January period as experienced in 1975/76.

Population development in the spring is known to be influenced by climatic factors. Watson (pers.comm.) has found that oviposition is influenced by soil moisture and temperature. The adverse effects

Figure 14-8 (c) Relationship between k_4 (winter-spring disappearance) and the R_i in May in the Wharepapa plot in the 1974/75 to 1976/77 generations.

Figure 14-8 (b) Relationship between $k_2 + k_3$ (late summer mortality + autumn-winter disappearance) and the R_i in February in (1) the ryegrass and ryegrass/white clover plots and (2) the Wharepapa plot. ▲ = data from groups of two sub-plots pooled per generation for the 1974/75 to 1976/77 generations at Wharepapa; ● = data from the ryegrass plot; ■ = data from the ryegrass/white clover plot in the 1975/76 and 1976/77 generations.

Figure 14-8 (a) Relationship between k_1 (summer mortality) and the population ranking index (R_i) in December in (1) the paspalum, ryegrass and ryegrass/white clover plots and (2) in the paspalum plot alone. ▲ = data from paspalum plot in generations 1974/75 to 1978/79; ● = data from ryegrass plot in generations 1974/75 to 1976/77; ■ = data from ryegrass/white clover plot in the 1975/76 generation.

$k_1(1) = 1{\cdot}41 - 0{\cdot}82\,Ri_{Dec}$

$k_1(2) = 1{\cdot}87 - 1{\cdot}09\,Ri_{Dec}$

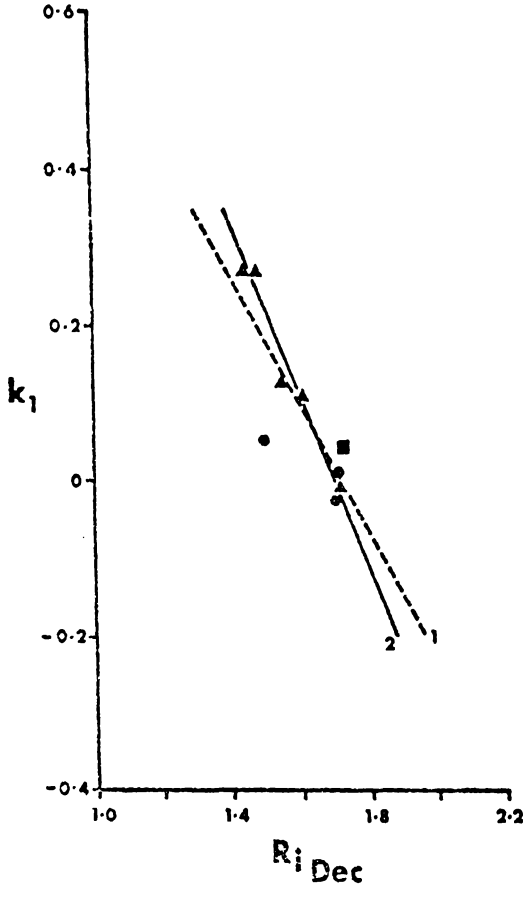


Figure 14–8 (a)

$k_{2+3}(1) = -0{\cdot}56 + 0{\cdot}28\,Ri_{Feb}$

$k_{2+3}(2) = -0{\cdot}62 + 0{\cdot}22\,Ri_{Feb}$

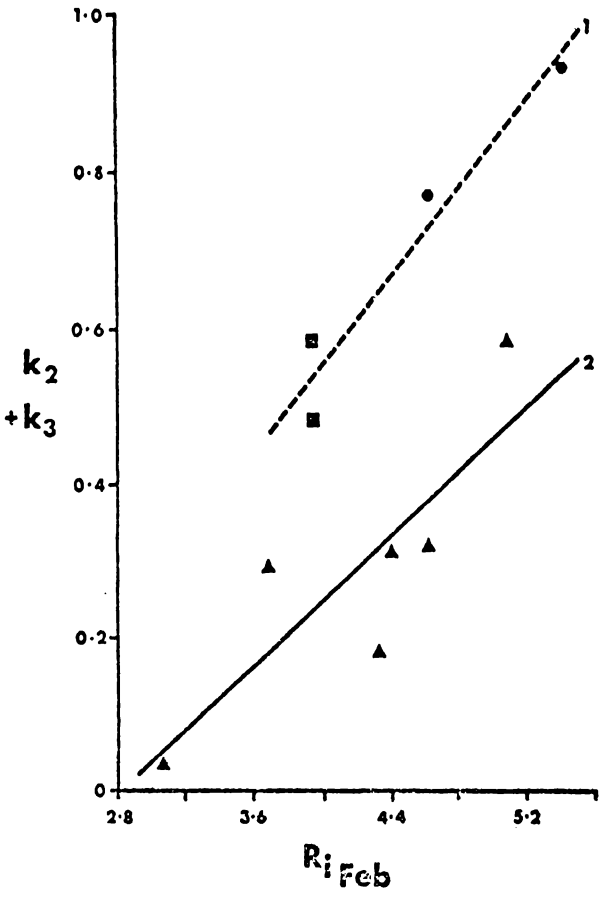


Figure 14–8 (b)

$k_4 = 1{\cdot}64 - 0{\cdot}14\,Ri_{May}$

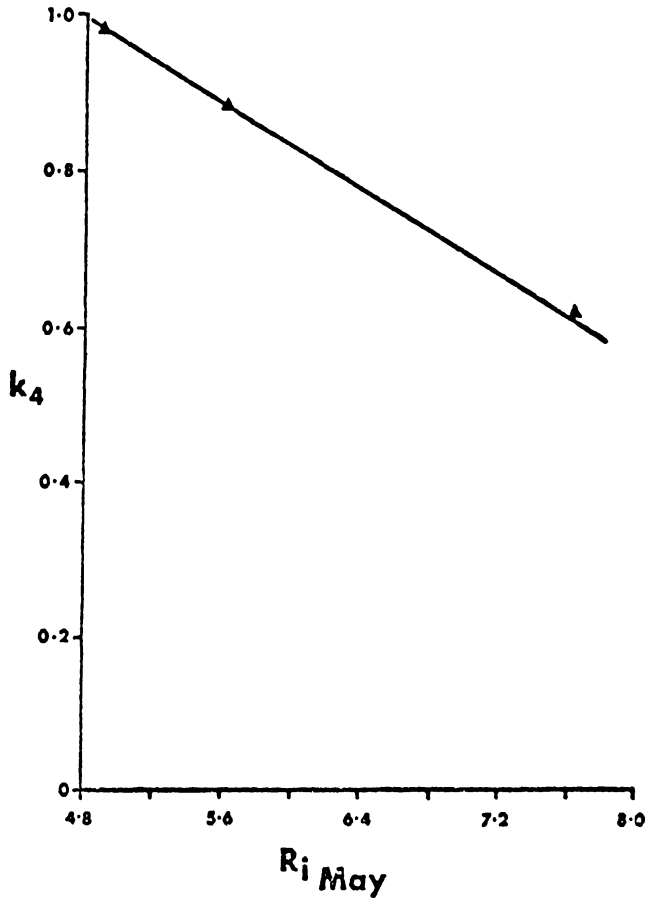


Figure 14–8 (c)

of low temperature and high soil moisture on the rate of egg development and hatching were shown in Chapter 4. No relationship could be shown from the data between the variation in mortality + summer mortality ($k_o + k_1$) and the R_i in December.

No significant relationships between R_i in February and k_2 or R_i in March and k_3 were evident for any of the plots. However, when the k_2 and k_3 mortalities were pooled, $k_2 + k_3$ for the ryegrass and ryegrass/white clover plots was significantly related to R_i in February ($P < 0.01$). The relationship is shown in Fig. 14-8(b). Over the period from February to June when $k_2 + k_3$ are operating, adult dispersal takes place. The relationship indicates that the greater the population development in February, the larger the population loss. As the data indicate that a greater proportion of the population was in the adult stage in the ryegrass plot at the commencement of the autumn dispersal period than in the paspalum plot, the contribution of dispersal to $k_2 + k_3$ mortality and disappearance may have been much greater in the ryegrass plot. This difference in R_i shown in Table 14-17, would be expected in view of the higher soil temperatures in ryegrass shown in Table 14-7.

As the values of $k_2 + k_3$ in the ryegrass/white clover plot were significantly higher ($P < 0.01$) than those of the paspalum plot in spite of similar population development levels, it is likely that other mortalities such as the influence of the white clover component of the diet were important in the ryegrass/white clover plot.

No significant relationship existed between $k_2 + k_3$ and R_i in February in the paspalum plot. This suggests that the black beetle

population was retained over this period in this plot, regardless of the level of population development. The population stability in the paspalum plot between February and June relative to the ryegrass and ryegrass/white clover plots was demonstrated in Chapter 10. Alternatively, it could be considered that the population did not develop fast enough to disperse before conditions became unfavourable for adult flight. In 1976 and 1977, when $k_2 + k_3$ in the paspalum were 0.24 and 0.33 respectively, only 9% and 8% of the population in February in the two years had developed beyond the third instar stage. In contrast, 36% and 65% of the population in the ryegrass plot had developed past this stage in February 1976 and 1977 respectively. The values of $k_2 + k_3$ of 0.77 and 0.93 in the ryegrass plot in the two years suggest that a greater proportion of adults were able to disperse from this plot.

Late summer mortality and autumn-winter disappearance ($k_2 + k_3$) was also found to be significantly related ($P < 0.05$) to R_i in February in the Wharepapa plot, and the relationship is shown in Fig. 14-8(b). The effects of adult dispersal from an area with high levels of winter soil moisture may be important in this relationship. The level of population decrease over this period is greater when the population is more advanced in February which suggests that adult dispersal out of the plot may be the major factor. It is of interest in comparing the two regression relationships in Fig. 14-8(b) that in spite of similar slope values, there is a large intercept difference suggesting that at a similar R_i in February, a greater population decrease between February and June will occur in the ryegrass and ryegrass/white clover

plots than in the Wharepapa plot. Such a situation could arise if the population in the latter plot, like that in the paspalum plot, is retained over the autumn dispersal period in spite of the level of population development.

Disappearance over the winter-spring period (k_4) was found to be significantly related ($P < 0.05$) to R_i in May in the Wharepapa plot. This inverse relationship shown in Fig. 14-8(c) suggests that mortality over the May to September period is greatest when the proportion of the population in the pre-adult stage in May is highest. As discussed previously, winter soil moistures were high at Wharepapa, with water frequently lying on the surface of the subplots. Under conditions such as this, mortality of over-wintering larvae and other pre-adult stages would be high. No significant relationship existed between k_4 and R_i in June for the paspalum, ryegrass or ryegrass/white clover plots or between k_5 and R_i in September for any of the plots. In contrast to the Wharepapa plot, the plots at Otakanini were much freer draining over the winter period.

These results demonstrate the importance of the level of population development in influencing population mortality. The presence of significant relationships between the R_i and k-values form the basis of the prediction of population density in specific pasture types if the relationship holds for a wide range of population levels and seasonal conditions. This concept will be examined further in the next chapter.

(3) Influence of pasture composition

The influence of pasture species on larval and adult ecology has been discussed previously. Laboratory and field studies have shown a number of life processes, and therefore black beetle population numbers, are adversely affected by legume species and phalaris, while other grass species favour growth and survival. As the insect is a pest causing severe pasture damage in some situations in some seasons (Plates 14-1 and 14-2), the effect of black beetle induced pasture damage was monitored in the paspalum, ryegrass and ryegrass/white clover plots at Otakanini to investigate whether changes in pasture composition induced by insect feeding play a role in determination of population trend.

Pasture production and composition were determined as described in Chapter 13. Sampling of the insect populations in the insecticide treated and untreated subplots showed that the insecticide treatments reduced black beetle numbers by 98%, and in the case of the ryegrass/white clover plot, white fringed weevil population numbers by 90%. Davidson et al. (1978a) found that the application of insecticide to pasture to remove scarab larvae caused a marked increase in grass growth relative to control plots which could not be attributed to the removal of the insects. They considered that this response may have been caused by temporarily increased cycling of nutrients from the decomposition of innocuous soil fauna or a change in microbial populations, although the effect of the chemicals on growth only lasted six months. Henderson and Clements (1974) also noted an increase in foliage yield following pesticide treatment. However, Martin (1974)



Plate 14-1 Area of black beetle larval feeding damage in ryegrass/white clover pasture in February.



Plate 14-2 Close-up of black beetle damage with pasture rolled back to show the root system destroyed by larval feeding.

found no significant increase in pasture yield following experiments with insecticides in New Zealand.

In this study no soil insect pests other than black beetle and white fringed weevil were present in the plots and nematode counts revealed that numbers of the plant parasitic nematodes present, (Heterodera trifolii, Meloidogyne sp. and Helicotylenchus sp.) were unaffected by the insecticide treatments. Earthworms were similarly unaffected. It is therefore considered that differences in pasture production and composition between the insecticide-treated and untreated plots can be safely attributed to the reduction in black beetle and/or white fringed weevil numbers in the former.

Pasture composition in the paspalum plot was maintained as a single species by the use of herbicides to remove legumes, weeds and other grass species. Total pasture production was assessed from four 3 month seasons, with the summer period commencing on 1 December. There was no winter production from the paspalum plot. Pasture production is shown in Table 14-18.

In spite of high numbers of black beetle over the summer larval feeding period in 1975-76 and 1976-77, paspalum pasture production did not differ significantly between insecticide-treated and untreated subplots which indicates that this grass is tolerant to black beetle feeding. No visible pasture damage was noted and pasture composition remained constant over the three generations. In this sward where paspalum was the only significant pasture species component, the magnitude of k-values and the resulting changes in black beetle population numbers cannot be attributed to

Table 14-18 Seasonal pasture production between 1975 and 1978 from the paspalum plot at Otakanini.

Year		Black Beetle/m^2 in February	Pasture Production (kg DM/ha) Summer	Autumn	Spring	Annual
1975-76	T*		990	103	1200	2293
	U**	59.8	912	125	967	2004
1976-77	T		1838	301	1032	3171
	U	56.7	1798	271	861	2930
1977-78	T		2454	214		
	U	***16.0	2368	198		

* Production from subplots, treated with insecticide to remove black beetle;

** Production from subplots not treated with insecticide;

*** Population estimate taken in March 1978.

Table 14-19 Seasonal pasture production between 1975 and 1978 from the ryegrass plot at Otakanini.

Year		Black Beetle/m^2 In February	Pasture production (kg DM/ha) Summer	Autumn	Winter	Spring	Annual
1975-76	T*		1360	880	1591	3040	6871
	U*	61.7	803	792	1621	3235	6451
1976-77	T		1435	1157	3575	3575	8046
	U	21.0	1659	1237	3784	3784	8529
1977-78	T		1413				
	U	12.3	1514				

* symbols as in Table 14-18

unfavourable effects induced by insect feeding and pasture damage. Likewise in the Wharenapa plot the tolerance of the kikuyu pasture to black beetle feeding means that this is unlikely to have contributed to the magnitude of k-values. The effect of black beetle populations on the ryegrass and ryegrass/white clover plots showed considerable differences when compared with the effect in the paspalum plot. Black beetle numbers were highest in the 1975-76 generation and in this season only, significant pasture damage occurred in the ryegrass plot (Table 14-19). The larval population reduced 1975-76 summer production by 41% and also caused a marked change in pasture composition. Herbage dissection in autumn 1976 revealed 82% ryegrass, 4% weeds and 14% litter in the insecticide-treated subplots compared with 69% ryegrass, 20% weeds and 11% litter in the untreated subplots. This ingress of non-graminaceous weed species which are an unfavourable food source for black beetle (Todd, 1959) became evident with the advent of the autumn rains.

Black beetle feeding in the ryegrass plot thus caused pasture damage which could be measured as a decrease in pasture production, and a significant change to a composition less favourable to the population than pure ryegrass.

Unlike the situation in the ryegrass plot, no significant production differences were obtained between insecticide-treated and untreated subplots over the 1975-76 summer period when black beetle numbers were highest in the ryegrass/white clover plot (Table 14-20). This plot also contained white fringed weevil. In the 1975-76 season, white fringed weevil numbers were low ($10/m^2$)

Table 14-20 Seasonal pasture production between 1975 and 1978 from the ryegrass/white clover plot at Otakanini.

Year		Black Beetle/m^2 in February	Pasture Production (kg DM/ha) Summer	Autumn	Winter	Spring	Annual
1975-76	T*		2162	570	1115	4388	8235
	U*	40.1	2388	662	1230	3711	7991
1976-77	T		2883	1236	2029	3428	9576
	U	16.0	2650	1153	2447	3359	9609
1977-78	T		1386	784			
	U	11.7	886	633			

* Symbols as in Table 14-18

Table 14-21 The % composition of the ryegrass/white clover plot at Otakanini, in 1976 as shown by herbage dissection.

Season	% Composition Ryegrass T*	Ryegrass U*	White Clover T	White Clover U	Weeds & Other Components T	Weeds & Other Components U
Autumn	43	16	51	83	6	1
Winter	71	23	26	75	3	2
Spring	69	65	24	32	7	3

* Symbols as in Table 14-18

and had no influence on pasture production or composition. In the subsequent years, weevil numbers increased to levels which had a significant effect on pasture composition, reducing the clover content and increasing the weed components. These results have been discussed with regard to the dynamics of white fringed weevil populations by East and King (1977) and King and East (1978).

Although total pasture production was not affected over the autumn and winter periods by black beetle feeding over the 1975-76 season, there were some significant changes in pasture composition as shown by the herbage dissection results in Table 14-21.

Black beetle feeding over the 1975-76 summer resulted in a significant reduction in the proportion of ryegrass in the sward over the autumn and winter periods, and a resultant increase in the white clover component. Although these differences had disappeared by the spring an unfavourable environment had been created for black beetle populations over the autumn and winter period.

Although life tables were not presented for the ryegrass/white clover plot, the population estimates shown in Appendix 14-1, demonstrate that the k-values were of a similar order of magnitude to those of the ryegrass plot (Appendices 14-7,14-8) with the exception of k_1 for the ryegrass/white clover in the 1976/77 generation. For this reason the discussion of the ryegrass k-values applies also to the ryegrass/white clover plot. In the 1976/77 generation, k_{2+3} and k_4 were 0.77 and 1.24 respectively in the ryegrass plot compared with 0.24 and 0.41 in the paspalum plot.

In view of the significant changes in pasture composition shown to be induced by black beetle feeding damage in the ryegrass and ryegrass/white clover plots, it could be concluded that the adverse effects of unfavourable pasture composition are likely to be involved in the large values of $k_2 + k_3$ and the population decreases observed in these plots between February and June.

However, the values of $k_2 + k_3$ and k_4 were also high at 0.93 and 0.31 respectively in the 1977/78 generation in the ryegrass plot (Appendix 14-8) when no significant pasture damage occurred. As shown in Table 14-21, pasture composition in damaged areas of the ryegrass/white clover plot was not significantly different from the control areas by spring 1976. This suggests that change in pasture composition does not provide the reason for the large decreases in black beetle populations in the ryegrass and ryegrass/white clover plots relative to paspalum between February and September.

Small plot studies of the interaction of plant species with adults in the autumn period, described in Chapter 10, showed that while autumn numbers remained high under paspalum in May and June, there was a large decrease in numbers, relative to paspalum, under ryegrass and ryegrass/white clover over the March to May-June period. Unfortunately these studies did not reveal the extent to which adult mortality and adult dispersal out of the plots influenced population numbers. Total available carbohydrates in the roots and rhizomes of paspalum plants in the plot at Otakanini have been found to be much higher than in roots of ryegrass plants from the ryegrass plot over the autumn period (King and Lauren, unpublished results).

This suggests that nutritionally, paspalum plants are a better food source than ryegrass plants for newly emerged adults in the autumn taking carbohydrate levels as an indicator. This may partly explain the apparent greater stability of the black beetle population under a paspalum sward, and why large population decreases occurred in the ryegrass and ryegrass/white clover plots over the autumn-winter period.

(4) Influence of parasites, predators and pathogens

During the course of the population studies at Otakanini and Wharepapa, monitoring was carried out to determine the influence of natural enemies as population mortality factors. No parasitism was noted at either site apart from the recovery of a few black beetle cadavers containing either the larvae or pupal coccoons of a species of Phoridae, probably attacked after the death of the host, and a few larvae at Wharepapa parasitised by the nematode, Neoaplectana sp. This finding is not surprising as the two attempts to introduce parasites for black beetle into New Zealand, namely the thynnid Pseudelaphroptera brevipilosa and the tachinid Microphthalma europea were unsuccessful (Cameron et al., 1978).

