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BEHAVIOURAL ANTECEDENTS OF ALTRUISM:

A Comparative Analysis

A thesis
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of the requirements for the Degree
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ABSTRACT

Altruism has two main aspects; the one philosophical and the other scientific. After a discussion of the main issues raised by the concept, two definitions having similar criteria were developed. Flight calls in male pheasants were then studied in order to place them either in one of the two altruistic categories or to relegate them to the egoistic category.

The establishment and maintenance of altruism in animal populations was examined in light of the dilemma presented by the classical genetic model for natural selection. A formula which will assist in the separation and delineation of the concept altruism from reciprocity and egoism was developed. The meaning of "others" was considered with respect to genetic coefficients of relationship. Modifications of a model for altruism were made which incorporated a factor covering the potential genetic contribution to future offspring by the altruist over that by the recipient(s). A further factor gave indications of possible values for the cost facet of altruism. These modifications help explain the preponderance of parental care in the animal world as opposed to geriatric care and suggest that older parents may be more altruistically disposed toward offspring than younger parents.

Based on a theory for the establishment and increase of altruistic genes in animal populations, a relationship was hypothesized to exist in the avian order Passeriformes between clutch averages (which were considered to be an index of "genetic investment") and prosocial behaviour. The positive correlations found supported this hypothesis.

Behaviours were then chosen from the mammalian order Artiodactyla for more exhaustive study. Mothering behaviour in sheep was examined for an altruistic bonding factor in the ewe towards the lamb which could be related to previous season twinning. Although the factor itself was not found, a serendipitous finding of sex ratio changes in back-crossed sheep was recorded.

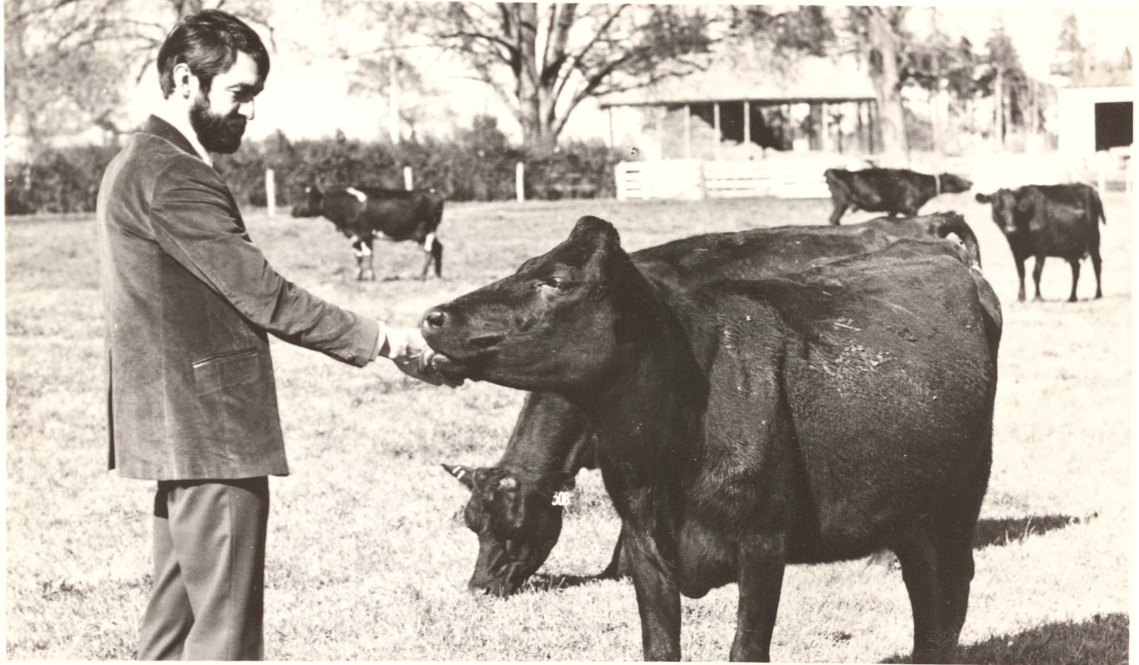
Social grooming in dairy cows was then investigated. The reduced stimulus world of the domestic cow decreases the number of modalities by which rewards may be returned to benefactors and the formula developed to delineate altruism from reciprocity and egoism could thus be more accurately applied. As little is known about social grooming in cows, herd parameters were recorded and several variables were correlated with the giving and/or receiving of grooming actions. Use of an identical twin herd furthered investigation into the meaning of "others" and it was found that grooming preferences fell into a five-point ordinal scale: self, twin, own age group, next nearest age group, and furthest away age group. Age proved to be the most pervasive variable correlated with non-twin social grooming, whereas within twin pairs grooming was most consistently correlated with milking order. The altruism found was also shown to be twin-linked (i.e. if one member of a twin pair was altruistic, its twin tended to be altruistic also).

Altruism is here considered almost coeval with egoism, that is almost as old as life itself. It is therefore reasonable to think of altruism as either a primary reinforcer or as being intrinsically motivating.

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"... under conditions of modern civilized life there is not a single factor exerting selection pressure in the direction of goodness and kindness, unless it is our innate feeling for these values."
(Lorenz, 1974, p.39).



Frontispiece: *Author being socially groomed by "Super Altruist" 307.*

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C H A P T E R I

INTRODUCTION

Research carried out in Sweden entitled "Sex as a Factor in the Behavior of Preadolescent Monkeys (*Macaca irus*) toward Infants" (Wood, 1970) formed part of the requirements for a M.Soc.Sc. degree from the University of Uppsala. An extension of the findings from that research, which supported the hypothesis that preadolescent (2 years $\pm$ 6 months) females show considerably more interest in infants (less than 36 weeks old) than do preadolescent males, led to a desire to uncover more information about affiliative sentiments. Many of the variables affecting mature maternal behaviour such as hormones released and connected to pregnancy, parturition and the resumption of the normal ovulatory cycle, would not appear to explain by themselves the increased interest of preadolescent females. Biological programming for such behaviour is one powerful interpretation of the results. One wonders how preadolescent female monkeys "know" in the ethological sense that they someday will be mothers and therefore show interest in handling young.