Predators were found at both sites and the numbers were most easily assessed at the December black beetle population sampling occasions when soil fauna were extracted from the sample cores by flotation. The numbers recovered at the two sites are shown in Table 14-22.

Predators appear to have increased in numbers between 1976 and 1977, particularly staphylinids at Wharepapa and elaterids at

Table 14-22 Numbers of predacious invertebrates recovered from the Otakanini and Wharepapa black beetle population study sites.

Sampling Date	Predator numbers/m^2					
	Wharepapa			Otakanini		
				Ryegrass		Paspalum
	Staphylinids	Elaterids	Carabids	Elaterids	Staphylinids	Elaterids
December 1976	*15.5	0	0	5.6	1.0	3.1
December 1977	**28.4	7.4	6.2	28.4	1.9	11.1

* includes 13.6/m^2 staphylinid eggs

** includes 21.0/m^2 staphylinid eggs

Otakanini. Staphylinid predators, Thyreocephalus orthodoxus (Olliff) and T. chloropterus (Erichson) were found at both sites, although they were more numerous at Wharepapa, possibly because of the cooler and moister situation. T. orthodoxus, which is the smaller of the two species, was the more numerous, as found by Cameron and Butcher (1978) from pitfall trapping at nearby Woodhill.

Butcher (1978) found that T. orthodoxus will eat black beetle eggs, larvae and pupae and laboratory observations showed that staphylinid adults would consume up to three second instar larvae, two third instar larvae or one pupa per week. Activity of T. orthodoxus adults as gauged by pitfall trapping peaked in October and November (Butcher, 1978) and peak egg numbers were found in early November in 1976. This suggests that the egg numbers at Wharepapa may have been higher than shown in Table 14-22 earlier in the spring.

The elaterids Conoderus exsul (Sharp) and C. striatus (MacLean) were found at both sites, with C. exsul being the dominant species at Otakanini where numbers were much higher than at Wharepapa. Farrell (1972) considered that Conoderus larvae were facultative predators of grass grub. Cameron and Butcher considered Conoderus spp. adults were capable of attacking small scarab larvae but not third instar black beetle larvae. They concluded that adults were probably also facultative predators of smaller black beetle larvae.

Several species of carabids were found at Wharepapa in the 1977 sample with the scaritids, Clivina spp. being the most numerous.

Cameron and Butcher (1978) found Clivina spp. adults reached $4/m^2$ in pitfall traps at Woodhill near Wharepapa but noted that Muggeridge (1939) recorded them as being phytophagous only.

Although no studies have been carried out to quantify the influence of predation on black beetle populations at Wharepapa and Otakanini, some predation undoubtedly occurred. The staphylinic predators are more likely to be of importance than the facultative elaterids, especially at Wharepapa. However, the most predacious stage, the adult, declines in numbers by the time peak black beetle oviposition occurs in most seasons and so the influence on k_1 mortality will be considerably reduced. As numbers of staphylinid adults had probably declined by the time the later larval instars had developed, the influence of predation as a component of k_2 mortality may not have been as great as in the k_1 mortality period. Relative to the pathogen complex, these predators are considered insignificant.

At both sites the faeces of birds such as magpies (Gymnorhina hypoleuca L.), starlings (Sturnus vulgaris L.) and mynahs (Acridotheres tristis L.) were found to contain fragments of black beetle adults. The excreta of hedgehogs (Erinaceus europaeus L.) was also found to contain adult fragments. This indicates that predation by these vertebrates is common. Some of the adults taken may however, have been dead or dying. During senescence, cadavers of adults are frequently found on the surface of the pasture and adults have been observed to move about the pasture surface during the day and at dusk where they could be eaten by feeding birds and hedgehogs.

Pathogens appeared to be the most significant natural enemies of black beetle populations at both sites. Of the pathogenic fungi, green muscardine Metarrhizium anisopliae was found infecting larvae, pupae and adults and Cordyceps sp. and the white muscardine Beauvaria sp. were noted in larvae and adults. The pathogenicity of these fungi is well established (Madelin, 1966). Infection of the population with these pathogens was minor, however, with only 2-3% of the population being infected at any one time.

Rickettsial infections were found in the Wharepapa population. Longworth and Archibald (1975) also found rickettsia in their plots at Wharepapa but did not consider it a significant pathogen.

The small RNA virus described by Longworth and Archibald (1975) in their black beetle population study plots at Wharepapa, also occurred in the plots used in this study at Wharepapa. However, relative to the major pathogen present at this site, a protozoan, the virus was of minor significance and only exceeded the 10% level of infection in February 1976. The virus was not found in black beetle populations at Otakanini.

The major pathogen in populations at Otakanini and Wharepapa was a coccidian protozoan, Adelina sp. The effect of this pathogen on insect hosts, including the possible role in black beetle population mortality (Longworth and Archibald, 1975; Archibald et al., 1975; Archibald, 1976), has been reviewed elsewhere in this thesis. The level of Adelina sp. has been monitored in black beetle populations since 1974 at Wharepapa and since 1975 in the paspalum plot at Otakanini, and is shown in Tables 14-23 and 14-24.

Table 14-23 The incidence of the protozoan pathogen *Adelina* sp. in black beetle populations in the Wharepapa plot.

Time of Sampling		1974	1975	1976	1977	1978
March	Population/m^2	164.4	81.4	59.2	17.3	33.9
	% *Adelina*	-	79	67	36	27
May	Population/m^2	119.0	39.5	40.7	19.1	NS*
	% *Adelina*	63	63	69	29	-
December	Population/m^2 (eggs and larvae)	163.4	162.2	11.7	16.7	109.2

*NS = no sample taken

Table 14-24 The incidence of the protozoan pathogen *Adelina* sp. in black beetle populations in the paspalum plot at Otakanini.

Time of Sampling		1975	1976	1977	1978
March	Population/m^2	61.0	45.0	41.9	16.0
	% Adelina	49	45	60	40
September	Population/m^2	25.9	13.6	11.7	NS*
	% *Adelina*	8	28	50	-
December	Population/m^2 (eggs and larvae)	112.9	62.9	40.1	50.3

*NS = no sample taken

No estimate of the level of Adelina infection is possible at the egg and small larval stages as the protozoan has a long developmental period. It is also suspected that infection of the developing larvae takes place when feeding commences. At both sites, a significant proportion of the population was infected with Adelina at the March, May and September sampling occasions. In a study of the influence of the pathogen on black beetle mortality at Wharepapa in plots adjacent to those of this study, Archibald et al. (1975) and Archibald (1976) found a good correlation between the number of black beetle infected with Adelina which died in the laboratory between sampling occasions from February to May, and the actual drop in the field population as shown by the sampling estimates. In the absence of a detailed study of the extent of adult dispersal from the plots over the autumn period, the significance of Adelina mortality on the observed population decline between March and May in the Wharepapa plot (Table 14-23) and between March and September in the paspalum plot (Table 14-24) cannot be determined.

No further study has been carried out to elucidate the relative importance of Adelina mortality in populations since those of Archibald et al. As the pathogen is debilitative, some pathogen induced mortality undoubtedly occurs, and will possibly contribute to k_2, k_3 and k_4 mortalities. No significant relationships were however shown to exist between the level of Adelina infection in the population and subsequent k-values.

In the paspalum plot, these mortalities had little effect in determination of population trend. At Wharepapa, k_4 was next in

importance to $k_o + k_1$ as the key factor influencing population change. As shown previously, a larger proportion of the population remained in the pre-adult stages at the beginning of the winter period in the Wharepapa plot. This may mean that pathogen induced mortality of this non-adult proportion over the winter was of greater significance at Wharepapa than in the paspalum plot. However, as discussed previously the higher mortality over the winter-spring period at Wharepapa may simply have been a winter soil moisture effect.

The adverse effect of Adelina on adult female fat reserves, essential for ovarian development was shown in Chapter 11. Adelina infection resulted in an overall reduction in potential fecundity of 91% in the trial population of adults, suggesting that over a period this effect will inevitably lead to a population decrease in the absence of adult immigration. In the Wharepapa plot pathogen infection of the black beetle population remained relatively high until the 1977/78 generation (Table 14-23), when the index of population trend was 158.6% (Appendix 14-11). It could be inferred from this that a reduction in Adelina infection resulted in more females ovipositing, so leading to an increase in the population through the influence on k_o, the variation in natality. Adult dispersal into the plots may however also be implicated in the population increase. This was shown in Chapter 10 to have a significant effect on summer larval population numbers at Otakanini.

The large negative value of k_o at Wharepapa in the 1975/76 generation (Appendix 14-9) suggests that any effect of the pathogen

on sterilizing the females has been insignificant relative to adult immigration before and during oviposition. Likewise in the 1976/77 generation, the effect of Adelina on oviposition appears to have been obscured by immigration.

The level of Adelina in the population in the paspalum plot in September increased markedly between 1975 and 1977 (Table 14-24). A further population estimate made in July 1978, showed that the level was $8.6 \pm 2.1/m^2$ and screening of black beetles from the sample revealed 100% infection with Adelina. In view of this increase in the incidence of the pathogen in the spring it was speculated before the December 1978 population estimate was made that a further large decrease in the population would occur with a low index of population trend. The December 1978 population estimate of $50.3/m^2$ and the index of population trend for the 1978/79 generation of 173% reveals that this did not take place. This suggests that adult female sterilization did not occur in the field as it did in the laboratory population, or alternatively significant adult immigration took place. As there is no evidence to prove that Adelina did not influence the potential fecundity of the resident female population at the start of the oviposition period, it is concluded that the effect of the pathogen on k_o was of less significance than that of adult immigration in spring.

Screening of the black beetle population in the ryegrass and ryegrass/white clover plots revealed the presence of Adelina. The absence of a March population sample, and the low population numbers present at the June sample have prevented any insight into the role of the disease in mortality in these plots.

In both the paspalum plot and the Wharepapa plot, k_o in conjunction with k_1 was the key factor determining population trend. Although there is indirect evidence for pathogen infection reducing fecundity in the field, the low level of precision of the December population, problems with timing the December estimate, variation in population development rate between generations and the effect of adult immigration has prevented the precise quantification of the role of Adelina in k_o.

(5) Combat mortality

In overcrowded situations, some species of Scarabaeidae regulate their densities through combat mortality affecting the larval stages (Kelsey and Hoy, 1950; Carne, 1956; Soo Hoo, 1968; Chadwick, 1970). Kelsey (1951), Wightman (1972a) and Kain (1975) noted grass grub larval combat in the laboratory, and East (1972) concluded from a small plot trial that larval combat among third-instar grass grub was severe at high population densities under conditions of food shortage. Both East and Kain considered that density dependent larval combat was of major importance in regulating grass grub populations.

The analysis of the population dispersion data in Chapter 13 showed that black beetle populations were aggregated, and at high densities the frequency distributions revealed a significant number of samples containing greater than one larva. In addition the measure of aggregation decreased between December and February probably reflecting locomotor movement of larvae through the soil in the course of feeding. Although no specific laboratory or field study was carried out to investigate black beetle larval

combat, it was noted that when several second and third instar larvae were confined in a small volume of soil, aggressive behaviour and wounding through larvae slashing at each other with their mandibles took place. At the highest larval densities recorded in summer, up to eight third instar larvae were recovered from a 10 cm diameter soil core.

It may be concluded from these observations that at least some larval combat is likely to take place over the summer in black beetle populations. This would contribute to k_1 and k_2 mortality. Examination of density relationships earlier in this chapter revealed no density dependence in k_1 but there was a suggestion that k_2 may have been density dependent in the paspalum plot. Combat mortality could therefore be important in k_2 in some generations.

If combat mortality does occur, it is likely that its influence on k_2 would be accentuated at very high population densities where pasture damage occurs. The highest population densities in February recorded in the paspalum and Wharepapa plots between 1975 and 1979 were 59.8/m^2 and 104.2/m^2 respectively. At these densities, no visual pasture damage occurred. In March 1974 a population level of 163.4/m^2 was recorded in the Wharepapa plot, suggesting a February level at least as high or greater. It was over this summer period that the farmer first noted pasture damage on the plot. As mentioned previously, pasture damage in the ryegrass and ryegrass/white clover plots was only noted in summer 1976, at which time the highest February population levels were recorded (40-60/m^2). The occurrence of severe pasture damage

at these population densities suggests that considerable larval movement would take place during feeding which would increase the chance of larval confrontation and possibly larval combat. Larval combat may therefore cause significant mortality at lower population densities in ryegrass pastures than where more tolerant grasses such as paspalum and kikuyu are dominant.

Black beetle larval population numbers are however very much lower than the usual range of grass grub densities found in improved pasture and reach epidemic proportions much more sporadically. For this reason it may be concluded that larval combat is unlikely to regulate black beetle populations in the manner of grass grub population regulation shown by East and Kain.

VI POPULATION MODELS

For the purpose of drawing together the influence that the various mortalities discussed in the previous section of this chapter have on black beetle population dynamics, population models were constructed. As Clark et al. (1967) pointed out, this is the only quantitative means of assessing the extent to which the life system of a particular insect is understood. Models are presented in this section for three contrasting pasture types, paspalum and ryegrass-ryegrass/white clover, based on the data from the plots at Otakanini and for the Wharepapa plot.

(1) Paspalum model

As k_o and k_1 were shown to be the key factors determining population change in the paspalum plot, these two mortalities become the important components in the model which is shown in Table 14-25.

Table 14-25 Population model 1 used to describe black beetle population dynamics in the paspalum plot at Otakanini.

k_o = −1.43 + 0.80 log (Potential Natality)

k_1 = 1.87 − 1.10 $R_{i_{December}}$*

$R_{i_{December}}$ = −2.406 + 0.099 ΣT_D**

$k_2 + k_3$ = 0.30 (average value from life tables)

k_4 = 0.30 (" " " " ")

k_5 = 0.12 (" " " " ")

k_6 = 0.06 + 0.184 log $N_{\text{Adults September}}$

*$R_{i_{December}}$ = the ranking of the level of population development in December

**ΣT_D = Sum of the mean daily temperatures in September, October and November recorded at Woodhill Forest.

There was a strong suggestion from the analysis of the mortalities that k_o may be density dependent (Fig. 14-5), although this could not be proved. For the purposes of the model, it is assumed that k_o is density dependent and it is predicted from the equation shown in Fig. 14-5. In Fig.14-8(a), k_1 was shown to be significantly related to R_i in December. The relationship between R_i in December and spring temperatures was investigated by plotting R_i for the Otakanini paspalum and ryegrass populations against the spring temperatures recorded at the nearby meteorological station at Woodhill Forest. For the purposes of the model the mean daily temperatures in September, October and November, preceding and during oviposition were summed to give ΣT_D. To increase the number of points, the black beetle population data of Esson (1973) were also included, with the spring temperatures from the nearest meteorological station site. The populations sampled by Esson in 1972 were at Awanui, Pakaraka and Te Kopuru in Northland and the temperatures used were recorded from Kaitaia, Kaikohe and Dargaville for the three sites respectively.

A highly significant linear relationship ($P < 0.01$) was found between R_i in December and the spring temperatures (Fig. 14-9). This relationship allows R_i in December to be predicted from the temperature records and in turn the values for k_1 can be predicted from R_i using the relationship for the paspalum plot in Fig. 14-8(a). k_1 is thus modelled as a function of spring temperature. As no relationships for $k_2 + k_3$, k_4 and k_5 and density in the paspalum plot were found, values for these mortalities in the model were set at average values derived from the life tables. The density

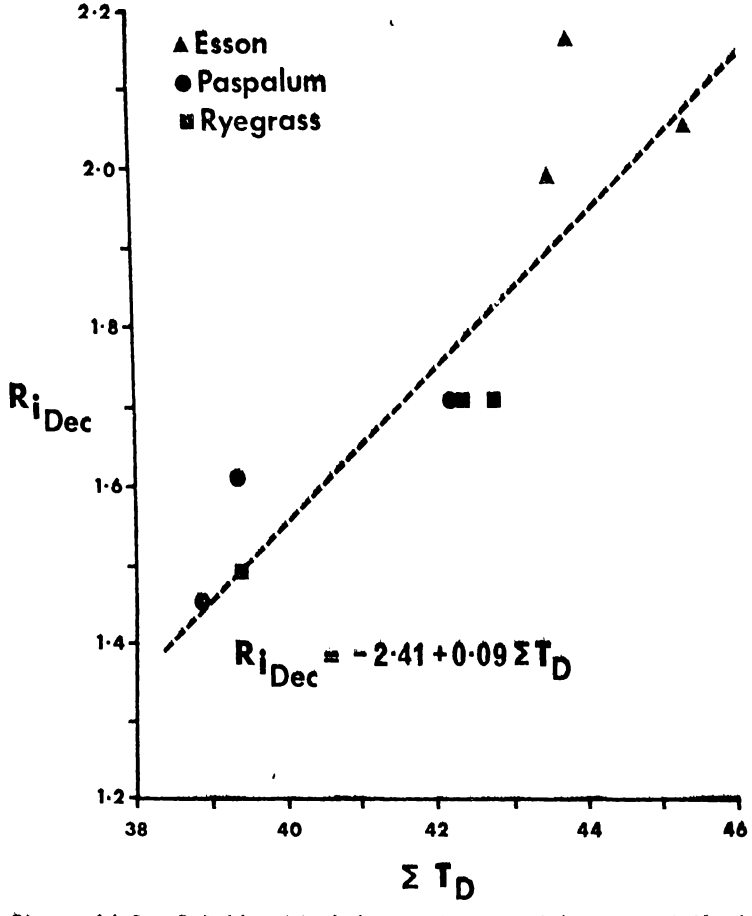


Figure 14-9 Relationship between the sum of the mean daily temperatures for the months of September, October and November (ΣT_D) and the black beetle population ranking index (R_i) in December using data from the trials of Esson (1973) and the paspalum and ryegrass plots at Otakanini.

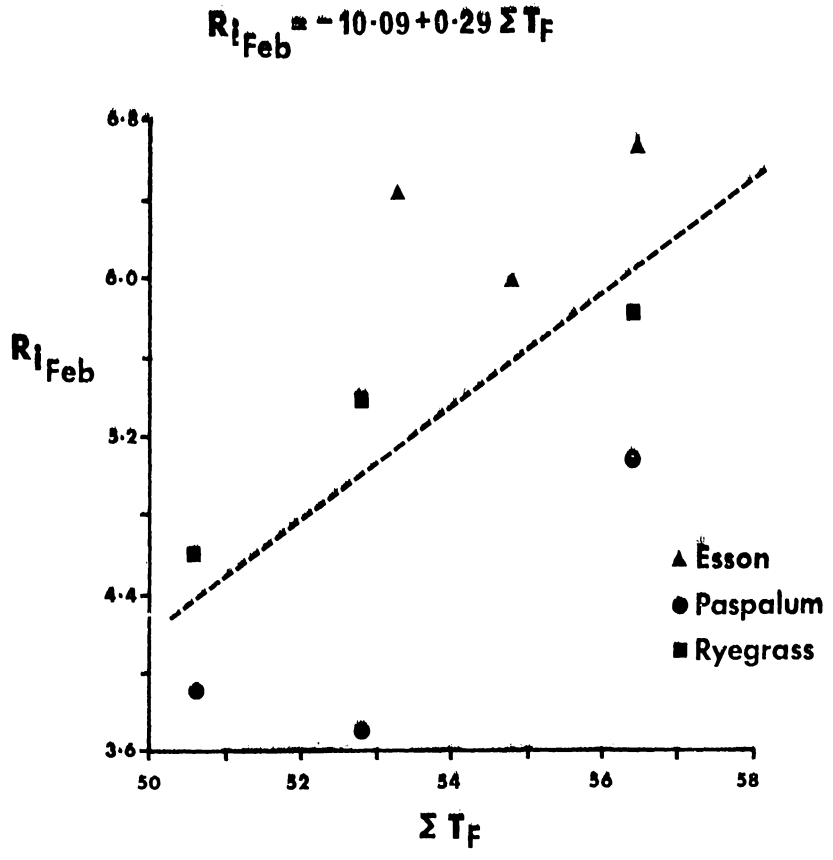


Figure 14-10 Relationship between the sum of the mean daily temperatures for the months of December, January and February (ΣT_F) and the R_i in February for the data from the trials of Esson (1973) and the paspalum and ryegrass plots at Otakanini.

relationship of k_5 previously demonstrated (Fig. 14-5) was also used in the model. Potential natality was calculated as in the life tables (Appendix 14-3). It is possible to derive ΣT_D and hence R_i in December for the population in the paspalum plot using temperature records from Woodhill Forest provided by the N.Z. Meteorological Service. The values over the period from 1956 to 1978 are shown in Appendix 14-17.

Black beetle population changes in paspalum since 1956 were simulated, using model 1 (Table 14-25). Todd (1964) noted that it was realised in 1957 that black beetle was a serious threat to the grassland economy in certain areas. Also, Todd (1959) reported that life history studies and insecticide trials were carried out at Clevedon (South Auckland) and at Hahei (on the Coromandel Peninsula) following severe pasture damage in the 1957/58 summer. Insecticide trials were also carried out on the south west coast of the Manukau Harbour in December 1958 where black beetle egg numbers were around $130/m^2$ (unpublished M.A.F. reports). These data show that black beetle population numbers over the existing distribution would have been high over the 1957 to 1958 period, and therefore were also likely to have been high in 1956. For this reason a February 1976 population density of $60/m^2$ is taken as the starting point for the simulation as this was the highest February density recorded over the study period in the paspalum plot at Otakanini.

The expected February population densities using the paspalum model over the period from 1956 to 1979 are shown in Fig. 14-11 and in Appendix 14-17. Observations over the period 1973 to 1979 have shown that black beetle damage only occurs in ryegrass based pastures

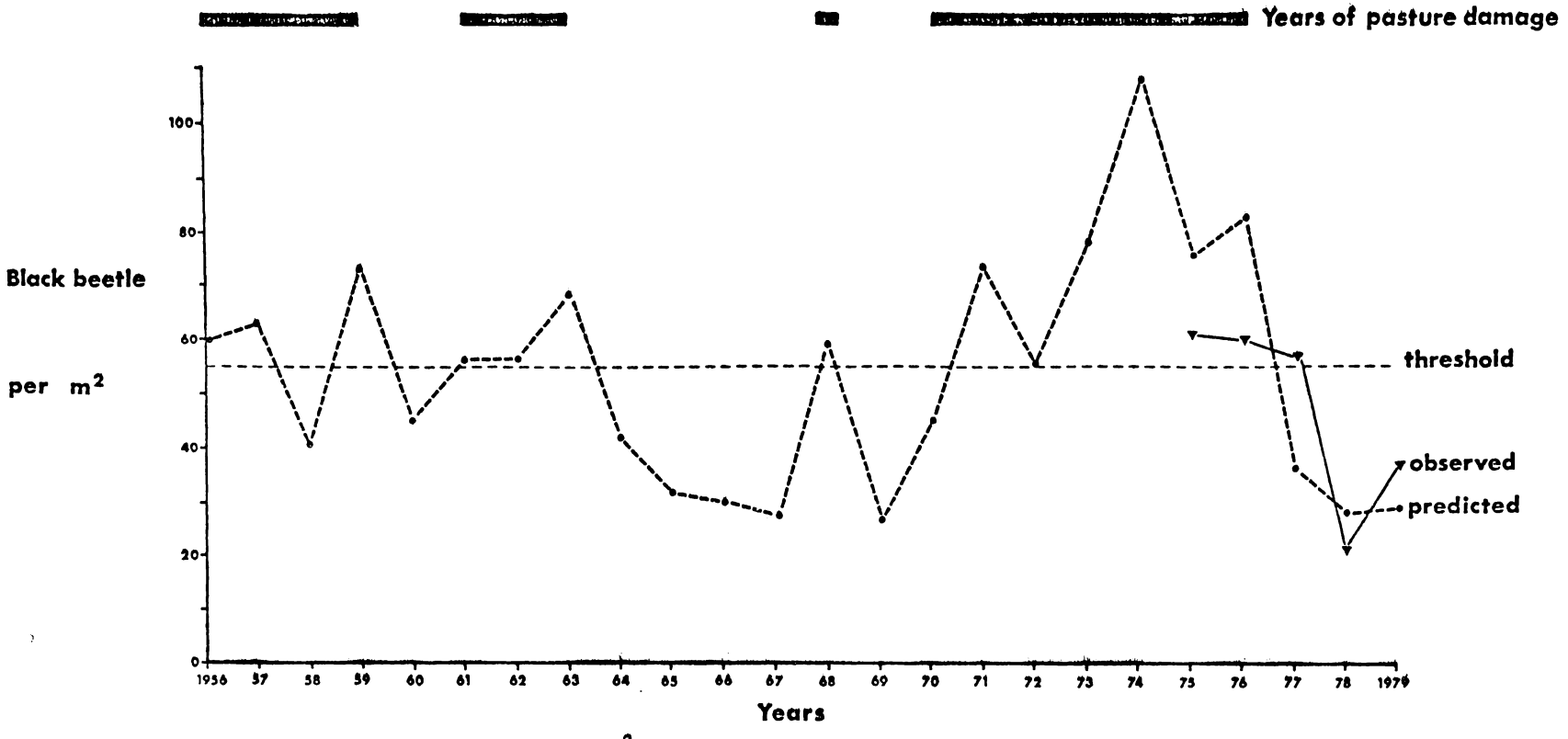


Figure 14-11 Black beetle population densities per m^2 in February predicted from the paspalum population model 1, and the years when pasture damage occurred over the period from 1956 to 1979. The observed population densities in the paspalum plot at Otakanini over the period 1975 to 1979 are shown for comparison with predicted densities.

when populations are high under paspalum. For example, February populations of 56–62/m^2 were recorded in the paspalum plot in 1975–77. The peak February population levels of 62/m^2 in the ryegrass and 40/m^2 in the ryegrass/white clover plots (Appendix 14–1) occurred in 1976 and caused considerable pasture damage, as discussed previously. For the purpose of providing a base-line, a simulated population of 55/m^2 in the paspalum plot was taken to represent years when pasture damage is likely to occur in ryegrass based pastures.

The years when simulated population numbers are close to or greater than this base-line are shown in Fig. 14–11. Years when severe pasture damage occurred as indicated in the literature and in trial reports are also shown in Fig. 14–11. The simulated population numbers suggest that during the late 1950's and early 1960's, in 1968 and from 1970 to 1976, pasture damage may have taken place. This predicted pattern of outbreaks ties in well with the historical information. Todd (1959,1964) reported high population numbers and pasture damage in the period 1957 to 1959 and again in the early 1960's. Unpublished Ministry of Agriculture and Fisheries trial reports noted that black beetle damage occurred in the Helensville area (near Otakanini) in 1961 and 1962. Bilkey (1973) stated that severe pasture damage from black beetle occurred in the early 1960's in the Dargaville area but over the 1964 to 1969 period damage was less noticeable, suggesting lower population numbers. The same report notes that severe damage occurred again in the 1970–73 period. Rosie (1969) reported that severe black beetle damage to pasture occurred in the Far North in

1968. Pasture damage over the 1973 to 1976 period was observed at the Otakanini Research Area and over much of the area of black beetle distribution (King, unpubl. reports).

The simulation of population densities using the paspalum model therefore reveals a good correlation with high population numbers and years of pasture damage. The observed population densities in the paspalum plot at Otakanini between 1975 and 1979 are shown in Fig. 14-11. These show reasonable agreement with the expected densities with numbers greater than $60/m^2$ in 1975 and 1976, followed by lower levels in 1978 and 1979.

The model is based on the unproven density dependence of k_o and the relationship between k_1 and spring temperatures. Due to the density dependence of the model, the simulated February population densities return to the values shown in Fig. 14-11, within two generations, regardless of the initial population density chosen. The importance of this density dependence to the model is shown when simulation is carried out using variants of the model. The population densities using these models are shown in Appendix 14-17. In model 2, k_6 is held at the average observed value of 0.22, with 0.30 representing a sex ratio of 1:1. All other parameters are the same as the initial model 1. February population numbers did not differ significantly from those predicted by model 1. When k_o is held at the average observed value of -0.10 (model 3), with all other mortalities as in model 1, the simulated densities reach unrealistically high levels. This demonstrates the importance of the density dependence of k_o to the model and the relative insignificance of the weak density dependence

in k_6. The removal of all density dependence from the model (model 4) with k_6 at 0.22 and k_o at -0.10 allows simulated population densities in February to reach a level of $10,000/m^2$. Such densities are some 100 times greater than those likely to be found in the field.

Simulation of black beetle population density with the model revealed that the variation in natality (k_o) and summer mortality (k_1) had to have negative or low values for a population increase to occur. Due to problems associated with obtaining accurate values of black beetle egg density at a time when oviposition had finished, it is difficult to apportion the mortality between the potential numbers of eggs in the population and the density in February. For this reason it is preferable to consider the combined action of k_o and k_1.

The simulation shows that when spring temperatures are high, negative values of $k_o + k_1$ are obtained indicating a February population density greater than that predicted from the fecundity of the females in the plot in September. Such a result could arise with changes in fecundity or adult immigration. If fecundity was density dependent (or greater in warm years) then k_o could possibly be expected to be negative. Alternatively, if the assumed fecundity of 10 eggs/female is too low and the figure was 20-30 eggs/female at all densities, then it would shift the k_o density relationship so that k_o was more often positive. Adult immigration during oviposition would also result in a population density in February greater than expected from the females in September. Watson (1978) reported that adult migration was greatly influenced by temperature and so it may be concluded that in years of warm

spring temperatures, the adult dispersal into an area would occur. This migration could result through adult movement from other over-wintering sites giving a general redistribution of the population.

(2) Ryegrass model

As only two life tables were constructed from the ryegrass plot it was not possible to carry out any investigation of the density relationships of individual mortalities. Consequently, there is no density dependence in the ryegrass model shown in Table 14-26. The mortalities k_o, k_4 and k_6 were set at average values. As all the September population was in the adult stage in the two generations used in the life tables, k_5 was taken as zero. The relationships between spring temperatures and R_i in December shown in Fig. 14-9 and between k_1 and $R_{i\ December}$ shown in Fig. 14-8(a) are used in the model to simulate summer mortality.

The relationship between R_i in February and summer temperatures was investigated by plotting $R_{i\ February}$ of the populations in the paspalum and ryegrass plots against the summer temperatures recorded at Woodhill Forest. For the purposes of the model, the mean daily temperatures in December, January and February over the period when summer mortality was occurring, were summed to give ΣT_F. To increase the number of points, the black beetle population data of Esson (1973) were included with the summer temperatures from the meteorological station sites as described for the calculation of ΣT_D.

The relationship between $R_{i\ February}$ and summer temperature is shown in Fig. 14-10. This relationship allows $R_{i\ February}$ to

Table 14-26 Population model used to describe black beetle population dynamics in the ryegrass plot at Otakanini.

k_o = -0.66 (average value from life tables)

k_1 = $1.41 - 0.82\ R_{i_{December}}$

$R_{i_{December}} = -2.406 + 0.099 \Sigma T_D$

$k_2 + k_3$ = $-0.56 + 0.28\ R_{i_{February}}$

$R_{i_{February}} = -10.087 + 0.286 \Sigma T_F^*$

k_4 = 0.78 (average value from life tables)

k_5 = 0

k_6 = 0.30 (average value from life tables)

ΣT_F = Sum of the mean daily temperatures in December, January and February recorded at Woodhill Forest.

Other symbols as in Table 14-25

be predicted from temperature records. The relationship between $R_{i\ February}$ and $k_2 + k_3$ for the combined data from the ryegrass and ryegrass/white clover plots was shown in Fig. 14-8(b). Although the relationship between $R_{i\ February}$ and ΣT_F was only weakly significant ($P > 0.05 < 0.1$), it has been included in the model for the purpose of allowing $k_2 + k_3$ to be varied.

When the model is used to simulate population changes in the ryegrass plot using an initial density of $62/m^2$ in February 1976, which was the actual population density (Appendix 14-1), the model predicts a density of $29/m^2$ in February 1977. This compares favourably with the actual density recorded of $21/m^2$. Due to the action of $k_2 + k_3$ and k_4 in 1977, a zero population level is predicted in September 1977 compared with an actual density of $1.2/m^2$. With the average value of k_o set at -0.66 to allow for adult immigration, a density of $3/m^2$ in February 1978 is predicted compared to that of $12/m^2$ from population sampling. This suggests that $k_2 + k_3$ and k_4 may have been over-estimated and/or k_o has under-estimated the influence of immigration.

The importance of k_o to the model is further illustrated when simulation is carried out using the actual population density of $27/m^2$ in February 1975 as the starting point. The model predicts a zero population level in September 1975 and therefore with k_o set at -0.66, a February 1976 density of $3/m^2$ compared to that of $62/m^2$ actually recorded. To reach such a level, k_o would have had to have been as high as -1.80 which means a September adult population of $18/m^2$ arising from immigration assuming a 1:1 sex ratio and 7 eggs/female. It was shown in Chapter 10 that immigration of about

3 adults/m^2 occurred in ryegrass/white clover pasture in the trial carried out in 1975. This result suggests that either a greater level of immigration than was recorded in the trial, did in fact occur, or alternatively that the model over-estimates the mortality between February and September.

This simulation reveals the deficiencies of the ryegrass model which are to be expected given the small amount of data on which it is based. It does however illustrate the marked contrast in the population dynamics of black beetle between the paspalum and ryegrass plots. In the latter plot a high level of adult immigration in spring appears to be necessary to compensate for the large values of k_2, k_3 and k_4. In view of the similarities evident in the pattern of black beetle population change observed in the ryegrass/white clover and ryegrass plots (Appendix 14-1), it seems reasonable to assume that high February population levels in ryegrass/white clover are also dependent on marked spring immigration.

(3) Wharepapa model

There was no significant relationship between spring temperatures and R_i in December in the Wharepapa plot. The variation in natality (k_o) was density independent as discussed previously. These factors have therefore prevented the development of a specific model for the population dynamics in the Wharepapa plot. To provide relationships for k_o and summer mortality (k_1) in the Wharepapa model, the relationships for k_o and k_1 were assumed from the paspalum model 1 (Table 14-25).

Two models were constructed as shown in Table 14-27. In Wharepapa model 1, late summer mortality plus autumn winter

Table 14-27 Population models used to describe black beetle population dynamics in the Wharepapa plot.

Model 1

k_o = -1.4 + 0.80 log (Potential Natality)

k_1 = 1.87 - 1.1 $R_{i\ December}$

$R_{i\ December} = -2.406 + 0.099 \Sigma T_D$

$k_2 + k_3$ = -0.62 + 0.215 $R_{i\ February}$

k_4 = 1.64 - 0.136 $R_{i\ May}$*

k_5 = 0.03 (average value)

k_6 = 0.36 - 0.132 log (Adults in September)

Model 2

$k_o + k_1$ = as for Model 1

$k_2 + k_3$ = 0.25 (average value)

k_4 = 0.82 (average value)

k_5 = 0.03 (average value)

k_6 = as for Model 1

*$R_{i\ May}$ = the ranking of the level of population development in May, other symbols as in Table 14-25 and 14-26.

disappearance ($k_2 + k_3$) was calculated from the relationship shown in Fig. 14-8(b) and winter-spring disappearance (k_4) from that shown in Fig. 14-8(c). Delayed development (k_5) was set at an average value of 0.03 calculated from the life tables and the proportion of females (k_6) as the inversely density dependent relationship shown in Fig. 14-6. In Wharepapa Model 2, k_o, k_1 and k_6 were calculated as for model 1, and $k_2 + k_3$, k_4 and k_5 were set at average values calculated from the life tables (Appendices 14-9 to 14-11).

Actual values of R_i in February and May were used to calculate $k_2 + k_3$ and k_4 using Wharepapa model 1. Spring temperature data from the adjacent Woodhill Forest (shown in Appendix 14-17) were used to calculate k_1 for both models. Taking the actual February population density in 1975 of 108.5/m^2 as the initial density, the densities predicted by the models between 1975 and 1979 were compared with the actual population densities. These are shown in Table 14-25. The densities predicted by the two models did not differ significantly. The very much higher actual densities in 1978 and 1979 compared with those predicted by the models, revealed that the models failed to allow for an increase in fecundity and/or the effects of adult immigration during oviposition in the spring. In both these years, cool spring temperatures were recorded at Woodhill (Appendix 14-17). In spite of this, there was a dramatic increase in the population level in 1979, suggesting the inadequacy of the relationships used for k_o and k_1.

Using the spring temperature data from Woodhill Forest (Appendix 14-17) and model 2, the population dynamics in the Wharepapa plot were simulated between 1967 and 1979. These are shown in

Table 14–28 Black beetle population densities (number per m^2 in February) predicted from the two models of population dynamics in the Wharepapa plot between 1975 and 1979, and actual densities at sampling.

Year	Actual Density	Predicted Density	
		Model 1*	Model 2
1975	109**	109	109
1976	63	78	68
1977	24	26	29
1978	46	22	21
1979	105	20	21

* Population model as shown in Table 14–28

** The actual population density recorded in February 1975 was taken as the initial density with each model.

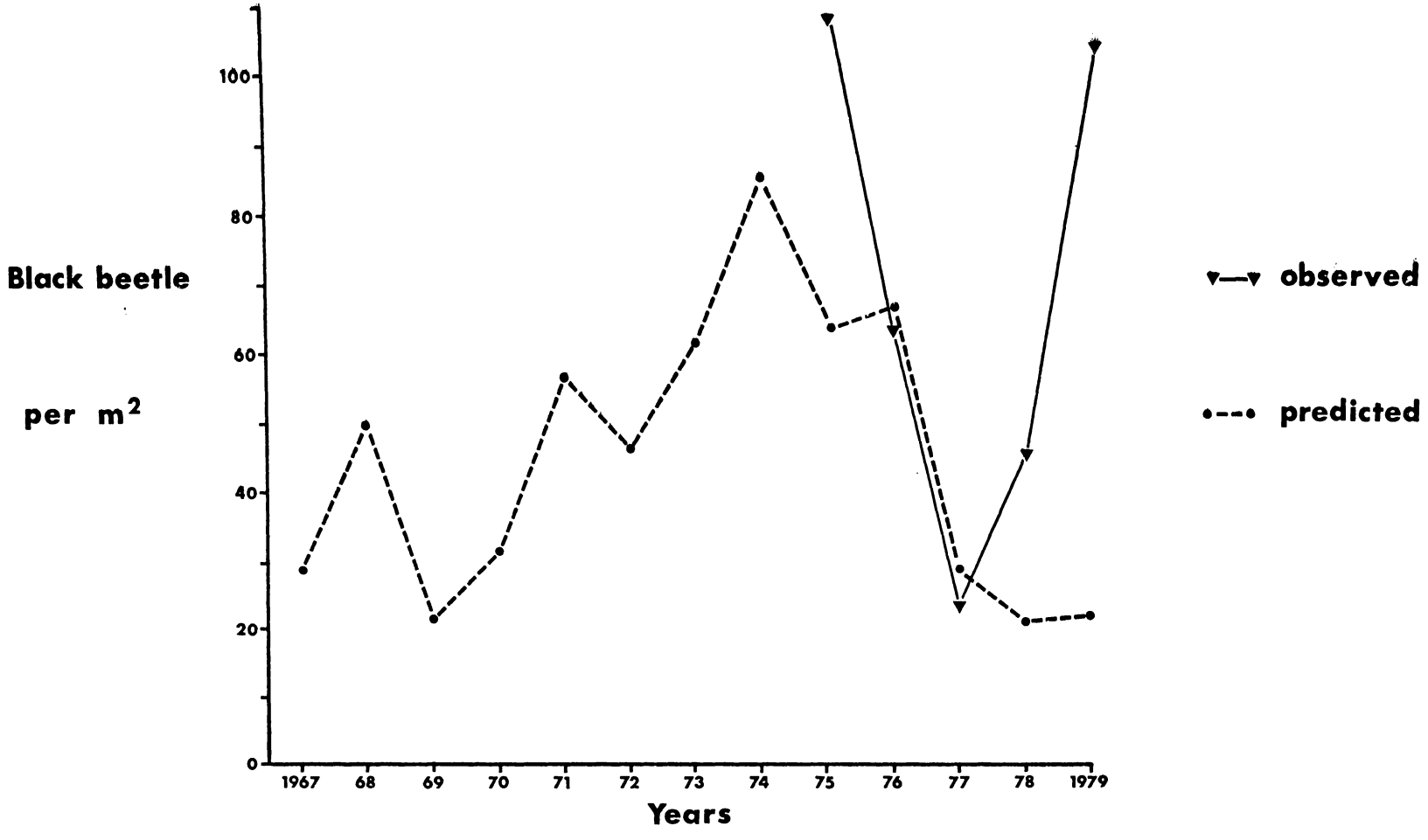


Figure 14-12 Black beetle population densities per m^2 in February predicted from the Wharepapa population model 2 over the period from 1967 to 1979, and the observed population densities in the Wharepapa plot over the period from 1975 to 1979.