Prosocial behaviour has been perhaps a neglected area for research purposes. Judging from the relative imbalance in favour of agonistic contra affiliative behaviours found in scientific journals, it apparently is considered more rigorous to study discord, agonistic encounters and dominance hierarchies than prosocial or caretaking, epimeletic behaviours.

Altruism more than other categories of prosocial behaviour seems to be particularly prone to "scientific" criticism. This may have historical-philosophical roots that,

for some, prejudice the case and preclude an objective analysis of criteria for the construct or an agreement as to which data ought to be subsumed under such a heading.

This thesis is being presented to explore behavioural antecedents of altruism with the aim of clarifying some of the entanglements surrounding such a psychological construct. Primarily, then, it was this construct which was under analysis, not so much the several behaviours from different quarters which were used to shed light on this central concern.

The broader aspects to be dealt with were:

- (a) The definition of altruism.
- (b) Specific criteria for the definition
- (c) Altruism's delineation from the related concepts reciprocity and egoism
- (d) Altruism's genetic reality
- (e) Closer examination of a pro-social behaviour in a specific animal to give the opportunity of a reappraisal of the findings occasioned by investigations into the first four aspects of altruism.

In order to reach point (a), it was necessary in Chapter II to examine the definitional complexities connected with altruism. The philosophical orientations present in the literature led to a discussion of twelve points. These were resolved insofar as this thesis is concerned, although it is hoped that these resolutions will have wider applicability.

A recent review by Krebs (1970) gives an adequate handling of the state of the human literature relating to altruism up to that point in time, but he omits relevant animal studies. This

omission is also taken into account and compensated for in Chapter II. The use of comparative analysis through animal studies in this thesis relates mainly to the fourth goal of comparative psychology as elucidated by Hodos and Campbell (1969) which is involved with the analysis of the general mechanisms for adaption and survival. This led to a greater interest in genetic factors than in specific behaviours per se.

In Chapter III the efficacy of the scientific definition of altruism delineated in Chapter II is used to exclude a heretofore accepted behaviour from the category of altruism. Specifically, flight calls (sometimes considered "warning" calls) in ring-necked pheasants are examined in the light of a hypothesis regarding sexual dimorphism and self-preservation.

Once the definition for altruism has been established, the problem arises as to whether or not it can be "fixed" in the gene pools of viable species. Several models are reviewed in Chapter IV in order to strengthen the case for the establishment of altruism. A model is also presented to delineate altruism from reciprocity and egoism.

In Chapter V a genetic model discussed in Chapter IV and substantiated in the research literature through work on social insects is tested by looking at antecedents of altruistic behaviour in the avian order Passeriformes.

Chapter VI discusses an experiment with primiparous ewes and their success at mothering twins in relation to the success rate of twins born to the same mothers the following year. A serendipitous investigation considers the possibility of sex ratios being affected by genetic crosses.

Chapter VII deals with social grooming in two herds, one of identical twin dairy cows and one of identical twin heifers. Herd diurnal grooming rhythms are noted both in terms of the number of interactions and amount of time involved. Breed, age, body weight, milk production, milking order and effects of feeding schedules are examined in relation to social grooming both given and received. The information so far gathered is then used in the formula devised in Chapter IV to categorise altruistic and egoistic cows. These categories are used to form a dichotomous scale which is then examined for significant correlations with the same variables used in the general study of social grooming listed above. The twin cow herd is also examined in regard to the relationships formed with others (i.e. twins, own age group, nearest age group, and furthest away age group).

Chapter VIII concludes the thesis, gives a general summary and also includes suggestions for additional research.

C H A P T E R I I

PHILOSOPHICAL ORIENTATION AND BACKGROUND INFORMATION

Before a scientific investigation of altruism in man or animals can be undertaken it becomes necessary to consider several global aspects of the term, to assess the background for its common usage and to clearly delineate adequate working assumptions. This is the basic aim of the present chapter. When Auguste Comte introduced altruism as a philosophical term in 1851, it was almost immediately taken up as part of the zeitgeist and made to fill an immense conceptual vacuum. It was assimilated by the disciplines of religion and ethical theory, economics, sociology, literature and politics. Altruism seemed to have a quality which appealed to the imagination of social reformers. Many kinds of altruism flourished in the U.S.A. between 1865 and 1900, probably due to major uncertainties in American thought. Budd (1956) felt the altruism of that period "... was too malleable. Too many of even its sincere prophets invented emphases that ranged from self-immolation to scientific alms-giving." (p. 52).

A relatively quiescent period seems to have followed from 1900 until the late 40's. This might be a reflection of the pessimism engendered by the desperation of two world wars. Shortly after and possibly as a result of this period, the need for studies in altruism again seems to have been felt. Sorokin (1950) exemplified the urgency for such studies in the preface to his book Explorations in Altruistic Love and Behaviour, "... there seems to be no effective defense against the Apocalyptic methods of destruction but the Sermon on the Mount practised in human behavior, incorporated into our social

institutions, and incessantly articulated by culture." (p.v).

An increasing trend to do research in altruism is evident in the academic world. Since 1950 several books have been published (Eibl-Eibesfeldt, 1973; Macaulay & Berkowitz, 1970; Nagel, 1970; Rosenhan, 1967), a few doctoral theses (Armsby, 1968; Friedrichs, 1957; Rettig, 1956), and articles in a rather large variety of journals (see Bibliography) ranging from philosophy to genetics, from behaviour modification to humanistic psychology, have been written in this area.

Given the variety of backgrounds drawn upon originally to gain an orientation into altruism, it is not surprising to see research being generated now in many different directions. Experimental results by one observer are scrutinised by research workers operating from other philosophical orientations, who then feel they can discard the results presented, not due to any particular defect in experimental methodology, but rather due to the inexactitudes found in the basic working definitions or axioms.