Fig. 14-12. As pointed out with reference to the simulation using the paspalum model, black beetle population densities were likely to be low in the mid-1960's. For this reason, simulation commenced in 1967 using an initial density of 29/m^2 which was the lowest recorded in the Wharepapa plot between 1975 and 1979. However, regardless of the initial starting density, February population levels return to those shown in Fig. 14-12 within three generations.

Population numbers predicted from the model peaked at 85/m^2 in 1974. This was the year that the farmer first noted damage on the Wharepapa site. In response to low spring temperatures since 1976, the predicted densities decreased to a level of 20/m^2 in 1979. In contrast, the actual population density in the plots increased to reach a level in 1979 similar to the 1975 density. The simulation using Model 2 has revealed reasonable agreement between high predicted numbers and years when black beetle caused pasture damage as shown in Fig. 14-11. However, the poor agreement between the predicted and actual densities in 1978 and 1979 indicates the unsuitability of the k_o and k_1 relationships derived from the paspalum model when applied to the dynamics in the Wharepapa plot. The relatively low population level recorded when the Wharepapa plot was sampled in July 1978 (Appendix 14-2) suggests that either fecundity was greater than the assumed value of 10 eggs/female and/or considerable adult movement occurred in the spring from more favourable overwintering sites adjacent to the plots which may have lower winter soil moisture levels. The reasons for this apparent dispersal taking place over a relatively cool spring are unexplained. It must be remembered however that because of very high soil moisture levels on the plots over the winter, induced by podzolised soil type, the dynamics of black beetle populations

at Wharepapa could be expected to be dissimilar to those in many other areas. For this reason the relationships describing the dynamics in a paspalum sward are unlikely to mirror the situation at Wharepapa.

CHAPTER 15

DISCUSSION OF POPULATION ECOLOGY SECTION

Extrapolation of the conclusions from this section outside the study areas is difficult without data from similar studies at other places in the black beetle distribution. In spite of this constraint, there is much to suggest that the population ecology of black beetle exhibits marked differences in comparison to other pasture scarabaeids in New Zealand. In this chapter, the sampling plan and population characteristics will be discussed, followed by an examination of the population dynamics of black beetle.

I SAMPLING AND POPULATION DISPERSION

(1) Population sampling

As reviewed in Chapter 3, much of the recent innovative research on the development of sampling methods and extraction techniques for soil inhabiting scarabaeids, designed to provide accurate population estimates for life table studies, was carried out by East (1972) and Kain (1975) for grass grub. Much of the black beetle sampling programme was inevitably derived from the techniques evolved from these studies. Understandably, the methods are very labour intensive as scarabaeid populations spend virtually all of their life cycle within the soil. However, where there are sufficient resources available, it would appear that the sampling and extraction techniques have widespread applicability for population studies.

The 10 cm diameter soil core was found to be much more efficient on the basis of cost and precision than the spade square as found by East (1972) and Kain (1975) for grass grub. The larger sample unit consistently overestimated black beetle larval, pupal and adult populations due to problems in accurately delineating the sample area and from individuals outside the sample area entering the sample hole from the dry powdery soil layer which is a product of larval feeding just below the soil surface. Due to the need to transport samples from the study site to the extraction laboratory to obtain population estimates of the egg and small larval stages, the 10 cm diameter soil core was also chosen as the sample unit to minimise the volume and weight of individual samples.

Cool storage of samples at 5 ^{o}C was found to be necessary to prevent the escape of the very mobile adult stage from the samples when extraction was delayed after sampling. At this temperature all life stages, living, dead and diseased, could be held intact for up to three weeks, with minimal change in condition. In practice however, samples were processed within one week of sampling using the extraction system of Kain and Atkinson (1976), developed for grass grub. This was found to be satisfactory for recovering eggs and small larvae of black beetle from the soil. For the larger larval stages, pupae and adults, it was found that hand sorting of the crumbled soil cores gave recovery efficiencies of 98% or better, without the need for the samples to undergo a washing and wet sieving system.

Milne (1959) considered that regular periodicity in the sample universe would be most unlikely to ever occur. No regular periodicity was evident in the Otakanini and Wharepapa study plots, and due to their relatively small size, uniform soil type and pasture composition,

the centric systematic area-sample system of Milne (1959) appeared to give reasonable results for black beetle population sampling. As discussed previously, a system of stratifying sampling on damage as done by East (1972) and Kain (1975) would have increased the precision of the sampling estimates considerably. This was not possible for black beetle however and the only relationship which may permit stratification would be pasture composition as noted in Chapter 9. It is evident that further investigation of this apparent oviposition preference for paspalum is necessary in pasture of mixed species composition where paspalum is present.

The problems of sampling black beetle populations were compounded by the very dynamic nature of the black beetle life cycle. The larval stages are of a very short duration with a long adult life and considerable overlap of the life stages compared with other scarabaeid pests. Oviposition was found to commence as early as September and extended into December, with female adults being found with fully developed eggs in the oviducts as late as February. This finding is in marked contrast to grass grub. Kain (1975) found that grass grub oviposition at a particular site took place over two to three weeks, and age-specific sampling was possible for the egg and other life stages when the population comprised 90% of the target developmental stage.

Such an approach was not possible with black beetle and as a compromise, sampling was carried out which gave considerable overlap of the life stages present at most sampling occasions. The major problem was the inability to obtain an accurate estimate of the egg population. In some generations, mistiming of the December sample grossly underestimated the egg population and resulted in large

apparent population increases between December and February. The extended oviposition period is one of the very real problems associated with population studies of black beetle, and the effect of this on the construction of life tables is discussed later in the chapter.

(2) Population dispersion

The analysis of the spatial distribution of the populations and the precision of the population data revealed the difficulties in the conduct of population dynamics studies on black beetle, relative to other scarabs such as grass grub. Low population densities give rise to apparent marked skewness of the data, invalidating normal parametric statistical techniques and necessitating the adoption of excessively large sample sizes in order to obtain reasonable precision. This characteristic was particularly evident in the black beetle populations in the ryegrass and ryegrass/white clover plots. In general, marked skewness was evident at the egg and early larval stages indicating an aggregated distribution. This skewness had decreased by March when the distribution followed the random dispersion described by the Poisson model. Skewness increased to a high level in the September samples, when zero counts were usually obtained from more than 90% of the sample units. This finding may simply be an artifact of the very low adult population density in September. Kain (1975) found a similar pattern of skewness with population development in grass grub, but in contrast to black beetle, at no stage did grass grub dispersion approach the random distribution described by the Poisson. East (1972) did however record a random distribution of third instar grass grub larvae using 4 cm diameter sample cores.

With some exceptions, the observed distribution of the December population estimates did not differ significantly from the negative binomial model. It is not possible to conclude if population development between December and February is the cause of the actual change in population dispersion because of the variability of the data. Black beetle oviposition does however take place in an aggregated manner in the soil even though eggs are deposited singly rather than in clusters as occurs with some other scarabaeids. Larval movement during feeding may reduce aggregation producing the more random pattern evident in February.

The number of samples required for the central limit theorem to apply was found to be considerably less than that required for a relative standard error of the black beetle population mean of 10%, which was similar to the findings of East (1972) and Kain (1975) for grass grub populations. The higher the density of black beetle eggs and small larvae at the December sampling, the lower the number of samples necessary to satisfy the central limit theorem and a 10% relative standard error of the mean. As skewness decreased in February, the sample size necessary for the two conditions decreased, but increased again in September, reflecting the low population numbers.

The low precision of the data from the ryegrass and ryegrass/white clover plots arising from the low population densities, high variances and very skewed distributions suggest this population data should be interpreted with caution. At the higher densities in the paspalum and Wharepapa plots, a reasonable level of precision was attained with relative standard errors of the sample mean being usually less than 20% and in February in particular, nearly always less than 10%.

The black beetle sampling data reveal that for life table studies and mortality analyses, the number of sampling occasions necessary and the sample size required for a reasonable level of precision is likely to be unacceptably high in terms of cost at other than relatively high population densities. This cost could be reduced significantly if some simple system of sample stratification could be developed. The results obtained do provide some worthwhile evidence on the optimum sampling occasion to minimise cost when an extensive survey is being undertaken. This situation could arise where population numbers are being regularly monitored on a wide range of soil and pasture types, aspects and farming systems to provide evidence of distribution changes or seasonal fluctuation. Clearly, such a programme is most feasible in the late larval instar and pupal stages in February, when the sample size required to provide accurate population estimates is at a minimum.

II POPULATION ECOLOGY

(1) Population change

(a) The role of weather in black beetle population change

At the commencement of population monitoring at Otakanini and Wharepapa in 1974, population numbers were considered high enough to cause economic damage over much of the black beetle distribution. On the evidence of changes in population trend, black beetle populations decreased at some stage over the study period in all plots, but on the basis of numbers in the 1978/79 generation are increasing again in the paspalum and Wharepapa plots. Following the damaging population levels of 1975/76, numbers in the ryegrass and ryegrass/

white clover plots have remained at sub-economic levels. Changes in these plots reflect the general situation in most of the established areas of black beetle distribution where population numbers have remained low since 1976 (Watson, pers.comm.).

Watson (1978) considers this pattern of population fluctuation is influenced by seasonal conditions, and that as black beetle is at the lower limits of its geographic range, it is therefore sensitive to climatic factors favourable and unfavourable for population survival, increase and dispersal. The observations from this study of the influence of spring and summer temperatures on populations as shown in the simulated dynamics strengthen this conclusion. Watson considered that black beetle tended to occur in high numbers in ryegrass-based pastures only in warm years with populations restricted in unfavourable seasons to localised nucleus areas where conditions remain favourable for survival. The population dynamics in the paspalum plot and to a lesser extent the Wharepapa plot, suggest that these pastures may be classed as refuge areas in unfavourable seasons.

From studies of black beetle flight in New Zealand, Watson concluded that opportunities for flight and hence immigration are severely limited by temperature. For this reason, true dynastid-type flight as discussed in Chapter 1, especially from adult over-wintering sites to larval development sites in spring, is likely to occur only infrequently as has been found since 1973. The population dynamics studies have shown the importance of adult dispersal to population change with winter unfavourable areas being repopulated in spring from favourable refuge areas. Conditions unfavourable for spring flight, along with generally low population

numbers except in localised areas, would help to explain why economically damaging populations have not occurred in ryegrass based pastures since 1976.

The data presented in Section 2 on the interaction of temperature with egg development, larval feeding and growth showed the importance of soil temperatures greater than 15 ^{o}C for optimum development. Records of soil temperatures at Otakanini during pre-adult development revealed that periods of temperatures below 15 ^{o}C occurred most frequently in early spring during oviposition and egg development. Watson (unpublished results) has found considerable variation in ambient soil temperatures existing between seasons. Consequently, spring temperatures are able to exert a major influence on population development.

The population studies have greatly clarified the pathways through which spring-summer and autumn weather influences population change. Among the key factors, summer mortality (k_1) in the paspalum and Wharepapa plots, late summer mortality + autumn-winter disappearance ($k_2 + k_3$) in the ryegrass plot and winter-spring disappearance (k_4) in the Wharepapa and ryegrass plots are all influenced by the rate of population development. It was found that k_1 could be modelled as a simple function of ΣT_D (i.e. spring temperatures) and hence variation in spring temperature was used to predict population change in the paspalum and Wharepapa models with an apparent accurate prediction of outbreak years of black beetle.

When oviposition or egg development was delayed in the spring giving a lower level of population development in December, summer mortality was greater in the paspalum, ryegrass and ryegrass/white clover plots. Although no significant relationship could be shown

between k_1 and the level of population development in the Wharepapa plot, this does not preclude a similar interaction to that at Otakanini. It would appear that mortality due to factors such as high summer soil moisture levels are accentuated in seasons when population development is slower.

Although the data did not reveal any relationship between temperature and the variation in natality (k_o), ΣT_D may influence k_o through an effect on immigration or fecundity or even an interaction between temperature and Adelina sp. This interaction with k_o could not be elucidated further due to the problems in separating the action of the k_o and k_1 mortalities.

The importance of population development over the summer to population change was demonstrated by the significant relationship between $k_2 + k_3$ and the level of population development in February in the ryegrass and Wharepapa plots. In seasons of lower than average summer temperatures, larval development is slowed and a lower proportion of black beetle are in the adult stage by autumn. This restricts the opportunities for dispersal by flight before the temperatures decline below the threshold conditions for autumn flight identified by Watson (1978). The population studies showed that it is probable that autumn dispersal is a major component of population decrease over the late summer and autumn to winter period, in ryegrass based pastures.

The level of mortality over the winter-spring period (k_4)in the Wharepapa plot was influenced significantly by the level of population development in May. Under the dense pasture cover at Wharepapa, the soil temperature and moisture conditions appeared to result in a significant proportion of the population being in the pre-adult stages

at the commencement of the winter. This resulted in considerable mortality over the winter when very high soil moisture levels were evident. It is notable that spring, summer and autumn weather influenced rate of development and therefore population change.

(b) Effects of pasture species

The effect of pasture plant species on black beetle populations is dependent on the favourable or unfavourable influence the species have on the ecology of the insect. The population levels found in the study plots demonstrate that white clover, lucerne and phalaris/white clover had an adverse effect on black beetle populations. The very good correlation evident between the effect of these species on the food consumption, growth and survival of larvae, fecundity and oviposition preference of adults described in Sections 2 and 3, and population numbers in the Otakanini plots, confirms the classification of favourable and unfavourable pasture plant species.

Ryegrass based pastures must be considered as intermediate between favourable and unfavourable species in their effects on populations. The dynamics in these pastures are characterised by wide fluctuations in population numbers relative to paspalum pasture and also probably to most kikuyu pasture. The large magnitude of $k_2 + k_3$ and k_4 in the ryegrass and ryegrass/white clover plots even in the absence of pasture damage suggests that while ryegrass is apparently a good spring and summer host on the evidence of adult fecundity and larval growth, it is an unfavourable adult habitat in autumn and winter and a high level of dispersal or mortality occurs in these pastures. The favourable nature of ryegrass as a summer habitat for larval development would appear on the basis of feeding

studies to be due to its favourable nature as a larval diet. As larvae may be primarily organic matter (O.M.) feeders, the relatively high level of O.M. in ryegrass pasture due to the senescence of plants in drought may also be important.

The high levels of $k_2 + k_3$ and k_4 may reflect better opportunities for autumn flight due to faster development. This effect would enable migration to occur from these ryegrass based pastures apparently unfavourable as overwintering sites. The population model indicates that outbreaks in ryegrass based pastures appear to depend on spring immigration. A high level of immigration must have taken place in the 1975 spring period for the very high damaging population levels of the 1975/76 summer to have been attained. The very restricted time period of the study prevented further insight into the importance of k_o. However, if the life table study had extended over a longer period and included a range of years from warm to cool, then it is possible that k_o (or $k_o + k_1$) may have been found to be a key factor for population change in the ryegrass and ryegrass/white clover plots, as well as the paspalum.

In contrast to the ryegrass based plots, the dynamics in paspalum were characterised by relatively stable populations with low k_2, k_3 and k_4 values. This may reflect a lack of dispersal opportunities (due to a reduced rate of population development) compared with ryegrass and/or preference by adults for the more favourable paspalum food source in autumn/winter. Successful overwintering as evidenced by low k_3 and k_4 values means that high summer larval populations in paspalum are not so dependent on spring immigration and paspalum therefore acts as a refuge in cool years.

Kikuyu pasture probably acts in a manner similar to paspalum, but this did not occur at Wharepapa which is somewhat atypical of other kikuyu areas due to its high winter soil moisture levels. The high value of k_4 in the Wharepapa plot may reflect this winter wetness.

The dynamics of black beetle populations show some similarities to the proposals of Wellington (1957,1960,1964) and Taylor and Taylor (1977), discussed in Chapter 3. Wellington considered that during harsh climatic conditions, populations of western tent caterpillar in marginal areas were killed, while those in favourable habitats survived to recolonize vacant areas when conditions permitted. Taylor and Taylor noted that 'environmental hostility' was transient, and that areas unsuitable for colonization eventually recovered their suitability and were re-occupied by migrants. The migration by black beetle from paspalum refuges to ryegrass based pastures could be considered to follow such a pattern.

The effect of mixtures of favourable or intermediate species and unfavourable species (e.g.ryegrass/white clover) on population change, appear to differ somewhat from intermediate species alone. Although values of $k_2 + k_3$ and k_4 were similar in both ryegrass and ryegrass/white clover, there is evidence for the adverse effect of the unfavourable species playing a role in these mortalities. Population development was reduced in the ryegrass/white clover plot in February relative to that in ryegrass. Rate of larval development in ryegrass/white clover was also shown to be slower compared with ryegrass in Chapter 6. As $k_2 + k_3$ was shown to be influenced by the rate of development in ryegrass/white clover it is possible that mortality due to the unfavourable white clover may have been as important as dispersal in determining the magnitude of the autumn-winter disappearance.

In mixtures of favourable and unfavourable species (e.g. paspalum/white clover), the adult oviposition/feeding preference for paspalum demonstrated in Chapter 9 might remove the effect of the unfavourable species or possibly delay it until larvae (which are indiscriminate feeders) develop.

(c) Comparison with other pasture scarabs

The effects of climatic variation on soil temperature and moisture are generally important in scarabaeid population fluctuation (e.g. Maelzer, 1961a; Milne, 1963; Davidson et al., 1972a,b; 1978b; East, 1972; Kain, 1975). Although East (1978b) notes that the ultimate regulation of population growth by density dependent mortality may be a general phenomenon, the frequency with which this mortality operates may depend on how often weather conditions allow the population density to reach the threshold for the mortality to operate. East and Kain found that fluctuations in grass grub populations occurred in response to unfavourable physical soil conditions. Davidson et al. considered that in the Australian environment, the effects of soil moisture and temperature on scarabaeid mortality override the density effects.

Although high soil moisture levels in summer and winter can be detrimental to black beetle populations, in the normal range of N.Z. soil temperatures, higher summer soil temperatures are likely to be favourable through their influence on the rate of population development. In contrast to black beetle, Kain concluded that fluctuations in grass grub populations occurred in response to unfavourable physical soil conditions such as high soil temperatures and/or low soil moisture levels in summer, and high levels of soil

moisture over the spring. This difference in the effects of weather on populations between grass grub and black beetle has a direct influence on the distribution of the two pests. In much of the more northern distribution of black beetle, grass grub populations do not occur. In areas of overlap of the two species, climatic conditions may result in soil moisture and temperature levels unfavourable to grass grub survival but favourable to black beetle survival.

Kain (1975) considered that adult dispersal plays no significant role in grass grub population change compared with natality and mortality in determining population numbers. This is in marked contrast to the situation with black beetle where the importance of dispersal is now well established.

(2) Population regulation

High variability of the life table data prevented proof of density relationships for most individual mortalities. Nevertheless, there appear to be two distinct patterns of black beetle population dynamics as demonstrated by the population models. One pattern typical of refuge areas is shown in paspalum pasture (and to a lesser extent by the kikuyu pasture at Wharepapa), where the simulated population never declined below $27/m^2$ (Fig. 14-11). The density dependent factor (k_o) is a vital component of the paspalum model since the removal of all density dependence from the model resulted in unrealistically high population levels being attained. In contrast, in ryegrass based pastures, black beetle populations fluctuate rapidly between high and low levels. At least in unfavourable years, population regulation probably does not occur at all in these pastures.

(a) Paspalum and kikuyu pastures

The possible density dependence of k_0 suggests that variation in natality is sensitive to population density. This may result from a reduction in female fecundity or longevity or less adult immigration into the pasture at higher densities. Alternatively the influence of disease on these parameters may be greater at higher population densities. In addition, there was some suggestion in the Wharepapa plot that disappearance over the autumn-winter (k_3) had some degree of density dependence. Density dependent mortalities are usually caused by natural enemies or by intraspecific competition. Disease is the only likely natural enemy known to be possibly important for black beetle in New Zealand in view of the findings of Archibald et al. (1975) and King and Mercer (1978).

There is some evidence to suggest that Adelina is an enzootic disease in black beetle populations, i.e., the disease is present in the population but not in outbreak proportions. Under some conditions, an enzootic may become an epizootic, so controlling populations (Burgess, 1973). Hurpin (1965) found that an epizootic of Nosema melolonthae in the scarabaeid Melolontha melolontha killed most individuals in a population during an outbreak. Although no density dependence could be proved in any of the mortality periods in the black beetle life tables where disease may have played a role, the fact that pathogenic micro-organisms can act as density dependent factors within a population was noted by Steinhaus (1954) and Franz (1961; cited in Surtess, 1971). Maddox (1966; cited in McLaughlin, 1971) reported a high incidence of a protozoan disease in an outbreak population of armyworm Pseudaletia unipuncta, but only a very low level of infection

in a sparse population. A similar relationship was noted between the level of infection with the fungus Metarrhizium anisopliae and porina Wiseana spp. density (Pottinger, pers. comm.).

Burgess (1973) noted that density dependence tends to stabilize populations, whereas delayed density dependence leads to oscillations that in turn favour enzootics and alternation of enzootic with epizootic. If Adelina was transmitted transovarially from one generation to the next, then delayed density dependence may occur in the field. As infection with coccidian protozoans however has only been shown to occur per os (McLaughlin, 1971), it is more likely that black beetle infection with Adelina is by ingestion of the spores from the soil by larvae, or by cannabalism. This would suggest that a degree of direct density dependence exists with higher infection rates occurring at higher population densities. Davidson et al. (1978b) considered that increased densities of scarab species on the northern tablelands of N.S.W. would result in increased disease infection levels. The density relationship of Adelina will depend on the pathogenicity of the disease and the longevity of the spores. It may therefore be concluded that although the existence of density dependent mortality was not proved, Adelina may act in this manner at the higher densities found in the paspalum and Wharepapa plots, so affecting k_0 and k_3.

In the absence of further knowledge as to how the mortality components of k_0 and k_3 respond to changes in population density, the true cause of any density dependence must remain unclear. As the influence of k_0 is associated with k_1 due to the timing of sampling problem, further population studies are necessary where a more accurate estimate of egg numbers is gained through intensively sampling over the oviposition period.

There is some evidence of the density dependence of k_2 in the paspalum plot which could arise from larval combat mortality. The simulated population densities in the paspalum plot showed that February levels of over $100/m^2$ could occur. Field population densities of over $100/m^2$ have also been found in some paspalum dominant sites in February (King, unpublished results). It is possible that larval combat may occur at these densities, even though pasture damage may not be visible due to the tolerance of this pasture species. A similar effect may occur in kikuyu, where field populations of up to $180/m^2$ have been recorded in February.

The significance of the density dependence of the proportion of females (k_6) in the paspalum plot is unclear. It was concluded in Chapter 14 that this may simply be an artifact arising from the number of subplots with no adult population present in the spring. In simulations of population change with the paspalum model, it was found that setting k_6 at an average value in model 2 resulted in similar population densities in February to those predicted with k_6 density dependent. The density dependence of k_6 is so weak compared with that of k_o that it is insignificant in population regulation even if it is real.

The lack of importance of the inverse density dependence of k_6 to population regulation in the Wharepapa plot was also evident from the Wharepapa model. It is concluded that even if the inverse density dependence was real, it was so weak as to be of little or no importance to population regulation.

As mentioned previously, there was some suggestion in the Wharepapa plot that autumn–winter disappearance (k_3) was density dependent. This mortality could be indirectly influenced by climatic

conditions. Favourable summer conditions result in greater survival, higher population numbers, advanced population development and hence a greater chance for autumn adult dispersal to take place. Such a mechanism could be interpreted as a means of population regulation.

(b) Ryegrass pastures

In contrast to paspalum and kikuyu, ryegrass is much less tolerant of larval feeding. Larval combat may occur in ryegrass based pastures at densities which cause severe pasture damage (40 to 60/m^2), possibly influenced by increased larval movement in response to a reduced food supply. Such densities appear to be reached only infrequently and so population regulation through combat mortality in ryegrass pastures is likely to be relatively rare.

Both East (1972) and Kain (1975) constructed population models for grass grub based on density dependent population regulation which included larval combat over the autumn-winter period. Grass grub populations however reach very much higher larval densities than black beetle. It is of interest in considering the possibility of density dependent combat mortality in black beetle populations, that Davidson (cited in Adena, 1978) considered there is no evidence of cannabalism or any other density dependent mortality factor in Sericesthis nigrolineata populations in Australian pastures. Consequently the simulation model of the population dynamics of this species is based on density independent processes (Adena, 1978), although the destruction of the soil environment which occurs at high densities could be deemed indirectly density dependent. These

findings suggest that S. nigrolineata may resemble black beetle in ryegrass pastures in its lack of density dependent regulation.

Adult dispersal in the autumn-winter period is likely to be one of the major components of $k_2 + k_3$ mortality in the ryegrass plot. As was the case with k_3 in the Wharepapa plot, this mortality may be related to density, although only indirectly. Favourable spring and summer temperatures are likely to favour survival and higher densities as well as a more advanced level of population development, and so adult dispersal in the autumn. However, the ryegrass life tables (Appendix 14-7 and 14-8) show that $k_2 + k_3$ was high, regardless of density and so there is no evidence for a density dependent relationship of $k_2 + k_3$.

It may therefore be concluded that population regulation in the sense of returning populations to an equilibrium level does not often occur in ryegrass based pastures due to the infrequent occurrence of seasonal conditions favouring adult spring dispersal and so high larval densities.

(3) Pest status and control strategies

Black beetle, like most of the serious pasture pests in New Zealand, was considered by Kain (1978) to occupy an intermediate place on the r - K continuum. This conclusion appears reasonable as Southwood (1977) stated that intermediate pests will achieve pest status in natural situations only occasionally. In contrast, the extreme r-strategists are pests virtually all the time.

The results of the population studies reported in this thesis would suggest that the position of black beetle on the continuum must be considered from the point of view of the suitability of the habitat.

Habitats in which tolerant grasses such as paspalum and possibly kikuyu form the major pasture components, appear to remain suitable both within and between generations, although it has been suggested by farm advisors (Langton, pers.comm.) that high black beetle populations over several generations will reduce the paspalum component, so changing the suitability of the habitat. On the other hand, pastures based on ryegrass which appear to be favourable for larval development only and which are highly susceptible to larval feeding damage, represent a much more unstable habitat. For these reasons, black beetle could be considered closer to a K-strategist or equilibrium species adapted to stable habitats in paspalum pastures, and closer to an r-strategist in ryegrass based pastures.

The most important feature of the synoptic three-dimensional landscape for animal population dynamics of Southwood (1977) and that modified for insects by Huffaker et al. (1977) is the natural enemy ravine which separates the endemic and the epidemic ridges, i.e. the action of natural enemies prevents endemic populations from becoming epidemic populations. Southwood considers that intermediate species may become pests because changes in the environment normally caused by man have reduced or eliminated the natural enemy ravine. Alternatively, man has introduced a species to a new area where it is free of natural enemies.

This situation is certainly true for black beetle, introduced from southern Africa into a pastoral environment, where apart from relatively localised areas of disease, no significant natural enemies appear to be present. Southwood noted that disruption of the natural enemy complex of intermediate species precipitates a release from the endemic to the epidemic ridge where stability is determined by intra-specific competition.

Kain (1978) noted that the pest status of a species, was a function of both insect density and host plant susceptibility, with the former variable being determined by both the position of the species on the r-K continuum and its position within its habitat range. Huffaker et al. (1977) considered that "towards the margins of a species geographic range, climatic factors may be largely responsible for population change". This is an important concept to consider when interpreting the pest status of black beetle which is near the edge of its geographic and ecological range in New Zealand (Watson, 1978). The population models indicate that seasonal temperatures have the major influence in determining changes in black beetle population numbers from generation to generation. The predictions of the model are in agreement with the history of sporadic black beetle pest outbreaks in New Zealand.

The approach to control strategies will have to vary depending on the habitat of black beetle, which influences what type of pest it is. Southwood considers one of the most important characteristic features of r-strategists is their high migratory tendency essential for their movement from a 'dying (or unfavourable) habitat', to a new one, while MacArthur and Wilson (1967) noted that r-species are adapted to temporary habitats. This would appear to describe black beetle in ryegrass/white clover pastures from the dispersal studies of Johannesson (1975) and Watson (1978), and the observations in this study.

Southwood observed that the most powerful tactic for the control of r-species rests with the rational use of insecticides. The simulation of population dynamics using the paspalum model and

extrapolation of this to ryegrass based pastures suggests that the sum of the mean temperatures in September, October and November must exceed 41.5 ^{o}C for a population increase to occur. Monitoring of these temperatures, associated with some sampling to determine adult population numbers, may allow the prediction of outbreaks and prophylactic applications of insecticides in early December. This is the best time for treatment as shown by Esson (1973), Watson and Webber (1976).

The use of insecticides may also have a place against populations in paspalum dominant areas, localised on a farm, particularly if these are considered as refuge areas in unfavourable seasons, and as over-wintering sites. Although this would only be feasible on a small localised scale, insecticide application against the adult, possibly in the form of baits, may reduce the level of re-invasion of pastures, when the distribution changes from localised to generalised.

Southwood considers that the most appropriate and dominant strategies with intermediate pests rest with biological or integrated control with a significant natural enemy component. In spite of the uncertainty as to the type of species black beetle is, the concept of biological control is an important one particularly in habitats tolerant of black beetle and supporting higher, more stable populations such as pastures containing paspalum or kikuyu. Further understanding of the relationship between Adelina induced mortality and black beetle may suggest ways in which the pathogenicity can be enhanced, or even the efficacy or desirability of introducing the pathogen into areas where it does not at present occur. Kain (1978) suggests that similar protozoan diseases regulate grass grub populations at low

endemic levels. In addition, the current attempts by Entomology Division, D.S.I.R. to introduce and establish natural enemies of black beetle from South Africa into New Zealand pastures, are a positive step to remedy the absence of significant natural enemies. Any success with this approach could set a lower stability point for black beetle populations.

Host plant resistance is recognised as being an appropriate control tactic for pests located at all positions on the r-K continuum (Southwood, 1977). The unfavourable nature of legumes and phalaris to black beetle populations has been detailed in this thesis. Although pure stands of white clover are seldom encountered in most farming systems in the absence of seed production, lucerne is an impcrtant forage crop in much of the area of black beetle distribution. In addition, herbage and dry matter production measurements from mixed phalaris/white clover pasture (King et al., unpublished results) have shown this pasture type to have considerable potential as a high producing dairy pasture. For this reason, resistant pastures containing phalaris may have a place as special purpose pastures in areas where black beetle has previously caused severe pasture damage.

The strategy of manipulating the composition of existing pasture to provide an unfavourable environment (e.g. to clover dominance) is fraught with hazards. East and King (1977) and King and East (1978) have pointed out that clover dominance can produce a rapid increase in legume-feeding pests such as grass grub and white fringed weevil. This possibility must be borne in mind where complexes of insect species occur.

The use of grazing management has been suggested as a control strategy for use in pest management systems (East, 1978a; Roberts, 1978;

Robertson et al., 1978). Reducing the pasture height over oviposition was shown in Chapter 9 to have no apparent effect on black beetle population levels. Similarly, grazing pressure did not influence population numbers or survival in a trial carried out at Otakanini (King et al., unpublished results), although the rate of population development was greater in shorter pasture over the summer. Although these trials did not suggest a possible control strategy using grazing management, there was a marked difference apparent in pasture damage from similar black beetle populations at different levels of grazing pressure. Hard grazing of pasture which was supporting an economically damaging level of black beetle over the summer accentuated the pasture damage. Lower grazing pressure places less stress on the plant and allows a greater chance of recovery once pasture growth commences again in the autumn.

In terms of the relative pest status of black beetle in paspalum and ryegrass pastures it is apparent that there is an equal need for control measures in both pasture types. Although pest outbreaks in ryegrass based pastures are spasmodic, the low tolerance of this pasture species to damage necessitates the use of control strategies to prevent the occurrence of severe pasture damage and the change to a less desirable pasture composition from an agronomic point of view. It is in this situation that the technique of prediction of pest outbreaks allowing some rationalisation of the use of insecticidal controls will be most valuable. In spite of paspalum pasture being more tolerant of black beetle feeding, evidence does exist that this component can be removed from the pasture over a number of years of damage. For this reason it

is important to protect this species as, especially in northern New Zealand, it forms a valuable summer producing component of the pasture. In addition, the role of paspalum areas in providing refuge areas for populations in unfavourable seasons necessitates the investigation of the use of control measures to reduce black beetle populations and through this, the ability of these areas to act as sources for re-infestation of ryegrass based pastures.

It may be concluded that in common with most soil-inhabiting insect pests, black beetle control strategies pose significant problems. The situation with black beetle in contrast to the dynamics of grass grub is confounded by the dispersive abilities of the adult and by the sporadic nature of the pest in ryegrass/white clover pastures. This introduces problems in developing a pest management system which are not encountered with insects such as grass grub. Kain (1978) concludes "that a major tactic in pest management strategies for r-pests operating in fringe habitats will undoubtedly be the prediction of pest outbreaks and the implementation of appropriate control measures".

While much research is necessary to further develop and improve control strategies, the work of Watson (1978) and the results of these population studies suggest that the prediction of black beetle outbreaks based on seasonal conditions is possible. It is apparent however that further intensive study of black beetle ecology is necessary to refine the population model. In particular, the effect of seasonal conditions on adult migration in the spring, on adult oviposition, fecundity and longevity, and on population development and mortality require further study. The main value of the approach adopted in this study was that the study of the dynamics under

different pasture types has been successful in identifying the major differences in the dynamics between species, i.e. between paspalum and ryegrass based pastures. However, the approach has severe limitations when dealing with an insect which has great dispersive abilities.

Price (1975) considered that the use of a single study plot can produce often spurious conclusions and that more emphasis should be placed on investigating the spatial dynamics of the insect. Likewise, East (1978b) concluded that without extensive population studies designed to monitor spatial changes in density, a complete picture of black beetle ecology was impossible. The study reported in this thesis has been invaluable in identifying the important parameters affecting population change and regulation. Research must now proceed to more extensive population studies in both ryegrass based pastures, and those containing paspalum, coupled with detailed studies of the factors influencing adult dispersal.

III SUMMARY

The results reported in this section represent the first attempt to sample black beetle populations intensively, and to quantify the population dynamics of the insect through the construction of life tables. In spite of the difficulties imposed by the very dynamic nature of the life cycle and the dispersive abilities of the adult, a number of points have emerged which make a considerable contribution to the understanding of the problems encountered in studying populations and to knowledge of the population ecology of black beetle.

1. The 10 cm diameter soil core was found to be more efficient on the basis of cost and precision than the spade square for sampling black beetle populations.
2. The extraction system of Kain and Atkinson (1976) was found to be satisfactory for recovering eggs and small larvae of black beetle from the soil samples.
3. Significantly more black beetle were found in the top 3 cm of the soil profile at all stages of the life cycle. No individuals were found at a depth greater than 9 cm and few at 6–9 cm.
4. The extended period of black beetle oviposition prevents the accurate estimation of the total egg density without intensive sampling over the oviposition period.
5. The frequency distributions of all population sampling estimates showed marked positive skewness. Within a developmental stage, the lower the population mean, the more skewed the distribution. Skewness was very marked at the egg and small larval stages, decreased by February and then increased reaching a high level at the low adult densities in September.
6. Generally, the observed population distribution in December did not depart significantly from that described by the negative binomial model, while in February, March, May and June the distribution was random and fitted the Poisson series.
7. Using a combination of stratified sampling with proportional allocation and centric systematic area sampling, relative standard errors of the sample mean were usually less than 20% at the higher population densities in the Wharepapa and paspalum plots. In February, the level of precision was nearly always better than a 10% relative standard error indicating that for survey purposes,

sampling should be carried out in February when the sample size required to provide precise population estimates is at a minimum.

8. Black beetle populations in the lucerne, white clover and phalaris/white clover plots remained at consistently low levels over the study period. This result and the adverse effects of these species previously established on larval and adult ecology, confirms their unfavourable nature and the importance of the plant-insect interaction to population dynamics.

9. Analysis of life tables showed that variation in natality and summer mortality were the key factors causing population change in the paspalum and Wharepapa plots along with winter-spring disappearance in the latter plot and the ryegrass plot.

10. Examination of the density relationships of individual mortalities revealed possible density dependence in the variation in natality, late summer mortality and the proportion of females in the adult population in September in the paspalum plot. In the Wharepapa plot autumn-winter disappearance may have been density dependent and the sex ratio inversely density dependent. All other mortalities appeared to be density independent.

11. There was no evidence that soil temperatures reached high enough levels to cause population mortality. There was strong evidence that high soil moisture levels in December and January can be an important contributor to summer mortality.

12. Temperature was shown to influence the level of population development. Significant linear relationships were derived between summer mortality and population development in December in the paspalum, ryegrass and ryegrass/white clover plots, and between

late summer mortality plus autumn-winter disappearance and population development in February in the Wharepapa, ryegrass and ryegrass/white clover plots. There was a similar relationship between winter-spring disappearance and population development in May in the Wharepapa plot.

13. Damage assessment studies showed that while some loss in pasture production occurred from population densities in February of 60/m^2 and 40/m^2 in the ryegrass and ryegrass/white clover plots respectively, the major effect of black beetle larval feeding was a change in pasture composition to weed and clover dominance. Paspalum was found to be tolerant of larval feeding with no damage being noted at population levels of 50-60/m^2 over several successive generations.

14. Large population decreases between February and September occurred in the ryegrass and ryegrass/white clover plots relative to the paspalum plot regardless of the occurrence of severe pasture damage. This indicated that population change in the ryegrass based plots was not a function of damage but rather of the unfavourable nature of these pastures as other than spring-summer environments and/or the rapid rate of larval development in ryegrass pastures.

15. Predators and parasites did not appear to be significant natural enemies in any of the study plots. The protozoan pathogen Adelina sp. was found to infect a significant proportion of the populations in the paspalum and Wharepapa plots in particular. As no relationships between percentage infection and mortality could be demonstrated, the influence of the pathogen on population trend remains unclear, although the evidence of an adverse effect on fecundity suggests it is potentially important.

16. Spring temperatures over September, October and November recorded at Woodhill Forest were found to be significantly related to the level of population development in December in the paspalum and ryegrass plots. Similarly, summer temperatures over December, January and February were related to population development in February in these plots.

17. Population models were constructed for the paspalum and ryegrass plots. The paspalum model was based on the density dependence of the variation in natality and the relationship between summer mortality, population development in December and spring temperatures. The ryegrass model was based on the latter relationships and that between late summer mortality plus autumn-winter disappearance, population development in February and summer temperatures.

18. Simulation of February densities predicted by the paspalum model showed moderately good agreement with observed densities and population trends over the study period. The use of spring temperatures recorded from Woodhill since 1956 to simulate population dynamics in the paspalum plot revealed a remarkably good correlation between high numbers in the simulated population and years of black beetle outbreaks. Density dependence was found to be essential to the paspalum model.

19. It was concluded that paspalum pastures probably act as nucleus or refuge areas for black beetle populations in unfavourable years. In paspalum, black beetle can be considered as more of a K-strategist adapted to a stable habitat. Adult migration in the spring or increased fecundity appears necessary for population increase to occur, and this plus summer mortality are influenced either directly or indirectly by spring temperatures.

20. Simulation of February population densities using the ryegrass model revealed the contrast in population dynamics compared to the paspalum, with black beetle appearing to be more of an r-strategist in ryegrass based pasture, adapted to the more unstable habitat of these pastures. Due to the large magnitude of population decrease between autumn and spring, adult migration before or during oviposition in the spring is necessary for populations in ryegrass based pastures to reach high levels. Since 1975, cool spring conditions appear to have prevented this happening. Except in favourable years leading to high population densities, density dependent mortalities which cause population regulation are probably absent in ryegrass based pastures.

21. It was concluded from these studies that until the model for ryegrass pastures can be further refined by the gathering of additional data on adult dispersal and population change, the paspalum model provides the best predictive tool. Some prediction of the need for control measures will be possible by assuming outbreaks can be expected when the sum of the mean daily temperature for September, October and November exceeds 41.5 ^{o}C.

22. Simulation of February population densities using a Wharepapa model, adapted from the paspalum model, revealed that adult spring immigration or increased fecundity was necessary for high population numbers to be reached. The dynamics of populations in this plot were however greatly affected by the very wet winter soil conditions resulting from a perched water table. This suggested that the results from Wharepapa are not typical of kikuyu dominated pasture sites.

CONCLUSIONS

In spite of black beetle being an important pest of pastures and crops in New Zealand, little attention has been given to the ecology of the insect. Research has concentrated on *ad hoc* controls which have not been widely adopted. The results of the studies on the ecology of black beetle reported in this thesis allow for the more rational use of existing controls, and the development of a pest management programme. The following general conclusions have been made.