Altruism has often been criticized on the grounds that a certain intent of behaviour is automatically implied. This criticism, however, is applicable to most of the terms with which we might elect to replace altruism. For example, prosocial or social grooming (rather than looking for edibles on another's fur). Amicable behaviour has suffered similar objections based on the idea that the acts referred to are not properly so described or interpreted (Barnett & Evans, 1964). Taking a reductionist point of view may lead us to identifying the maternal-care giving or epimeletic behaviour (Scott, 1956) of cats to their young as merely licking. However, what we gain in precise

physiological terms we may more than just lose in sociological or biological understanding.

Krebs (1970) in his summary of the altruistic literature considered that researchers had avoided the definitional problem by using operational definitions. In a similar vein, Macaulay & Berkowitz (1970) said in the introduction to their book on altruism that "... there are several definitional problems that are yet to be solved. We will begin by trying to dispose of (or evade) one of them: What is "Altruism"?" (p.2). Evasion, however, can hardly be considered a satisfactory basis upon which to establish a foundation for research.

A clearer conceptualization of altruism would facilitate inter-disciplinary communication of research findings. As a step in this direction, the following thirteen usages of the term altruism are examined to derive important issues which should be considered when forming a working definition of the term. These usages also illustrate the diversity of thinking in this area.

1. "Altruism ... Regard for others, as a principle of action; opp. to egoism or selfishness." Encyclopaedia Britannica - World Language Edition of the Oxford Dictionary (1962,p. 51).
2. "Learning theorists view altruistic behavior as a product of modelling, conditioning, discrimination training, and rewards for self-sacrifice." Sarason (1972, p. 405).
3. "The primary problem [regarding altruism] is whether there is purposive behavior in which one animal helps another at some cost to himself (in material wealth, such as food, or in the expenditure of energy), when

- the behavior has not been induced by reward or by threat of punishment." Hebb, (1971, p. 409).
4. "Altruism is self-destructive behavior performed for the benefit of others." Wilson (1971, p.321).
 5. Dobzhansky (1968) defined "Altruistic" as "... behavior benefiting the group (family, clan, tribe) to which the individual so behaving belongs and detrimental to that individual himself." (p.238).
 6. Trivers (1971) in his article on the Evolution of Reciprocal Altruism, stated that "Altruistic behavior can be defined as behavior that benefits another organism, not closely related, while being apparently detrimental to the organism performing the behavior, benefit and detriment being defined in terms of contribution to inclusive fitness." (p. 35).
 7. "Biological altruism, broadly defined, includes all behaviors by which some individuals benefit others of the same species, without benefiting themselves. The benefits may be voluntary or involuntary and direct or indirect: e.g., genetic shortening of life span is altruism if it prevents older individuals from competing to the disadvantage of younger ones. (But "reciprocal altruism" [Trivers, 1971, p. 35] is not altruism by this definition, because probabilities of benefits are mutual)." Darlington, Jr. (1972, p.293).
 8. Rice & Gainer (1962) felt that altruism could be operationally defined as "behavior of one animal that relieves another animal's 'distress'." (p. 123).
 9. "Empathic or vicarious control of behavior is in fact

a requirement of the truly altruistic act."

Aronfreed (1968, p. 139).

10. According to Kreb's (1970) analysis of Leeds' (1963) criteria, an "altruistic act;
 - a) is an end in itself; it is not directed at gain,
 - b) is emitted voluntarily, and
 - c) does good." (p. 259).
11. Maslow (1966) talks about " ... the godlike in human beings, of altruism ..." (p. 15).
12. "Altruism, on the other hand (as opposed to egoism), may denote the theory that we ought always to aim at other people's happiness, on the ground that this is the best means of securing our own as well as theirs." (Moore, 1965, p. 96).
13. "ALTRUISM, a philosophical term used in ethics (q.v.) for the theory of conduct which regards the good of others as the end of moral action. It was invented by Auguste Comte and adopted generally as a convenient antithesis to egoism. As a theory of conduct, its adequacy depends on the interpretation given to the term "good". If "the good" is taken to be pleasure and the absence of pain, altruism would seem a reasonable principle. Most men would agree that a moral agent has an obligation to further the pleasures and alleviate the pains of other people, while it would seem contrary to ordinary usage to say that a man has a duty to further his own pleasure or to spare himself pain or is to be blamed for not doing either of these things. The same arguments hold if happiness is taken as the end of life. But if "good" is used more widely to include knowledge, aesthetic experience, virtue of character and personal holiness, then altruism fails as a complete theory of morals, for a moral agent has a duty of self-improvement in these fields, as well as his duties to others.

Some utilitarians (e.g., Herbert Spencer and Sir Leslie Stephen; see UTILITARIANISM) held that these distinctions between self and others were unsatisfactory. Both egoism and altruism conceived society as an aggregate of units. The true moral aim was the welfare neither of others nor of self but of society (the social organism). This view claimed the support of evolutionary theory. Society was thought of as preserved and developed by the harmonious co-operation

of the individuals composing it, just as an organism is by the harmonious interaction of the cells of which it is made up. This analogy was dangerous for two reasons: it does not seem possible to speak of the good of a society except in terms of the goods of its individual members; and these theories do not make clear whether the society to which individual actions are referred is one society or many. In ordinary usage there are many societies, each with its own members, but it is not an adequate theory of morals to limit the moral agent's duties to actions serving the particular society to which he belongs.

The principle of altruism recalls the Christian maxim "Do unto others as you would they would do unto you". But "others" in this maxim means not "other Englishmen" or "other Christians" but "other men regardless of the particular societies to which they happen to belong." (Mabbot, 1970, p. 691c).

The above usages of altruism suggest twelve issues to be considered when defining the term. These issues are:

- I. Should altruism be reserved as a "higher human" quality?
 - II. What are the implications of purposive behaviour with relation to altruism?
 - III. Is altruism defined by intention or action?
 - IV. How is altruism related to egoism?
 - V. Is altruism a moral principle or a behavioural category?
 - VI. Is altruism amenable to empirical, scientific investigation?
 - VII. Can an absence of behaviour be altruism?
 - VIII. Is the existence of other's "need" or "distress" necessary to elicit altruism, or does it occasionally "overflow"?
 - IX. Is altruism innate or learned?
 - X. Is reward a concomitant of altruism?
 - XI. Is reciprocal altruism a contradiction in terms?
 - XII. What genetic relationship should the giver have to the recipient for the giving to be considered altruistic?
- Or, what is the meaning of "others"?