1. In contrast to black beetle eggs which are relatively tolerant of a wide range of soil moisture levels, first instar larvae are very susceptible to extremes of soil moisture. High spring soil temperatures favour optimum development of the early life stages. Food consumption and growth by the two later instars increases linearly with increasing temperature.
2. It is concluded from the relatively high temperature requirements of black beetle pre-adult stages that black beetle is only likely to buildup to pest status following warm spring-summer conditions, and the distribution in New Zealand will be limited by soil temperatures.
3. Development of black beetle from eggs to third instar larvae is possible on a soil diet high in organic matter (O.M.) in the absence of living plant material. First instar larvae appear to feed primarily on O.M. Aggregation of larvae at sites high in O.M. but not at plants has been previously shown to occur. It is concluded that as O.M. stimulates feeding

in the presence of plant roots, black beetle may be primarily saprophagous. Larvae were shown to develop in the top few cm's of the soil profile where soil O.M. levels are higher. Feeding activity in this area inevitably results in ingestion of plant roots.

4. Pasture plant species have a profound influence on many aspects of black beetle ecology. It is concluded from both laboratory and field investigations of larval growth and survival respectively, that all grass species tested with the exception of phalaris, are favourable species. Phalaris and the legumes tested are unfavourable. Larval growth and survival is lower on a grass-legume mixture than on grass alone.

5. Adult females accumulate body fat in late autumn with a peak being reached in June. Fat levels decline as ovarian development proceeds up to oviposition. Diet has an influence on fat levels.

6. Various aspects of adult ecology are influenced by pasture species. Fecundity is dependent on whether the diet is a grass, with the exception of phalaris which is resistant, or a legume. It is concluded that the effect of an unfavourable legume species on fecundity is a function of the length of the period the female feeds on the species in the spring from September to oviposition. Over this period final ovarian development and egg differentiation take place. Adult aggregation and oviposition are also influenced by pasture species composition, with aggregation of adult and egg stages occurring under paspalum in a mixed grass-legume pasture.

7. It is concluded that in seasons of warmer than average spring temperatures, adult dispersal into a pasture can have a significant influence on summer larval population levels. As more adults are retained in paspalum swards compared with other grass or legume dominant swards over the autumn-winter period, a strong pasture species-adult interaction operates in the autumn which affects adult dispersal and/or mortality.

8. As black beetle has a long period as an adult relative to other stages in the life cycle, it is concluded that factors such as the effects of pasture species and disease (especially Adelina sp.) on adults are potentially important in black beetle population ecology.

9. It has been established that the equipment and techniques developed for sampling grass grub populations, and the system of differential flotation in saline solutions to extract grass grub eggs and small larvae from soil cores, are equally satisfactory for use in studies on black beetle. A sampling plan using a combination of stratified random sampling with proportional allocation and a centric systematic area sample is most satisfactory for sampling black beetle populations, when considered in terms of precision and cost.

10. Black beetle is a difficult insect to sample in population studies. Adult dispersal and the large overlap of the different life stages cause problems in the estimation of populations for the construction of life tables and other quantitative purposes. It is concluded that for life table studies, a level of precision approaching a 20% standard error of the mean would have to be accepted, in terms of reasonable

cost, at other than very high population densities. The adoption of a stratified sampling system however could reduce cost. For survey purposes, sampling should be carried out in February when the sample size required to provide accurate population estimates is at a minimum.

11. The validity of the classification of favourable and unfavourable pasture plant species is confirmed by the very good correlation evident between the effects of grasses and legumes on pre-adult and adult ecology, and population numbers in the pasture plots at Otakanini.

12. In spite of difficulties in sampling black beetle populations, it is possible to construct life tables for this insect and determine the importance of mortalities on its populations. Key factors influencing population change were variation in natality and summer mortality in paspalum pastures, and variation in natality, summer mortality and winter-spring mortality in kikuyu based pasture. Late summer mortality, autumn-winter and winter-spring disappearance and spring migration of adults were the major determinants of population change in ryegrass pastures. The components of these mortalities are adult migration, variation in fecundity, the influence of high soil moisture levels and disease.

13. Summer larval population densities of between 40-60/m^2 cause severe pasture damage in ryegrass based pastures. Production losses occur but more importantly, pastures become legume and weed dominant. Paspalum and kikuyu based pasture is much more tolerant of feeding damage than ryegrass, and summer populations greater than 100/m^2 and 160/m^2 respectively, are necessary to cause damage.

14. A significant relationship was found between spring temperature, the level of population development in December and summer mortality. There was also a significant relationship between summer temperature, the level of population development in February and autumn and winter mortality/disappearance. In view of these relationships it is concluded that temperature has a major influence on the ecology of black beetle in the field.

15. These relationships have provided the basis for the prediction of population numbers through simple models. The model for paspalum pastures is based on the relationships between spring temperatures and summer mortality, and the density dependent variation in natality which is thought to reflect changes in adult immigration and/or fecundity with changes in population density. In a simulation exercise, the model accurately predicted the occurrence of outbreaks over the preceding 26 years when spring temperature records were used. It was concluded from the model that density dependence is an important component of population regulation in paspalum pastures, as such mortalities prevent unrealistically high population densities from being reached.

16. Ryegrass only provides a favourable spring and summer environment for black beetle populations. Populations decline significantly between autumn and spring in ryegrass based pastures. It is concluded from the ryegrass population model that high populations will only occur in ryegrass based pastures when significant adult spring immigration from favourable overwintering areas

takes place. Under New Zealand conditions, black beetle populations remain low in ryegrass swards in all but warmer than average years. Population regulation in the sense of populations returning to an equilibrium density does not occur often in ryegrass based pastures.

17. A model of the dynamics in the kikuyu based pasture at Wharepapa suggests spring immigration of adults is necessary for high population levels to be attained. The relatively high autumn to spring mortality/disappearance at Wharepapa appears due to the very wet winter soil conditions there. It is concluded that the situation may differ from that in kikuyu dominant pasture on drier soils.

18. There appear to be major differences in the population dynamics of black beetle between paspalum refuges and ryegrass based pastures. Black beetle can be considered as closer to an r-strategist in ryegrass based pastures, adapted to a relatively unstable habitat, and closer to a K-strategist in the more stable habitat of paspalum pastures. This suggests differences in practical control strategies by farmers between the two situations.

19. The rational use of insecticides is a powerful control tactic in ryegrass based pastures. This study has shown that mean temperatures in September, October and November can be used in the model developed to predict summer population levels. Predictive modelling in conjunction with strategic population monitoring could therefore be used to decide the use of prophylactic applications of insecticide in early December. In addition, it

is concluded that selective use of insecticide in paspalum refuge areas could prevent significant migration to susceptible areas in warm years, restricting the overall damage by black beetle.

20. Due to their density dependent action, it is concluded that the use of biological controls, including the introduction of natural enemies to reduce population numbers in the more stable habitats of paspalum and possibly kikuyu dominant pasture, is a worthwhile area for practical exploitation.

21. The results achieved in this study also suggest that utilisation of host plant resistance could provide an effective control strategy against black beetle. Lucerne is resistant to black beetle and because of its drought tolerance could be a valuable forage or pasture species in areas prone to black beetle. It is concluded however that lucerne will not provide a complete alternative to pasture as this crop is highly susceptible to infestation by white fringed weevil and lucerne aphids. The use of phalaris and white clover as a special purpose pasture mixture or in combination with other pasture plant species, could provide an effective strategy to reduce black beetle pasture damage, although further developmental research is required.

22. In terms of the objectives of this study, it is concluded that an understanding has been gained of the reasons for population fluctuations within different pasture types. However, the greatest benefit must result from the understanding derived of the reasons for population change and regulation, and the techniques developed to predict pest outbreaks. These should allow a more rational and integrated use of control measures.

23. Finally, it is concluded that this study has shown the need in ecological research on pest species for a well designed population study, with adequate sampling, to provide the quantitative basis in order to determine the manner in which mortalities operate and the way they affect numbers. This allows finite conclusions to be made and the development of models which can verify the validity of the conclusions. As black beetle has never been subjected to quantitative research, this study has been exploratory and broad based. Nevertheless, it has provided solutions and has pointed to new areas for investigation.

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Appendix O-1

A list of the plant species referred to in the thesis.

ryegrass	*Lolium perenne* L.
phalaris	*Phalaris aquatica* = *tuberosa* L.
cocksfoot	*Dactylis glomerata* L.
tall fescue	*Festuca arundinacea* Schreb.
yorkshire fog	*Holcus lanatus* L.
blue grass	*Poa pratensis* L.
paspalum	*Paspalum dilatatum* Poir.
kikuyu	*Pennisetum clandestinum* Hochst.
prairie grass	*Bromus unioloides* (Willd) Beauv.
digitaria	*Digitaria pentzii* Stent.
brown top	*Agrostis tenuis* Sibth.
poa	*Poa annua* L.
white clover	*Trifolium repens* L.
lucerne	*Medicago sativa* L.
lotus	*Lotus pedunculatus* Cav.
sweet clover	Melilotus spp.
red clover	*Trifolium pratense* L.
lupin	*Lupinus angustifolius* L.
cowpea	*Vigna* spp.
pea	*Pisium* spp.
bean	*Phaseolus* spp.
carrot	*Daucus carota* L.

Appendix 4-1 First instar black beetle larval growth at four temperatures when kept in a soil medium in the absence of plants.

10°C		15°C		20°C		25°C	
*Weight Change	**G.R.	Weight Change	G.R.	Weight Change	G.R.	Weignt Change	G.R.
0.357	0.090	0.091	0.024	0.63	0.153	5.67	0.855
0.007	0.002	-0.168	-0.045	0.63	0.153	2.94	0.557
0.280	0.071	-0.007	-0.002	1.12	0.257	5.04	0.798
-0.119	-0.032	0.049	0.013	1.12	0.257	1.82	0.386
-0.56	-0.159	0.056	0.015	1.33	0.298	4.06	0.696
-0.119	-0.032	0.462	0.115	1.33	0.298	3.15	0.586
0.042	0.011	0.616	0.150	0.84	0.199	3.85	0.672
0.084	0.022	0.91	0.214	1.4	0.311	3.08	0.577
0.231	0.059	0.812	0.193	1.12	0.257	2.45	0.488
0.70	0.169	0.84	0.199	1.05	0.243	4.20	0.712
-0.091	-0.024	0.441	0.110	0.91	0.214	2.10	0.359
				0.98	0.228	1.54	0.337
				1.47	0.324		
				1.47	0.324		

* weight change = gain or loss in mg/larva/week

** G.R. = Growth Rate = gain or loss in mg/mg of larva/week

Appendix 5-1 Second instar larval weight change (mg/week) and growth rate (G.R. = mg/mg of larvae/week) feeding on plant roots.

White clover		Ryegrass		Paspalum	
Weight Change (mg)	G.R.	Weight Change	G.R.	Weight Change	G.R.
-4.3	-0.073	-4.41	-0.042	5.88	0.007
-2.6	-0.027	2.73	0.070	9.59	0.147
-0.2	-0.002	13.0	0.119	16.8	0.189
-1.5	-0.039	14.14	0.098	9.52	0.105
-0.7	-0.021	17.78	0.133	17.64	0.182
-11.3	-0.132	10.15	0.098	2.1	0.035
-0.5	-0.014	1.75	0.021	9.45	0.091
0.9	0.009	9.94	0.077	9.31	0.133
6.1	0.095	11.48	0.140	4.48	0.056
7.7	0.077	0.63	0.007	16.66	0.161
3.6	0.051	7.63	0.070	10.99	0.154
6.2	0.082			1.68	0.035
2.7	0.047			11.55	0.161
				0.98	0.077
				7.70	0.105
				5.11	0.049
				11.9	0.119

Appendix 6-1 Numbers of black beetle recovered from plant treatments in February when seeded with eggs in December. N = 150.

Treatment	Black Beetle Recovered/Replication					
	I	II	III	IV	V	Total
ryegrass	6	16	0	5	18	43
paspalum	8	13	5	1	5	31
ryegrass/lotus	2	8	6	6	0	22
lotus	0	0	10	2	0	12
white clover	3	1	3	1	4	12
phalaris	6	0	4	0	1	11
phalaris/white clover	2	1	1	0	2	6

Appendix 6-2 Numbers of black beetle recovered from plant treatments in January when seeded with second instar larvae in December. N = 75.

Treatment	Black Beetle Recovered/Replication					
	I	II	III	IV	V	Total
paspalum	47	53	13	13	21	147
ryegrass	10	5	47	8	22	92
ryegrass/lotus	1	5	10	5	25	46
lotus	9	12	5	8	10	44
phalaris/white clover	6	7	12	8	9	42
phalaris	10	1	16	2	12	41
white clover	4	5	7	6	10	32

Appendix 6-3 The influence of pasture species on larval growth and survival. Second and third instar larvae recovered from plant treatments in February.

Treatment	REPLICATES								
	I		II		III			IV	
	L_2	L_3	L_2	L_3	L_1	L_2	L_3	L_2	L_3
ryegrass	0	1	1	1	0	4	15	0	0
ryegrass/ white clover	0	0	11	1	1	4	10	0	0
white clover	0	0	11	0	0	5	0	0	0

Appendix 8-1 Changes in ovarian development and fat level in adult female black beetles in paspalum at Otakanini during 1977.

	30 March		1 June		26 July		13 October		17 November	
	% Fat	O.D.*	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.
1.	19.6	2	42.4	1	11.7	2	13.7	5	5.5	5
2.	10.5	2	34.7	2	22.9	3	21.6	4	4.1	5
3.	9.2	1	36.0	2	20.7	3	24.1	3	3.6	5
4.	20.9	2	36.3	2	29.3	4	12.1	4	12.3	5
5.	19.3	2	45.9	2	5.8	2	6.5	3	4.0	5
6.	25.2	2	41.3	2	9.3	2	13.3	3	3.9	5
7.	20.7	2	44.3	2	22.1	3	9.9	5	5.4	5
8.	19.9	2	39.8	2	5.8	3	11.0	3	5.5	4
9.	15.2	2	48.2	3	20.8	2	15.6	4		
10.	21.9	2	39.6	2	27.3	2				
11.	16.3	2	26.6	2	39.4	3				
12.	21.5	2	38.8	2	19.8	2				
13.	16.0	2	41.7	2						
14.	18.8	2	41.7	4						
15.	18.2	2	43.2	2						
16.	11.8	2								

*O.D. = Ovarian Development Ranking

Appendix 8–2 Comparison of % fat level in male and female black beetle adults, July 1977.

	Te Kowhai			Paspalum pasture, Otakanini		
	Female		Male	Female		Male
	% Fat	O.D. Ranking	% Fat	% Fat	O.D. Ranking	% Fat
1.	12.4	2	28.3	11.7	2	7.5
2.	36.5	2	35.4	22.9	3	14.9
3.	37.3	3	37.4	20.7	3	18.3
4.	33.6	2	27.2	29.3	4	9.5
5.	32.7	2	22.1	5.8	2	19.8
6.	33.5	2	13.7	9.3	2	8.4
7.	34.2	2	22.7	22.1	3	13.0
8.	13.4	2	29.9	5.8	3	11.0
9.	36.4	3	29.0	20.8	2	8.6
10.	28.8	2	26.0	27.3	2	21.7
11.	38.4	3		39.4	3	
12.	33.8	2		19.8	2	
13.	23.9	2				
14.	36.1	2				
15.	45.4	2				
16.	33.7	2				
17.	37.2	2				

Appendix 8-2 continued

Te Kowhai

Female

	% Fat	O.D. Ranking
18.	28.0	2
19.	32.6	3
20.	25.3	2
21.	13.7	3

Appendix 8-3 Differences in O.D. ranking and % fat body between female black beetle at different sites in 1977.

	26/1/77		27/1/77		13/9/77		8/9/77		4/10/77		21/10/77		13/10/77		17/11/77		16/11/77	
	Te Kowhai		Otakanini		Te Kowhai		Otakanini		Te Kowhai		Te Aroha		Otakanini		Te Aroha		Otakanini	
	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.	% Fat	O.D.
1.	12.4	2	11.7	2	28.8	3	19.4	3	19.9	3.5	27.9	4	13.7	5	28.7	5	5.5	5
2.	36.5	2	22.9	3	23.3	3	15.7	3	19.1	3.5	24.3	4	21.6	4	36.2	4	4.1	5
3.	37.3	3	20.7	3	31.4	3.5	12.0	2	22.7	4	23.7	5	24.1	3	19.0	5	3.6	5
4.	33.6	2	29.3	4	21.3	3.5	14.7	3	13.8	4	17.3	5	12.1	4	32.8	5	12.3	5
5.	32.7	2	5.8	2	29.3	3.5	14.1	3	37.5	4	20.7	5	6.5	3	27.3	5	4.0	5
6.	33.5	2	4.3	2	28.1	3.5	18.7	3	22.4	3.5	22.3	5	13.3	3	35.9	5	3.9	5
7.	34.2	2	22.1	3	27.9	3.5	12.9	3	21.7	3	17.9	3	9.9	5	24.1	4	5.4	5
8.	13.4	2	5.8	3	25.8	3	25.1	3	23.9	3.5	17.8	5	11.0	3	34.4	4	5.5	4
9.	36.4	3	20.8	2	28.0	3			12.2	3	6.2	2	15.6	4	31.6	5		
10.	28.8	2	27.3	2	28.8	3			20.3	3	21.3	4			25.7	5		
11.	38.4	3	39.4	3	24.2	4			26.0	4	8.1	5			15.5	5		
12.	33.8	2	19.8	2	25.7	5			13.8	3	19.4	3			26.9	5		
13.	23.9	2			29.7	3												
14.	36.1	2			29.9	3												
15.	45.4	2			23.2	3												
16.	33.7	2			21.3	3												

Appendix 8-3 continued

	26/7/77		13/9/77	
	Te Kowhai		Te Kowhai	
	% Fat	O.D.	% Fat	O.D.
17.	33.2	2	38.2	4
18.	28.0	2	23.2	3.5
19.	32.6	3	29.7	3
20.	25.3	2	15.7	4
21.	13.7	3		

Appendix 8-4 Difference in O.D. ranking and % fat body between female black beetle adults from maize and paspalum. Otakanini, June 1977.

	Paspalum Pasture		Maize Stubble	
	% Fat	O.D.	% Fat	O.D.
1.	42.4	1	37.6	2
2.	34.7	2	45.1	4
3.	36.0	2	10.2	2
4.	36.3	2	19.8	2
5.	45.9	2	8.7	2
6.	41.3	2	20.3	3
7.	44.3	2	22.6	1
8.	39.8	2		
9.	48.2	3		
10.	39.6	2		
11.	26.6	2		
12.	38.8	2		
13.	41.7	2		
14.	41.7	4		
15.	43.2	2		

Appendix 8-5 % Fat in female black beetle adults between September and oviposition on different diets.

	Population A	Population B	Population A	Population B at Oviposition	
	September	September	Carrot Diet	Paspalum Diet	Ryegrass Diet
			At Oviposition		
1.	19.4	28.8	19.1	17.7	7.6
2.	15.7	23.3	35.3	5.8	7.9
3.	12.0	31.4	25.8	5.8	15.2
4.	14.7	21.3	35.6	6.2	8.3
5.	14.1	29.3	23.8	6.7	8.8
6.	18.7	28.1	20.4	4.9	8.4
7.	12.9	27.9	27.8	6.4	
8.	25.1	25.8	34.2	5.0	
9.		28.0	24.2	14.6	
10.		28.8	16.4	10.4	
11.		24.2		15.0	
12.		25.7		6.7	
13.		29.7		10.2	

Appendix 8-5 continued

	Population B
	September
14.	29.9
15.	23.2
16.	21.3
17.	38.2
18.	23.2
19.	29.7
20.	15.7

Appendix 8-6 Relationship between dry weight of female black beetle adults and weight of fat body in September 1976.

Wet Weight (mg)	Dry weight (mg)	Weight of fat body (mg)	% fat (Dry weight basis)
222.2	75.0	10.5	14.0
246.8	94.1	16.3	17.3
227.0	76.6	15.5	20.8
224.1	85.6	18.0	21.0
213.4	84.6	24.8	29.3
227.4	85.3	26.0	30.5
238.5	95.7	32.7	34.2
245.2	109.3	40.7	37.2
216.3	107.9	40.8	37.8
239.6	116.1	56.0	48.2

Appendix 8–7 Potential fecundity of female black beetle adults determined by dissection at the commencement of oviposition in November.

Eggs laid in first batch	Ova present in female at dissection	Total potential fecundity
1	69	70
3	53	56
2	45	47
3	41	44
3	33	36
4	47	51
2	26	28
1	40	41
2	44	46
4	45	49
2	31	33
1	43	44
3	46	49
2	56	58
2	53	55
5	59	64
3	62	65
1	60	61
9	54	63
10	55	65

Appendix 8-8 Fecundity of female black beetle adults when the food supply is removed after the commencement of oviposition.

Eggs laid before food removed	Eggs laid after food removed	Total fecundity per female
2	4	6
7	5	12
1	0	1
4	6	10
1	14	15
3	8	11
1	5	6
1	5	6
1	6	7
5	0	5
1	6	7
1	3	4
3	10	13
1	1	2
10	14	24
1	3	4
1	13	14
1	6	7
2	1	3
1	8	9

Appendix 8-9 Fecundity of female black beetle adults continuously fed on a carrot diet.

Eggs laid in first batch	Total Eggs laid	Alive at end of trial (X)	Eggs laid in first batch	Total Eggs laid	Alive at end of trial (X)	Eggs laid in first batch	Total Eggs laid	Alive at end of trial (X)
2	66	X	2	48	X	1	63	X
1	69	X	1	31	X	4	63	X
1	26		3	71	X	0	0	X
2	10		2	19		1	44	X
1	10		2	78		1	81	X
4	67	X	2	56	X	1	70	X
1	23		1	46	X	3	7	
3	51		7	49	X	3	3	X
1	64		3	54	X	1	83	X
1	28		2	26		6	93	X
5	71		2	44		4	26	
2	63	X	1	2		8	76	X
1	58	X	1	1		1	41	X
2	10	X	1	27	X	2	61	X
0	0	X	0	0	X	1	31	X
7	34		6	88	X	2	50	X

Appendix 8-9 Fecundity of female black beetle adults continuously fed on a carrot diet (continued).

Eggs laid on first batch	Total Eggs laid	Alive at end of trial (X)	Eggs laid in first batch	Total Eggs laid	Alive at end of trial (X)	Eggs laid in first batch	Total Eggs laid	Alive at end of trial (X)
2	62		1	24		6	74	X
3	15		1	27	X	2	50	X
3	6		2	6		3	44	
1	4		2	68	X	1	66	X
1	38	X	1	36		2	57	X
2	91	X	2	62	X	11	76	X
1	50		2	2		2	6	X
3	36		15	94	X	3	65	X
3	67		1	1		2	64	X
1	57	X	1	17		2	2	X
2	7		2	73		5	41	
1	80	X	9	97	X	1	51	X
2	63	X	2	53		10	47	X
1	72		2	4		1	51	X
1	82	X	1	42	X	0	0	X
1	72	X	2	30	X	3	42	
1	5		5	18		8	16	
1	35	X						

Appendix 8-10 The fecundity of female black beetle adults on a diet of paspalum, ryegrass or white clover roots.

Eggs laid/female on paspalum roots	Eggs laid/female on ryegrass roots	Eggs laid/female on white clover roots
0	1	0
6	0	0
0	14	0
20	10	0
1	0	0
7	8	0
12	9	0
21	0	0
8	4	0
0	2	3
19	2	0
18	19	6
7	0	0
1	12	0
19	0	0
0	36	0
4	0	0
8	0	0
5	3	0
19	5	13
5	0	3
0	1	4
4	9	0
7	1	0
5	3	25
12	5	0
8	2	0
9	6	4
7	8	2
20	3	1

Appendix 8-11 Fat analysis of a subsample of black beetle adult females from Te Kowhai in September and used in the fecundity trial reported in Table 8-8.

Insect Dry Weight (mg)	% Fat
83.6	28.8
74.0	23.3
101.0	31.4
59.1	21.3
83.4	29.3
82.7	28.1
81.8	27.9
56.6	25.8
87.8	28.0
89.0	28.8
80.7	24.2
94.8	25.7
84.4	29.7
83.3	29.9
77.1	23.2
78.3	21.3
112.2	38.2
78.2	23.2
82.1	29.7
75.0	15.7

Appendix 8-12 Fat analysis of a subsample of female black beetle adults from Elstow, Te Aroha in mid-November and used in the fecundity trial reported in Table 8-9.

Insect dry weight (mg)	% Fat
88.7	28.7
125.9	36.2
84.2	19.0
105.1	32.8
119.3	27.3
102.8	35.9
80.1	24.1
117.8	34.4
109.0	31.6
79.1	25.7
81.0	15.5
99.0	26.9

Appendix 8-13 The number of black beetle recovered from the field fecundity trial reported in Table 8-9.

	Treatments : Black beetle per cylinder					
Cylinder	Ryegrass		40:60 Ryegrass:White clover		White clover	
Number	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
1	1	0	5	8	0	2
2	2	1	1	2	2	4
3	1	1	0	0	6	4
4	0	8	0	0	1	5
5	2	4	6	0	0	0
6	1	5	3	0	0	5
7	9	7	3	12	3	5
8	0	4	1	7	5	0
9	2	2	1	9	0	0
10	2	2	0	3	0	1
11	13	5	0	3	7	1
12	1	0	0	5	1	10
13	0	0	0	4	0	3
14	9	5	4	13	1	2

Appendix 9-1 Number of black beetle eggs and larvae recovered from the pasture height, oviposition trial (1) at Otakanini, 1976.

Treatments	Replicates									
	1	2	3	4	5	6	7	8	9	10
1. No insecticide - mown to 3 cm	3	1	1	0	1	1	0	0	2	0
2. No insecticide - long pasture	0	1	1	0	0	0	0	0	0	0
3. Insecticide - mown to 3 cm	0	1	0	1	0	0	0	0	0	0
4. Insecticide - long pasture	2	0	0	0	0	0	0	0	0	0

Appendix 9-2 Number of black beetle eggs and larvae recovered from the pasture height, oviposition trial (2), Ruakura, 1977.

	Cage A				Cage B			
	Long Pasture		Short Pasture		Long Pasture		Short Pasture	
Pot No.	Eggs	L_1 Larvae*	Eggs	L_1 Larvae	Eggs	L_1 Larvae	Eggs	L_1 Larvae
1	0	0	11	4	6	8	6	10
2	14	1	8	5	2	10	5	1
3	2	2	6	0	0	0	6	2
4	9	9	14	0	4	14	1	5
5	4	11	6	2	6	0	5	16
6	9	4	0	1	4	4	7	13
7	2	2	9	3	0	5	0	4
8	11	0	7	2	0	12	0	0
9	5	0	1	0	2	3	15	0
10	3	0	0	0	5	0	0	0

* = first instar larvae

Appendix 10-1 Numbers of black beetle adults recovered in July when seeded into plant treatments as third instar larvae in March 1976.

	Replicates											
	I		II		III		IV		V		Total	
Treatment	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Paspalum	10	11	15	7	10	9	14	9	8	6	57	42
Ryegrass	3	2	3	2	3	3	3	2	2	2	14	11
Phalaris	0	0	1	0	1	1	0	0	1	1	3	1
White clover	0	0	0	0	0	0	1	0	0	0	1	0
Lotus	0	0	1	0	0	0	0	0	0	0	1	0
Ryegrass/lotus	1	0	0	1	0	2	0	2	0	0	1	5
Phalaris/white clover	1	0	0	0	0	0	0	0	1	1	2	0

Appendix 10-2 Numbers of black beetle adults recovered in May when seeded into plant treatments as adults in March 1977.

	Treatments					
	Paspalum		Ryegrass/white clover		Ryegrass	
Replicate	♂	♀	♂	♀	♂	♀
1	14	11	4	4	1	0
2	11	12	7	0	2	1
3	7	13	2	0	0	1
4	11	11	3	0	0	0
5	12	12	0	1	3	1
Total	55	59	16	5	6	3

Appendix 10-3 Weight of adults and body fat and % fat (dry weight basis) of female black beetle adults taken from paspalum pasture, Otakanini, at the start of trial (2) in March 1977.

Beetle No.	Dry Weight (mg)	Weight of fat (mg)	% Fat
1	77.6	15.2	19.6
2	75.8	13.4	17.7
3	81.7	8.6	10.5
4	60.6	5.6	9.2
5	74.7	15.6	20.9
6	72.6	3.8	5.2
7	81.5	6.8	8.3
8	64.8	12.5	19.3
9	81.8	12.4	15.2
10	95.2	24.0	25.2
11	72.9	15.1	20.7
12	71.5	14.2	19.9
13	59.4	9.0	15.2
14	68.4	15.0	21.9
15	67.0	10.9	16.3
16	87.8	18.9	21.5
17	68.1	10.6	16.0
18	73.8	13.9	18.8
19	73.8	13.4	18.2
20	70.4	8.3	11.8

Appendix 10–4 Weight of adults and body fat and % fat (dry weight basis) of female black beetle adults taken from the paspalum treatment at the end of trial (2) in May 1977.

Beetle No.	Dry weight (mg)	Weight of Fat (mg)	% Fat
1	103.0	43.7	42.4
2	114.5	39.7	34.7
3	120.0	43.2	36.0
4	123.2	44.7	36.3
5	138.7	63.6	45.9
6	135.0	55.7	41.3
7	110.3	48.9	44.3
8	138.3	55.1	39.8
9	107.8	52.0	48.2
10	110.4	43.7	39.6
11	87.1	23.2	26.6
12	104.9	40.7	38.8
13	122.3	51.0	41.7
14	118.0	49.2	41.7
15	127.9	55.3	43.2

Appendix 10–5 Weight of adults and body fat and % fat (dry weight basis) of female black beetle adults taken from the ryegrass and ryegrass/white clover treatments at the end of trial (2) in May 1977.

Beetle No.	Dry weight (mg)	Weight of Fat (mg)	% Fat
1	63.1	2.6	4.1
2	75.0	1.6	2.1
3	75.6	3.7	4.9
4	74.3	1.1	1.5
5	79.9	7.8	9.8
6	68.8	2.2	3.2
7	67.2	2.5	3.7
8	59.8	1.8	3.0

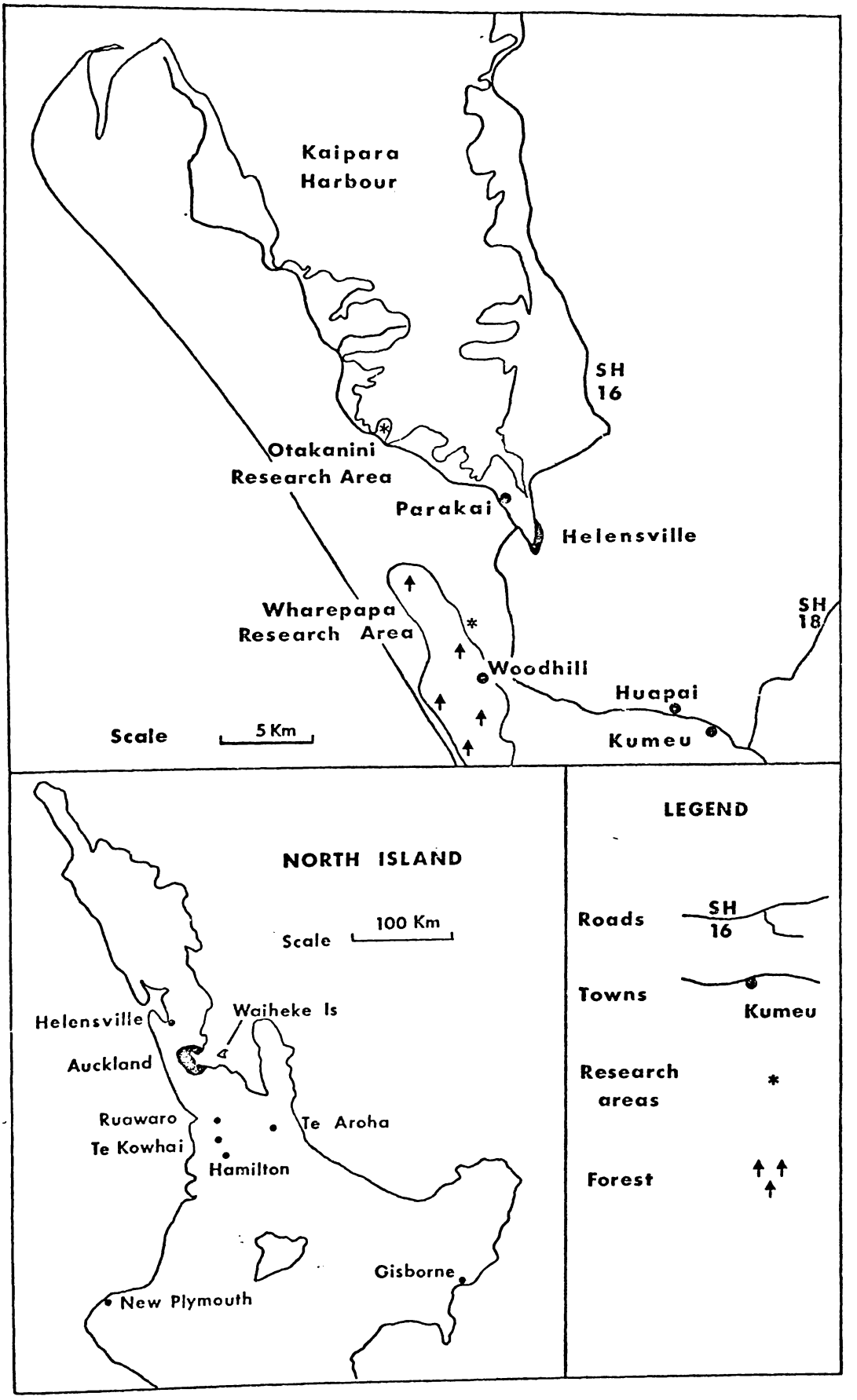
Appendix 11-1 Percentage body fat in adult female black beetle from Otakanini with and without *Adelina* sp.

Beetle No.	Maize - June		Paspalum - July		Paspalum - September		Paspalum - October	
	Adelina	No Adelina	Adelina	No Adelina	Adelina	No Adelina	Adelina	No Adelina
1.	6.1	37.6	8.8	11.7	8.9	19.4	8.0	13.7
2.	5.4	45.1	14.9	22.9	11.2	15.7	9.0	21.6
3.	6.0	10.2	13.2	20.7	15.8	12.0	6.2	24.1
4.	7.9	19.8	12.6	29.3	14.7	14.7	17.5	12.1
5.	5.4	8.7	5.8	5.8	9.6	14.1		6.5
6.	7.5	20.3		9.3	7.3	18.7		13.3
7.	7.6	22.6		22.1	4.8	12.9		9.9
8.	7.7			5.8	12.5	25.1		11.0
9.	4.2			20.8				15.6
10.	5.4			27.3				
11.	5.5			39.4				
12.	5.7			19.8				

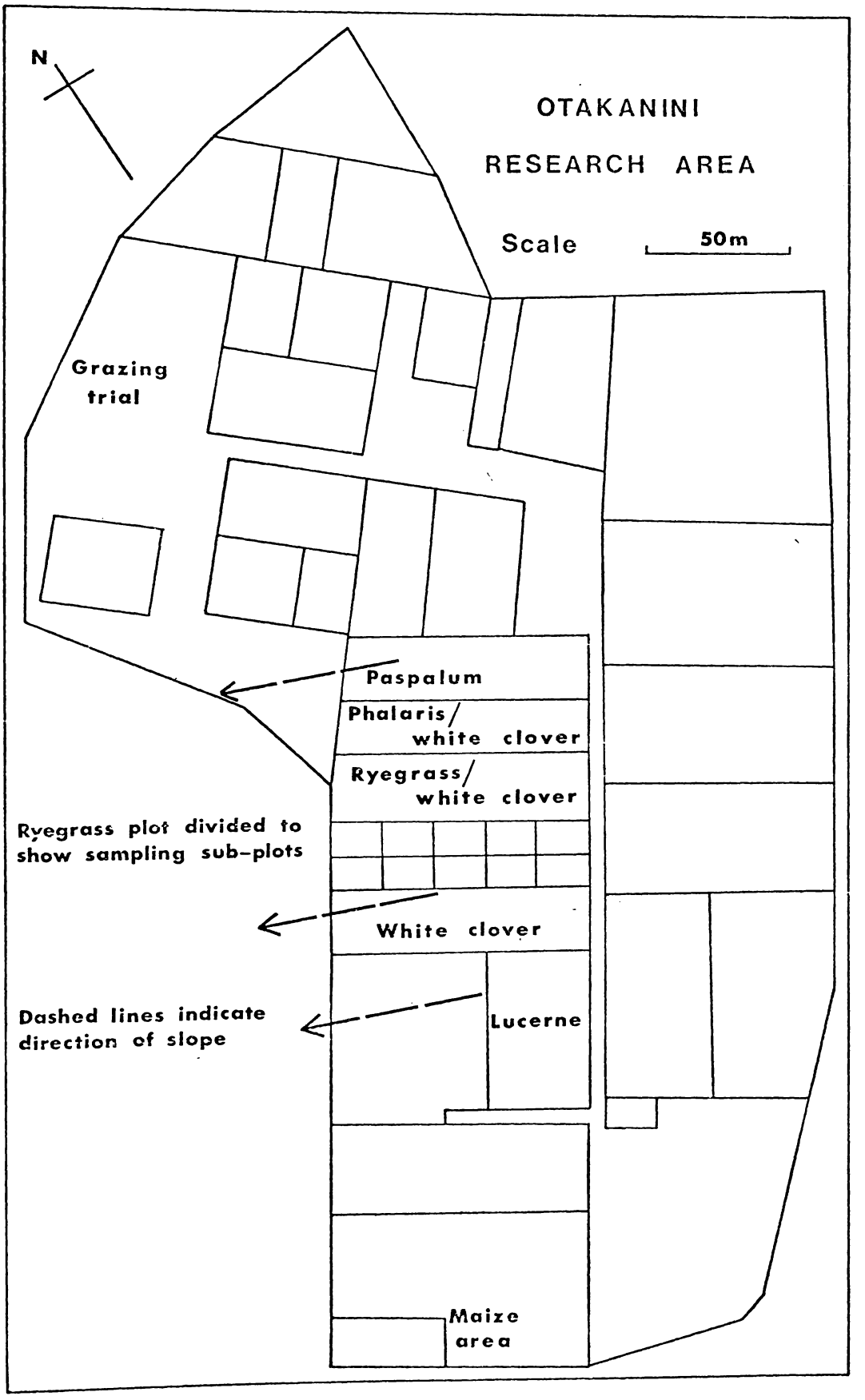
Appendix 11-2 Relationship between oven dry weight of adult black beetle females, weight of body fat and the incidence of *Adelina* sp. from the maize stubble area at the Otakanini Research Area in June 1977.

	Oven Dry Weight (mg)		Weight of Fat (mg)	
Sample No.	Adelina	No Adelina	Adelina	No Adelina
1.	47.8	97.7	2.9	36.7
2.	66.6	119.8	3.6	54.0
3.	58.1	92.6	3.5	9.4
4.	60.8	90.2	4.8	17.9
5.	52.3	63.3	2.8	5.5
6.	54.8	85.4	4.1	21.0
7.	59.1	63.5	4.5	19.3
8.	50.4	103.3	3.9	MS*
9.	54.5		2.3	
10.	58.8		3.2	
11.	71.0		3.9	
12.	52.8		3.0	

* Sample lost during extraction



Appendix 13-1 Location of the Otakanini Research Area where the black beetle population studies were carried out.



Appendix 13-2 The layout of the six different pasture type plots in which the black beetle population studies were carried out at the Otakanini Research Area.

Appendix 14-1 Black beetle population estimates (mean no./m^2 ± standard error of the mean) in each pasture plot at the Otakanini Research Area.