These issues will now be elaborated more fully. Most of the issues are left open in the following discussions. This is related to the nature of axioms used for building definitions; not being amenable to proof, they can only be presented. Following this, the stance taken in this research for each issue will be given (p. 51).

I. SHOULD ALTRUISM BE RESERVED AS A HIGHER HUMAN QUALITY?

Wirth (1966) interpreting Maslow, stated that he "... argues that [research] training based solely on the mechanistic model [of the physical sciences] tends to sponsor safe investigations, limited to enquiries that may be managed easily by the methodology. This has the effect of ruling out significant but more intractable questions that deal with the whole person - with subjective or self-knowledge, with deeper knowledge of "a single person," and with the higher human qualities such as altruism and integrity." (p. x.).

Two questions obtrude here,

1. whether or not altruism should be reserved as a "higher human quality", and
2. whether it is necessary to employ techniques not traditionally used in rigorous empirical scientific investigation to gain a more thorough understanding of altruism.

The second issue will be pursued later.

As frequently used it appears that in altruism one has discovered the dividing principle, or "divine touch" of deity, giving man a quality no animal possesses. For example, Zuckerman (1932) said that: "The reflex character of the reaction of a monkey who rushes to the aid of a tormented fellow

has been emphasized sufficiently not to require summarizing here. Its 'blind' character is demonstrated by the fact that the monkey responds in the same way to an 'assault' upon a dead companion. Monkeys and apes do not recognise death, for they react to their dead companions as if the latter were alive but passive. Thus the 'blind' character of their social responses would seem to deny them any claim to altruism." (p.305). And, as recently as 1966, Eimerl & DeVore in a similar vein stated that "Apparently non-human primates do not appreciate the significance of death, or so their behaviour suggests." (p.88). For evidence to support this view they mention George Schaller (1965) who once saw a female gorilla, with a two day old infant that had died, carrying the dead infant for four days before she finally abandoned it.

A consideration of the behaviour towards the dead observed in many human societies (where an assault on recently deceased relatives would not be tolerated either) would question the validity of the opinion above that altruism on these grounds should be reserved as a human quality.

Leeds (1963) mentioned three criteria which would tend to substantiate a "higher human" view of altruism.

1. The person who engages in giving, treats it as an end in itself. He anticipates no other satisfaction or gain than the pleasure of contributing to the welfare of others.
2. The person gives voluntarily. He is acting beyond the call of duty and not fulfilling stipulated role obligations.
3. On balance, the person "is doing good" as judged by the recipient and spectators to the action. (Krebs (1970) agreed that these criteria were in fact the attributes ascribed by laymen to altruism.)

The third criterion presents some difficulties, since it means that the operation of contingent factors, not reasonably foreseeable by the agent, may make his action non-altruistic. This problem seems to apply to any moral principle which judges individual actions by actual (i.e. "intended" or "reasonably foreseeable") results. These difficulties may be avoided by referring to types of actions rather than consequences, thus allowing one to ignore the odd case where, say, attempting to save someone's life turned out for some reason to have bad consequences for the recipient.

There seem to be strong emotive egocentric aspects for man having altruism as opposed to animals. One indication of this would be the general public's positive reactions to Adlerian psychology. Adler reorganised the Freudian psychoanalytic world, with its concentration on the id. Hall & Lindzey (1970) stated that "By endowing man with altruism, humanitarianism, co-operation, [Adler] restored to man a sense of dignity and worth that psychoanalysis had pretty largely destroyed ..." (p.127). Goldiamond (1968) agreed that some people when discussing conscience, morality and altruism would state that it is; "These behaviors - which make us human - ..." (p.32).

As Auguste Comte coined the term, his original statement should help clarify the picture regarding man's exclusive claim to altruism and provide an orientation for further discussion.

"We have now to consider the culminating point of the affective series; the social or altruistic propensities, ... Although, as I have already explained, it is only in our own race that this characteristic property can be fully manifested, its first appearance should be noted in Biology, as the best preparation for examining it afterwards more thoroughly in Sociology. That these higher instincts are shared by many animal species is beyond question. They exist sometimes in a higher degree of intensity than in Man; and independently of this they are not complicated with

social institutions and intellectual influences. Here consequently it is that their true character can be rigorously defined, so as to leave no room for uncertainty. Without the aid afforded by the observation of animals, our feeble reasoning powers would never have been able to withstand the sophistical attempts of theology and ontology to disprove the existence of innate sympathetic instincts; and indeed they still remain unacknowledged by minds who reject the validity of this appeal. ... Evidently the principal feature of Progress in all living things is that the general consensus which we have seen to be the essential attribute of vitality should become more perfect. It follows that happiness and worth, in individuals as well as in societies, depend on adequate ascendancy of the sympathetic instincts. Thus the expression, Live for Others, is the simplest summary of the whole moral code of Positivism. And Biology should indicate the germ of this principle, presenting it in a form uncomplicated by disturbing influences." (Comte, 1875, p.564).

The Darwinian tone in this passage is remarkable in that Comte published this work a full eight years prior to Darwin's Origin of the Species. The original French version (1851) is quoted in Appendix A.

The large number of experimenters using animals in their studies of altruism also suggests that one does not helpfully differentiate man from the animal kingdom along this dimension. Hebb (1971) much in accordance with the spirit of Comte's reasoning felt that "... the only decisive evidence of the existence of altruism, as such, comes from the large-brained infrahuman mammals." (p.409).

Tables I, II & III show the variety of animals studied and the type of helping behaviour or altruism discussed or observed. It starts with insects and extends along the scale of complexity to the subhuman primates and then man. These charts are a descriptive sample rather than an exhaustive listing of studies in the field, and illustrate briefly the range of investigations undertaken in this area.

Table I Representative Summary of Range of Species in which
Altruistic Behaviours have been Observed
(Invertebrates)

Researchers	Species Studied	Kind of Altruism or Helping Behaviours Discussed or Observed	Issues Raised (see p.10)
Eberhard (1972)	Sphecid Wasp (<i>Trigonopsis cameronii</i>)	"... altruistic behaviour associated with group living, most notably the failure to steal prey from nest mates ..." (p.1390).	VII
Darlington Jr. (1972)	Ants	"genes for altruism" in tri-determinant systems.	VII,XII,IV
Hamilton (1964)	Social insects (Hymenoptera)	Production of female workers vs. queens, and the genetic evolution of altruism.	XII
Wilson (1971)	Termites (<i>Nasutitermes</i>)	Altruism of individuals and of colonies - soldier caste defends others.	XII
	Fire ants (<i>Solenopsis saevissima</i>)	Injured workers leave the nest more readily than their uninjured sisters.	XII
	Harvesting ant (<i>Pogonomyrmex badius</i>)	"Dying workers tend to leave the nest altogether." (p.321)	XII
	"Higher" social insects	Alarm communication.	XII
Sakagami and Akahira (1960)	Honey bee workers (<i>Apis mellifera</i>)	Possess barbed stings that tend to remain embedded when the insects pull away from their victims, causing part of their viscera to be torn out and the bees to be fatally injured.	XII
Williams (1971)	Social insects	Altruistic behaviour by individuals who refrain from breeding and devote their lives to assisting the queen or royal couple and their young.	XII,VII
Limbaugh & Pederson & Chase (1961)	Shrimps (<i>Stenopus scutellus</i> & <i>Hippolyasmata californica</i>)	Shrimps that clean fishes.	XI
Trivers (1971)	Fish (<i>Labroides dimidiatus</i>) (Fish should be in Table II)	Cleaning symbioses and evolution of reciprocal altruism	XI

Table II Representative Summary of Range of Species in which Altruistic Behaviours have been Observed (Vertebrates)

Researchers	Species Studied	Kind of Altruism or Helping Behaviours Discussed or Observed	Issues Raised (see p.10)
Trivers (1971)	Birds	Warning calls	XI
Tinbergen (1965)	Male cardinal (<i>Pyrrhuloxia Richmondia Cardinalis</i>)	Fed several goldfish during a period of several days. (see fig. 2)	VIII
Skutch (1961)	Birds ("Helpers")	A "helper" is a bird which assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age which is neither its mate nor its dependent offspring. Brief accounts of the activities of helpers in over 130 species are given in an annotated list.	XII
Brown (1970)	Mexican Jay (<i>Aphelocoma ultramarina</i>)	Altruistic behaviour as shown by co-operative breeding (feeding the young of other parents, defence of territory, detection and mobbing of predators).	VIII
Lorenz (1935)	Jackdaws	Attack anyone who holds a conspecific in his hand, including the caretaker, when he is holding a tame Jackdaw.	VIII
Stanford (1952)	Bob-white quail (<i>Colinus virginianus</i>)	Unmated bob-white quail of either sex adopt orphaned young. 46.7 per cent of the 182 males sampled adopted orphaned young, whereas only 23.1 per cent of the 182 females sampled adopted the orphaned young.	VIII
Rice & Gainer (1962)	Albino Rats (of the Wistar strain)	More likely to press a bar when it lowered a struggling rat than when it lowered a styrofoam block.	VIII
Rice ¹ (1965)	Rats	Would press a bar to remove a companion from a tank of water.	VIII
Mykytowycz and Dudzinski (1972)	Rabbits - male (<i>Oryctolagus cuniculus</i>)	Bucks were seen to protect adults. Dominant males were observed to separate fighting does, this behaviour benefitted the young defenceless kittens.	VIII
Kilgour (personal communication 1973)	Sheep - Romney	Operational altruism in sheep may in part be defined as the picking up and mothering of another's lamb.	VIII
Carrington (1958)	Elephants (<i>Loxodonta africana</i>)	"... if a calf is orphaned, it will always find another cow in the herd who will accept it as her foster-child." (p.63).	VIII

1 reported by Krebs (1970).

Table II Cont'd.

Haber reported by Fox (1971)	Wolves (<i>Canis lupus</i>)	Observed altruism in wolves when they brought food to an injured alpha wolf.	VIII
H. & J. van Lawick- Goodall (1970)	Jackals (<i>Canis aureus</i>)	"... it is common for the older offspring of a pair of jackals, particularly the female offspring, to remain with the parents and help look after the next litter." (p. 142). These extra caretakers chase away hyenas, regurgitate food for their small siblings and spend long periods grooming them.	XII
Hebb & Thompson (1956)	Dogs	Prevented children from swimming by persistently "rescuing them".	I
Schaller (1972)	Lions	"Lactating lionesses permit small cubs of any litter to suckle on them, almost indiscriminately, ... cubs of several litters may occupy the four teats of one lioness." (p.149).	XII
Siebenaler and Caldwell (1956)	Dolphins (<i>Tursiops truncatus</i>)	"Co-operation" support for breathing after one of the group has been stunned. Two adults are required to assist each injured conspecific. The helpers must however regularly desert the injured one in order to blow. (See Fig. 4).	VIII
Eibl-Eibesfeldt (1970)	Rhesus Monkeys (Rhesus Macaques)	Will attack their keeper when he catches an animal from the group and it gives the alarm call.	VIII
Masserman (1968)		"Some macaques continued to starve for days rather than pull a lever to secure readily available food if they had learned that this also subjected another macaque to an electric shock." (p.255).	VII
Nissen (1931)	Chimpanzee	Large male "saving" a youngster from "danger" in "open field" situation.	II
Nissen and Crawford (1936)	Chimpanzee	Food sharing - begging.	VIII
Stevenson-Hamilton (1947)	Baboons	A cheetah being chased away by a large male baboon after the cheetah had tried to cut out some juveniles from the group.	VIII

Table III Some of the many altruistic behaviours that have been observed and recorded in Homo sapiens