	PASTURE PLOTS					
Sampling Date	Paspalum	Ryegrass	Ryegrass/ White clover	Lucerne	White clover	Phalaris/ White clover
December 1974	60.4 ± 8.6	25.9 ± 6.2	NS	17.3 ± 4.9	17.3 ± 5.4	NS
February 1975	61.1 ± 4.3	27.1 ± 3.9	NS	2.5 ± 1.2	7.4 ± 1.2	NS
March 1975	46.9 ± 5.7	NS	NS	NS	NS	NS
June 1975	35.8 ± 5.1	NS	NS	NS	NS	NS
September 1975	25.9 ± 3.9	NS	NS	NS	NS	NS
December 1975	112.9 ± 15.3	62.9 ± 8.9	45.0 ± 8.9	7.4 ± 2.4	13.0 ± 5.6	8.6 ± 3.6
February 1976	59.8 ± 6.2	61.7 ± 6.6	40.1 ± 4.9	3.7 ± 1.7	17.9 ± 3.6	10.5 ± 2.6
March 1976	45.0 ± 5.6	NS	NS	NS	NS	NS
June 1976	35.2 ± 5.4	10.5 ± 2.5	13.6 ± 3.0	2.5 ± 1.1	7.4 ± 1.5	6.8 ± 2.0
September 1976	14.2 ± 3.0	0.6 ± 0.6	NS	NS	NS	NS
December 1976	62.9 ± 10.5	23.4 ± 5.8	3.7 ± 1.7	0.6 ± 0.6	0.6 ± 0.6	3.7 ± 2.1
February 1977	56.7 ± 6.7	21.0 ± 3.4	16.0 ± 3.0	0	4.9 ± 2.2	0
March 1977	41.9 ± 4.3	NS	NS	NS	NS	NS
June 1977	26.5 ± 3.9	2.5 ± 1.2	4.3 ± 1.6	NS	NS	NS
September 1977	11.7 ± 2.5	1.2 ± 0.6	NS	NS	NS	NS

Appendix 14-1 continued

	Pasture Plots		
Sampling Date	Paspalum	Ryegrass	Ryegrass/ White clover
December 1977	40.1 ± 8.1	8.0 ± 3.1	5.6 ± 2.5
February 1978	NS	12.3 ± 2.8	11.7 ± 3.3
March 1978	16.0 ± 3.1	NS	NS
June 1978	8.6 ± 2.1	NS	NS
September 1978	NS	NS	NS
December 1978	50.3 ± 11.7	11.7 ± 4.5	NS
February 1979	37.0 ± 5.1	NS	NS

NS = no sample taken in this period.

Appendix 14-2 Black beetle population estimates (mean/m^2 ± standard error of the mean) at Wharepapa.

Sample Date	Mean/m^2	± standard error
December 1974	163.4	17.0
February 1975	108.5	8.8
March 1975	81.4	7.9
May 1975	39.5	2.8
September 1975	9.9	3.0
December 1975	162.2	17.0
February 1976	63.4	5.4
March 1976	59.2	4.3
May 1976	40.7	3.5
September 1976	4.3	1.6
December 1976	11.7	4.1
February 1977	29.0	4.1
March 1977	17.3	3.3
May 1977	19.1	3.7
September 1977	2.5	1.1
December 1977	16.7	5.2
February 1978	NS*	-
March 1978	33.9	5.6
May 1978	NS	-
July 1978	16.0	2.5
September 1978	NS	-
December 1978	109.2	15.9
February 1979	104.2	3.3

*NS = no sample taken in this period.

Appendix 14-3 Life table for the 1975/76 black beetle generation in the paspalum plot at Otakanini.

Time of sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1975	*L_{III} + pre-pupae + pupae	61.1	1.79	
	k_2 (late summer mortality)			0.12
March 1975	L_{III} + adults	46.9	1.67	
	k_3 (autumn-winter disappearance)			0.12
June 1975	Overwintering larvae + adults	35.8	1.55	
	k_4 (winter-spring disappearance)			0.14
September 1975	spring larvae + adults	25.9	1.41	
	k_5 (delayed development)			0.04
September 1975	spring adults** proportion females = 0.52	23.4	1.37	
	k_6 (proportion females)			0.28
	Potential natality***	122.6	2.09	
	k_o (variation in natality)			0.04
December 1975	eggs + L_I*	112.9	2.05	
	k_1 (summer mortality)			0.27
February 1976	L_{II} + L_{III}*	59.8	1.78	
	K (Total mortality)			1.01

Index of population trend = 98.0%

*L_I, L_{II}, L_{III} are first instar, second instar and third instar larvae respectively.

**It is assumed for the purpose of constructing the life table that larvae present in September will die before reaching the adult stage.

***Potential natality = No. spring adults/m^2 x proportion of females x average fecundity assumed from Section 3 to be 10 eggs/female on a paspalum diet.

Appendix 14-4 Life table for the 1976/77 black beetle generation in the paspalum plot at Otakanini.

Time of sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1976	L_{II} + L_{III}	59.8	1.78	
k_2 (late summer mortality)				0.13
March 1976	L_{III} + pre-pupae + pupae	45.0	1.65	
k_3 (autumn-winter disappearance)				0.11
June 1976	overwintering larvae + adults	35.2	1.54	
k_4 (winter-spring disappearance)				0.41
September 1976	spring larvae + adults	13.6	1.13	
k_5 (delayed development)				0.14
September 1976	spring adults	9.9	0.99	
	proportion females = 0.63			
k_6 (proportion females)				0.20
	Potential natality	49.3	1.69	
k_o (variation in natality)				-0.13
December 1976	eggs + L_I	66.6	1.82	
k_1 (summer mortality)				0.07
February 1977	L_{II} + L_{III}	56.7	1.75	
K (total mortality)				0.93

Index of population trend = 94.8%

Appendix 14-5 Life table for the 1977/78 black beetle generation in the paspalum plot at Otakanini.

Time of sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1977	L_{II} + L_{III}	56.7	1.75	
k_2 (late summer mortality)				0.13
March 1977	L_{III} + pupae + adults	41.9	1.62	
k_3 (autumn-winter disappearance)				0.20
June 1977	overwintering larvae + adults	26.5	1.42	
k_4 (winter-spring disappearance				0.35
September 1977	spring larvae + adults	11.7	1.07	
k_5 (delayed development)				0.17
September 1977	spring adults	8.0	0.90	
	proportion females = 0.70			
k_6 (proportion females)				0.15
	Potential natality	56.0	1.75	
k_o (variation in natality)				0.15
December 1977	Eggs L_I	40.1	1.60	
k_1 (summer mortality)				0.27
February 1978	L_{II} + L_{III}	21.4*	1.33	
K (total mortality)				1.42

Index of population trend = 37.7%

* calculated from March 1978 estimate of $6/m^2$ by assuming k_2 = 0.13 in 1978.

Appendix 14-6 Life table for the 1978/79 black beetle generation in the paspalum plot at Otakanini.

Time of Sample	Predominant Stages	No./m^2 (N)	log.N	k
*February 1978	L_{II} + L_{III}	21.4	1.33	
k_2 (late summer mortality)				0.13
March 1978	L_{III} + pupae	16.0	1.20	
k_3 (autumn-winter disappearance)				0.26
June 1978	over-wintering larvae + adults	8.6	0.94	
k_4 (winter-spring disappearance)				0.29
**September 1978	spring larvae + adults	4.5	0.65	
k_5 delayed development				0.14
***September 1978	spring adults	3.2	0.51	
	† proportion females = 0.57			
k_6 (proportion females)				0.24
	Potential natality	18.2	1.26	
k_o (variation in natality)				-0.44
December 1978	eggs + L_I + L_{II}	50.3	1.70	
k_1 summer mortality				0.13
February 1979	L_{III} + pre-pupae + pupae	37.0	1.57	
K (total mortality)				0.75

Index of population trend = 172.9%

* Calculated from March 1978 estimate of 16/m^2 by assuming k_2 = 0.13 in 1978

** Calculated from June 1978 estimate of 8.6/m^2 by assuming k_4 = 0.29 in 1978

*** Estimated from September 1975 - September 1977 data where approximately 70% of population was in the adult stage.

† Estimated value from the mean of previous generations data.

Appendix 14-7 Life table for the 1976/77 black beetle generation in the ryegrass plot at Otakanini.

Time of sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1976	L_{III} + pre-pupae + pupae	61.7	1.79	
* k_{2+3} (late summer mortality + autumn-winter disappearance)				0.77
June 1976	adults	10.5	1.02	
k_4 (winter-spring disappearance)				1.24
September 1976	adults	0.6	-0.22	
k_5 (delayed development)				
September 1976	adults	0.6	-0.22	
	proportion females = 0.50			
k_6 (proportion females)				0.30
	Potential natality	2.1**	0.32	
k_o (variation in natality)				-1.05
December 1976	eggs + L_I	23.4	1.37	
k_1 (summer mortality)				0.05
February 1977	L_{III} + pre-pupae + pupae	21.0	1.32	
K (total mortality)				1.31

Index of population trend = 34.0%

* Mortalities k_2 and k_3 assessed together as no population sample was taken in March.

** Potential natality = no. adults/m^2 in September x proportion of females x average fecundity assumed from Section 3 to be 7 eggs/female on a ryegrass diet.

Appendix 14-8 Life table for the 1977/78 black beetle generation in the ryegrass plot at Otakanini.

Time of sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1977	L_{III} + pre-pupae + pupae	21.0	1.32	
k_{2+3} (late summer mortality and autumn-winter disappearance)				0.93
June 1977	adults	2.47	0.39	
k_4 (winter-spring disappearance)				0.31
September 1977	adults	1.2	0.08	
k_5 (delayed development)				0
September 1977	adults	1.2	0.08	
	proportion females = 0.50			
k_6 (proportion females)				0.30
	Potential natality	4.2*	0.62	
k_o (variation in natality)				-0.28
December 1977	eggs + L_I	8.0	0.90	
k_1 (summer mortality)				-0.19
February 1978	L_{III} + pupae	12.3	1.09	
K (total mortality)				1.07

Index of population trend = 58.6%

Appendix 14-9 Life table for the 1975/76 black beetle generation in the Wharepapa plot.

Time of Sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1975	L_{III} + pre-pupae + pupae	108.5	2.04	
k_2 (late-summer mortality)				0.13
March 1975	L_{III} + pupae + adults	81.4	1.91	
**k_3 (autumn-winter disappearance)				0.31
May 1975	L_{III} + adults	39.5	1.60	
k_4 (winter-spring disappearance)				0.61
September 1975	adults	9.9	0.99	
k_5 (delayed development				0.02
September 1975	spring adults	9.3	0.97	
	proportion females = 0.75			
k_6 (proportion females)				0.125
	Potential natality*	69.8	1.84	
k_o	(variation in natality)			-0.37
December 1975	eggs + L_I	162.2	2.21	
k_1 (summer mortality)				0.41
February 1976	L_{III} + pre-pupae + pupae	63.5	1.80	
K (total mortality)				1.24

Index of population trend = 58.5%

* Potential natality = No. of spring adults/m^2 x proportion of females x average fecundity assumed to be 10 eggs/female.

** As the Wharepapa plot was sampled in May and not in June in contrast to the plots at Otakanini, k_3 is taken as the difference in the log. densities between March and May, and k_4 between May and September.

Appendix 14-10 Life table for the 1976/77 black beetle generation in the Wharepapa plot.

Time of Sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1976	L_{III} + pre-pupae + pupae	63.5	1.80	
k_2 (late-summer mortality)				0.03
March 1976	L_{III} + pupae	59.2	1.77	
k_3 (autumn-winter disappearance)				0.09
May 1976	L_{III} + pupae + adults	40.7	1.61	
k_4 (winter-spring disappearance)				0.98
September 1976	adults	4.3	0.63	
k_5 (delayed development)				0
September 1976	spring adults	4.3	0.63	
	proportion females = 0.86			
k_6 (proportion females)				0.07
	Potential natality	37.0	1.57	
k_o (variation in natality)				0.50
December 1976	eggs	11.7	1.07	
k_1 (summer mortality)				-0.39
February 1977	L_{II} + L_{III}	29.0	1.46	
K (total mortality)				1.28

Index of population trend = 45.7%

Appendix 14-11 Life table for the 1977/78 black beetle generation in the Wharepapa plot.

Time of Sample	Predominant Stages	No./m^2 (N)	log.N	k
February 1977	L_{II} + L_{III}	29.0	1.46	
k_2 (late-summer mortality)				0.22
March 1977	L_{III} + pre-pupae + pupae	17.3	1.24	
k_3 (autumn-winter disappearance)				-0.04
May 1977	L_{III} + adults	19.1	1.28	
k_4 (winter-spring disappearance)				0.88
September 1977	adults	4.3	0.64	
k_5 (delayed development)				0.07
September 1977	spring adults	3.7	0.57	
	proportion females = 0.50*			
k_6 (proportion females)				0.30
	Potential natality	18.5	1.27	
k_o (variation in natality)				0.05
December 1977	eggs + L_I	16.7	1.22	
k_1 (summer mortality)				-0.44
February 1978	L_{III} + pre-pupae + pupae	46.0**	1.66	
K (total mortality)				1.04

Index of population trend = 158.6%

* A 1:1 sex ratio was assumed as all adults in the September sample were males.

** Calculated from March 1978 estimate of 33.9/m^2 by assuming k_2 = 0.13 in 1978.

Appendix 14-12 Paspalum plot. Values of log number of black beetle per m^2 and k-values for the determination of the key factor by regression of k_1 on K and for the tests of density dependence of the k_1's.

Groups of 3 sub-plots /generation; sub-plot 10 deleted

Plot	Feb	k_2	Mar	k_3	June	k_4	Sept	k_5	Sept A	k_6	PN	$k_o + k_1$	Feb	K
1975/76 Generation														
1	1.22	-.32	1.54	.07	1.47	.02	1.45	0	1.45	.29	2.15	.17	1.98	.23
2	1.94	.43	1.51	-.21	1.72	.25	1.47	.10	1.37	.28	2.09	.45	1.64	1.30
3	1.76	.09	1.67	.35	1.32	-.04	1.36	.08	1.28	.39	1.89	.44	1.45	1.31
1976/77 Generation														
1	1.98	.22	1.76	-.01	1.77	.47	1.30	.02	1.28	.33	1.95	.04	1.91	1.07
2	1.64	.05	1.59	.25	1.34	.29	0.63	.37	0.26	.10	0.50	-1.02	1.52	.04
3	1.45	-.03	1.48	.33	1.15	.36	0.79	.53	0.26	.10	0.50	-1.06	1.56	.23
1977/78 Generation														
1	1.91	.30	1.61	-.02	1.63	.32	1.31	.10	1.21	.21	1.99	.79	1.20	1.70
2	1.52	-.15	1.67	.49	1.18	.72	0.46	.10	0.36	.10	0.60	-.26	.86	1.00
3	1.56	.07	1.49	.60	0.89	0	0.89	.36	0.53	.20	0.99	.25	.74	1.48

Appendix 14-13 Wharepapa plot. Values of log. number of black beetle per m^2 and k-values for the determination of the key factor by regression of k_i on K and for the tests of density dependence of the k_i's.

Plot	Feb	k_2	March	k_3	May	k_4	Sept	k_5	Sept A	k_6	PM	$k_o + k_1$	Feb	K
1975/76 Generation														
1	1.87	.30	1.57	.27	1.30	.61	0.69	0	0.69	.30	1.39	-.26	1.65	1.22
2	2.18	.13	2.05	.45	1.60	.43	1.17	0	1.17	.18	1.99	.32	1.67	1.51
3	2.12	.09	2.03	.32	1.71	.84	0.87	.17	0.69	.30	1.39	-.55	1.94	1.17
4	1.90	.05	1.85	.18	1.67	.58	1.09	0	1.09	.22	1.87	-.01	1.88	1.02
1976/77 Generation														
1	1.65	-.06	1.71	.36	1.35	.96	0.39	0	0.39	.30	1.09	-.56	1.65	1.00
2	1.67	-.08	1.75	.40	1.35	.48	0.87	0	0.87	.22	1.69	.12	1.57	1.14
3	1.94	.13	1.81	-.11	1.92	1.53	0.39	0	0.39	.30	1.09	-.26	1.35	1.59
4	1.88	.07	1.81	.27	1.54	.85	0.69	0	0.69	.30	1.39	.30	1.09	1.79
1977/78 Generation														
1	1.65	.26	1.39	.04	1.35	.46	0.99	.12	0.87	.30	1.57	-.11	1.68	1.07
2	1.57	.48	1.09	-.21	1.30	.91	0.39	0	0.39	.30	1.09	-.08	1.17	1.40
3	1.35	.05	1.30	-.09	1.39	1.00	0.39	0	0.39	.30	1.09	.13	0.96	1.39
4	1.09	0	1.09	.10	0.99	.60	0.39	0	0.39	.30	1.09	-.17	1.26	.83

Appendix 14-14 Paspalum plot. Regression coefficient values and 95% confidence limits for the tests of density dependence of k_i's carried out when the slope of k against $\log_e N_1$ differed significantly from zero. Pooled data from 1974/75, 1975/76 and 1976/77 generations.

Test of Y on X	regression coefficient (b)	± 95% confidence limits
k_o - log PN	0.804	0.399
log N Dec - log PN	0.196	0.399
log PN - log N Dec	0.822	1.677
k_1 - log N Dec	0.257	0.482
$k_o + k_1$ - log PN	0.716	0.449
log N Feb - log PN	0.284	0.499
log PN - log N Feb	0.849	1.348
k_2 - log N Feb	0.829	0.298
log N Mar - log N Feb	0.171	0.298
log N Feb - log N Mar	1.216	2.117
k_3 - log N Mar	1.110	2.502
k_4 - log N June	0.149	0.745
k_5 - log N Sept	-0.298	0.343
k_6 - log N Sept Adults	0.184	0.088
log N Survivors - log N Sept Adults	0.816	0.088
log N Sept Adults - log N Survivors	1.208	0.128

Appendix 14–15 Wharepapa plot. Repression coefficient values and 95% confidence limits for the tests of density dependence of k 's carried out when the slope of k against log N_1 differed significantly from zero. Pooled data from 1975/76, 1976/77 and 1977/78 generations.

Test of Y on X	regression coefficient (b)	± 95% confidence limits
$k_0 + k_1$ - log PN	0.422	0.550
k_2 - log N Feb.	0.058	0.361
k_3 - log N Mar.	0.445	0.336
log N May - log N Mar.	0.550	0.336
log N Mar - log N May	1.033	0.628
k_4 - log N May	0.606	0.798
k_6 - log N Sept. Adults	-0.132	0.051
log N Survivors - log N Sept. Adults	1.122	0.062
log N Sept. Adults - log N Survivors	0.885	0.049

Appendix 14–16 Development ranking index (R_1) of black beetle populations in the paspalum, ryegrass and ryegrass/white clover plots at Otakanini, and the Wharepapa plot.

Plot	R_1 at sampling			
Paspalum	December	February	March	June
1974/75	1.71	5.08	7.29	7.45
1975/76	1.47	3.90	5.33	6.98
1976/77	1.61	3.70	4.96	6.39
1977/78	1.45	NS*	4.96	7.14
1978/79	1.55	4.98	6.47	NS
Wharepapa	December	February	March	May
1974/75	1.94	4.86	6.78	7.61
1975/76	1.34	4.36	4.69	4.89
1976/77	1.0	3.37	4.75	5.61
1977/78	1.44	NS	4.63	7.0
1978/79	1.44	4.36	6.25	NS
Ryegrass	December	February	March	June
1974/75	1.71	5.81	NS	NS
1975/76	1.71	4.61	NS	7.29
1976/77	1.49	5.38	NS	6.75
Ryegrass/white clover	December	February	March	June
1975/76	1.72	3.93	NS	7.27
1976/77	1.33	3.92	NS	6.29

*NS = not sampled

Appendix 14-17 Values of spring temperature (ΣT_D) at Woodhill Forest, predicted ranking index (R_i) of black beetle populations at Otakanini in December, and simulated population densities in February between 1956 and 1979 using four population models and assuming an initial density of $60/m^2$.

			Predicted black beetle population numbers/m^2 in February			
Year	ΣT_D *	R_{iDec} **	***Model 1	Model 2	Model 3	Model 4
1956	41.9	1.74	60	60	60	60
1957	40.1	1.56	63	65	87	97
1958	42.7	1.82	41	45	78	100
1959	40.3	1.58	73	74	132	199
1960	41.6	1.71	45	46	118	138
1961	41.4	1.69	56	58	142	204
1962	42.1	1.76	56	58	129	288
1963	40.1	1.56	68	69	174	501
1964	39.4	1.49	42	43	135	525
1965	39.2	1.47	32	32	92	191
1966	39.1	1.46	30	30	82	155
1967	42.3	1.78	28	29	56	126
1968	38.4	1.40	59	60	96	229
1969	40.8	1.63	27	28	56	159
1970	42.7	1.82	45	46	64	182
1971	41.1	1.66	76	76	113	363
1972	42.8	1.83	55	56	123	490
1973	43.8	1.93	78	79	214	1047
1974	42.2	1.77	108	110	407	2754
1975	42.8	1.83	76	78	457	4898
1976	39.4	1.49	83	85	562	10,000
1977	38.9	1.45	36	37	295	8710
1978	39.1	1.47	28	29	155	5370
1979	-	-	29	30	98	4365

* ΣT_D = Σ Mean daily temperature for September, October and November

** R_i = index of level of population development

*** = Population models are detailed in Chapter 14