Researchers		Kind of Altruism Discussed or Observed	Issues Raised (see p.10)
Staub ¹ (1968)	Children	Candy left for others.	VII
Ugurel-Semin (1952)	Children	Developmental aspects of children sharing edible nuts generously.	IX
Durkheim (1966)	Adults	Altruistic suicide.	II
Trivers (1971)	Adults	One human being saving another from drowning.	XI
Latane and Rodin (1969)	Adults	Helping an injured woman.	VIII
Darlington and Macker (1966)	Adults	Volunteering to give blood.	XI
Hornstein, Fish and Holmes (1968)	Adults	Returning "lost" wallets.	X
Feldman (1968)	Adults	Likelihood of mailing an unstamped letter for another person.	III
Trotter (1971)	Adults	Living donors of kidney transplants.	VIII
Darley and Batson as reported by Trotter (1971)	Adults (Seminarians from the Princeton Theological Seminary)	Helping a young man lying in an alley between two buildings coughing and groaning and possibly in pain, in relation to time pressures placed on the seminarians.	IV

¹ reported by Krebs (1970).

II. WHAT ARE THE IMPLICATIONS OF PURPOSIVE BEHAVIOUR WITH RELATION TO ALTRUISM?

"The primary problem [regarding altruism] is whether there is purposive behavior in which one animal helps another at some cost to himself ..." (Hebb, 1971, p. 409). A key word in this statement is purposive. Smith (1971), in a recent discussion of the existence or possibility of purpose, said that "In describing and evaluating human behaviour, it is commonly assumed that the behaviour is purposive and derives from a conscious awareness of features of the environment." (p. 34). Consciousness could not, according to Bowes (1971), be extended to animals. She reasoned "A dog too feels a desire to eat, that is a propensity which may be said to be mental, without however that involving a conscious experience of felt awareness that is feeling this desire ... It seems to me that if the dog did have this capacity, it would have symbolically codified its experience in language as human beings do and used some such term as "I"? It does not seem to me that a conscious awareness of private experience is possible without the use of "I" or a similar term." (p. VIII). In this connection it is interesting to note that of the one hundred and sixty words of American Sign Language acquired in an enriched learning programme for Chimpanzees, two of the words learned were "me" and "mine" (Fouts, 1974).

Purposive frequently seems to imply consciousness. However, consciousness is also a rather elusive variable to pin down. Dewey (1959) believed that "Psychologically speaking, our native impulses and acts are neither egoistic nor altruistic, that is, they are not actuated by conscious regard for either one's own good or that of others." (p. 324). Thomas (1970) has stated that

"Discussions of where in the hierarchy of animals or at what point in the development of a child consciousness first appears, are clearly terminological. If awareness of the environment, indicated by discriminatory reactions, is the criterion of consciousness, then even the protozoans are conscious. If awareness of awareness is required, then it is doubtful whether the great apes and human infants are conscious." (p. 370).

According to Tolman (1951) "All that can be conveyed about consciousness and ideation from the rat to the scientist or even from one scientist to another is that they perform certain functions." (p. 215).

Lorenz (1966) seemed to feel that "purposive" behaviour as used by Tolman (1951), is similar, if not identical, to the construct "Appetitive behaviour" used by the Ethologists. Eibl-Eibesfeldt (1970) in discussing appetitive behaviour, said

"... animals that for a time have had no opportunity to perform a certain behavior pattern are in a state of specific readiness to perform precisely the behavior pattern they were unable to perform. ... The observer at first notes merely a general restlessness of the animal - one has the impression "as if it were searching for something." ... If it does not find adequate releasing objects, it may on occasion accept substitute objects. Female rats are so ready to retrieve during the first few days following parturition that they will repeatedly grasp their own tail, retrieve it in their mouth, and deposit it in their nest. ... appetitive behavior, is variable and adaptable to changing situations. The animal must be capable of mastering detours that lie between it and a desired goal that is remembered, as when a dog in a mood to hunt proceeds toward a chicken yard known to him. Once he has found the releasing situation, the more automatically discharged fixed action patterns of prey catching run off. Their occurrence not only changes the releasing stimulus situation ... but results also in a change of mood ... Appetitive behavior can also ... be demonstrated by electrical brain stimulation. Cats that are eating stop when stimulated in certain points of the hypothalamus and attack a rat which has until then been ignored. If they do not see prey they search, and they learn a maze when they find as a reward a rat they are allowed to attack. ... The specific readiness to act or the mood of an animal is also shown in a noticeable

lowering of the threshold for certain releasing stimuli. A predator in a mood to hunt will react most readily to stimuli that release hunting-behavior patterns. If prevented from hunting for some time it will even accept substitute objects, and in some instances the response may occur in vacuo following a prolonged absence of the appropriate releasing stimuli ... At the same time the thresholds for other behavior patterns, for example those belonging to the area of sexual behavior, are raised such that very strong releasing stimuli are required to detract the animal from its hunting and switch it to sexual behavior." (p. 44).

Using the term appetitive or purposive serves the function of psychological economy. However, when empirical insights into the various physiological correlates of a given behaviour are increased we may find it expedient to discard this particular hypothetical construct. When purposiveness is used in its most effective form for understanding behaviour in general, including altruism, it seems to imply:

1. lowered thresholds of stimulus sensitivity;
2. increases in general arousal level;
3. going through the memory "bank" to find modes of action that have been successful in the past for attaining a given goal;
4. rank ordering, and using, one of these modes as the situation requires;
5. and all this is done against a background drive, which Tolman (1959) calls the drive against effort and uncertainty and/or that for little effort and for certainty.



Fig.1 *"Mismothering"* (after Tinbergen 1965).

III. IS ALTRUISM DEFINED BY INTENTION OR ACTION?

Sorokin (1961) stated that "As an empirical phenomenon altruistic love means a specific behavior of living forms striving - instinctively or consciously - to be helpful to other organisms." (p.641). Nagel (1970) stated in an ostensibly similar vein that "By altruism I mean not abject self-sacrifice, but merely a willingness to act in consideration of the interests of other persons without the need for ulterior motives." (p.79). However, both Sorokin and Nagel unwittingly confuse us here. Do they mean altruism is the striving, willingness, i.e. intent, or do they mean altruism is the specific behaviour, i.e. act? Maybe altruism for Sorokin means "specific behavior" and for Nagel means willingness.

Sorokin (1961) continued "If altruistic love remains in the state of a purely psychological experience and does not manifest itself in respective altruistic overt actions, then it becomes an "unfulfilled" or not "fully realized" love." (p.642).

The discussion on purposiveness would seem to indicate that altruism could be the result of an "appetitive" behaviour, and would in fact be most clearly defined, as such, on the consummation of the act following such behaviour. It would seem that inferences, already weak, about "states of mind" would be considerably more so if the act did not reach completion. The man who contributes \$5,000 to charity is considered altruistic by the arrangers of the charity, because they are familiar with the large number in the same socio-economic bracket who do not contribute financially. The man's colleagues, however, may feel that he is just contributing to reduce his income taxes, or to assuage a guilty conscience. Indeed, Rawlings (1968) stated that "A major theoretical approach to the study of altruistic behavior is to

view such behavior as a reaction to guilt or anxiety. Guilty persons may expiate their guilt by punishing themselves or doing something good ..." (p. 377).

Krebs (1970) felt that "Behavioral researchers have generally avoided the definitional issue [for altruism], which involves establishing the intention behind apparently self-sacrificial other-oriented acts, by employing operational definitions." (p.262). However, this is not surprising when one realizes that a great many psychologists feel they cannot establish, at least scientifically, "black box" intents behind any behavioural acts.

Campbell (1965) accepted the importance of intent but questioned its relationship with moral theory when he said that "Under a broader framework we must now, in some cases, be willing to see altruistic social motives as irrational and immoral, or at least amoral." (p.307).

Some would logically conclude that the fact that one acts altruistically does not mean that one is altruistic, and if one is altruistic, one may still be considered (for the same behavioural act) immoral or amoral.

IV. HOW IS ALTRUISM RELATED TO EGOISM?

In turning to psychoanalytical theory for assistance in clarifying this issue, we only find further confusion. Freud (1963) spoke of altruism in relation to egoism:

"We termed the cathexis of energy which the ego directs towards the object of its sexual desires 'libido', all the others, which are sent out by the self-preservative instincts, we termed 'interest'." (p. 414).

"When we speak of egoism, we have in view only the individual's advantage; when we talk of narcissism we are also taking libidinal satisfaction into account." (p.417).

"The opposite to egoism, altruism, does not, as a concept, coincide with libidinal object-cathexis, but is distinguished from it by the absence of longings for sexual satisfaction. When someone is completely in love, however, altruism converges with libidinal object-cathexis. As a rule the sexual object attracts a portion of the ego's narcissism to itself, and this becomes noticeable as what is known as the 'sexual over-valuation' of the object. If in addition there is an altruistic transposition of egoism on to the sexual object, the object becomes supremely powerful; it has, as it were, absorbed the ego." (p.418);

but when we put sentence one with three, altruism seems to all but vanish.

More recently altruism has been connected with the super-ego. For example Friedrichs (1960) felt that altruism is "... the inhibiting or controlling of ego's behavior to provide for satisfaction of alter's impulses or desires." (p.497). Similarly, Cattell and Horowitz (1952), in using an Objective Personality Test to investigate the structure of altruism, concluded that "If this test is penetrating the unconscious, as its construction supposes, the altruistic behavior measured here seems motivated by powerful super-ego pressures together with disregard of the external pressures of current society." (p.117). This, however, is difficult to understand as his subject population consisted of 60 undergraduate women students (probably from the University

of Illinois) and according to English & English (1970) the super-ego is, among other things, "... a system within the total psyche developed by ... incorporating the moral standards of society as perceived by the ego." (p.535). One wonders what external pressures these other students were bringing to bear on their contemporaries which were supposed to be disregarded rather than internalized.

Leaving psychoanalytic considerations aside and speaking more generally about the relationship between altruism and egoism, Wispé (1968) raised the question of the great moral paradox. If man is egoistic in the first place why should sympathy be one of his features or characteristics? An extreme position is taken by Cooley (1964) who said "I hold altruism, when used to denote a supposed peculiar class of impulses, separate from another supposed class called egoism, to be a mere fiction, ..." (p.375). Moore (1965) similarly suggested, from a philosophical orientation, that as opposed to egoism, altruism "... may denote the theory that we ought always to aim at other people's happiness, on the ground that this is the best means of securing our own as well as theirs." (p.96). In other words we ought to be egoistically altruistic.

"Altruism and egoism are coeval and as old as life itself" according to Holmes (1945, p.111), who quoted Aristotle as having said that "... all life is concerned with the realization of two ends, the preservation of the individual and the perpetuation of its race." Holmes (1945) felt that "Egoism and altruism have their roots in these two life activities." (p.111). The roots of altruism may be considered to have their origin where perpetuation of the species involves co-operation between two organisms (for the purpose of sexual reproduction and the survival of offspring).

Consequently, whereas asexual reproduction and egoism may be considered as old as life itself, altruism may only be considered as old as sexual reproduction. (See also Chapter IV).

V. IS ALTRUISM A MORAL PRINCIPLE OR A BEHAVIOURAL CATEGORY

Cassirer (1966), among others, considered that "... a knowledge of nature, is possible only on the assumption of universal determinism." (p.300). However, it seems that choice is the essence of morality. For example Hospers (1965) suggested that some (particularly indeterminists) feel that with regard to several alternative courses of action "Morality makes no sense unless you are really free to choose between them." (p.265). "It seems to me [Waddington, 1960] that a readiness to discuss the problems of ethics implies an acceptance that some significance can be attached to the concepts of organization and of Free Will, ..." (p.64). Determinants of a behaviour, if they can be identified, would seem to rule out its also being classified as moral. Concern for the welfare of others is another one of the distinguishing features of a moral system, as opposed to a system of conventions or manners which involves the form rather than the motivation of behaviour. Llano (1896) believed that the characteristic feature of moral consciousness is the feeling of duty or obligation, more generally known as conscience. By conscience he meant "... an abstract feeling of fear of punishment most vividly exhibited in the feeling of remorse following the commission of an immoral act; to which it must be added, that it is exclusively an egoistic feeling, inasmuch as it is a painful state experienced by the individual on his own account, and not a sympathetic or altruistic sentiment." (p.376).

Consequently three conditions which seem to be implied a priori when one is discussing moral principles are

1. concern for the welfare of others,
2. freedom of choice between alternative behaviours, and
3. obligation or duty.

A priori laws may be considered instances of prima-facie duties, i.e. laws which hold only if they are not overruled by a superior moral obligation.

A fourth point brought up in such contexts is, of course, the requirement of reward or rather lack of it. The resolution of this point for ethical systems is still a bit unclear. Scriven (1966) concluded, in relation to reward, that "The moral significance of unselfish behavior is that it helps others "for their own sake", implying "not for what others will do in return"; it is not made less moral by the fact that it gives satisfaction to the doer." (p.235). In other words, intrinsic rewards are allowable but not extrinsic rewards.

It has regularly been maintained by moral philosophers that the chief test which can be applied to an ethical system is to ask if it can be harmonized with common sense ethics; i.e. with those ethical judgements which we feel constrained to make, prior to philosophical persuasion, in our ordinary ethical thinking. (Ewing, 1966).

Whether altruism is considered as a moral principle or as a behavioural category seems to be intimately connected to the approaches or avenues one chooses for further pursuance of the subject.

VI. IS ALTRUISM AMENABLE TO EMPIRICAL, SCIENTIFIC INVESTIGATION?

There appear to be, according to Ewing (1966), four methods or alternatives to choose between when attempting to analyze an ethical concept such as altruism. Three of these correlate rather well with three of Kerlinger's (1967) four general ways or methods of knowing.

- | | |
|--|--|
| 1. The method of tenacity | |
| 2. The method of authority | A. metaphysical analysis |
| 3. The a priori method (or
method of intuition) | B. analysis in terms of
other ethical concepts |
| 4. The method of science | C. naturalistically (in
terms of the concepts
of a natural science,
including psychology) |
| | D. it may be declared unan-
alyzable |

(Kerlinger, 1967, p. 6)

(Ewing, 1966, p. 754)

Although substantial amounts of valid knowledge are acquired via the first three methods of knowing, Kerlinger (1967) felt "... that more dependable knowledge is attained through science because science ultimately appeals to evidence: propositions are subjected to empirical test." (p.8).

The function of science according to Braithwaite (1964) "... is to establish general laws covering the behaviour of the empirical events or objects with which the science in question is concerned, and thereby to enable us to connect together our knowledge of the separately known events, and to make reliable predictions of events as yet unknown." (p.1). So far, however, according to Sorokin (1961) "Scientific knowledge concerning altruistic love is, ..., almost negligible." (p.643).

Sorokin (1961) in order to remedy this lack, reduced altruistic love to five basic dimensions in an attempt to first describe and then measure its occurrence. These dimensions were:

1. Intensity - ranging from zero to infinity, from giving a few cents to the hungry to the sacrificing of one's life for the well-being of a loved person.
2. Extensity - ranging from the zero point of egoism (love of oneself) to the love of all mankind, of all living creatures and of the whole universe.
3. Duration - altruistic love ranging from the shortest possible moment to years, decades, often the whole life of an individual or of a group.
4. Purity - varying from love motivated by selfish expectations of advantage to the pure love motivated exclusively by love for love's sake, or by the love of a person for the person's sake. Pure love knows no bargain, no reward. It asks nothing in return.
5. Adequacy - fluctuating from the "blind" to the "wise" love. In the inadequate love there is always a discrepancy between the subjective motives and purposes of love and the objective consequences of the unwise or inadequate actions through which the love is expressed. (p.642).

Several of these dimensions certainly seem amenable to objective analysis and yet the issue of intent also appears to filter through, confounding the possibility of measurement.

In choosing a method to use for gaining greater insight into altruism several factors have to be considered. For example, from a utilitarian, pragmatic point of view it would seem that,

for the most part, intent is only identifiable by the consequences of the act, that the predisposing feelings for altruism are adequately termed empathy and sympathy, and that scientifically the term altruism may be reserved for a particular behavioural classification.

In looking at altruistic behaviour from an empirical deterministic orientation several major theoretical problems arise in connection with morals. The analysis of ethics, in terms of the concepts of a natural science, is regarded by some as a strong argument for such an approach. Others reason that a naturalistic analysis is, by its very nature, a strong argument against just such an approach. (Ewing, 1966, p. 754). An example of this is the definition of "good" as pleasant and what is desired by most, or as what is in accord with the main trend of evolution. This view might consider that an ethical system for man ought to bring about a cultural harmony with man's social-biological background. However, naturalistic theories are generally criticized for not developing the concept of "ought" as distinct from what "is". Flew (1967) in this line quoted Einstein as saying "Scientific statements of facts and relations ... cannot produce ethical directives." (p.42). Another criticism is that the naturalist's concept of "goodness" does not seem to call forth any real sense of obligation. Ethical conclusions, it is also objected, cannot be established in the way they should be if a naturalistic analysis were correct. Statistics about human psychological attitudes or introspective observations cannot prove that something is good or right. It is felt by some that a naturalistic account takes away the specific character of ethics (Ewing, 1966, p.755). However, science can, of course, increase the body of

knowledge to which ethics may then be related. Naturalists seem to make their greatest contribution towards understanding an ethical variable not so much by building ethical systems as by developing theories which may help explain the origin of ethical beliefs and attitudes from nonethical factors.

Altruism as a behaviour may be investigated scientifically. As a moral principle in an ethical system, however, it must be given over to the philosophers who may regard the intent rather than the behavioural act as the defining element, i.e. the intent to do something "good" as a result of experiencing sympathetic or empathic feelings.

One thing that can be done with such a variable through science is to more carefully delineate its area. In this case, if either a network of determining factors is shown to be operative for a given behaviour or contingent reinforcers are found, then that behaviour may be considered to no longer belong to the category delineated by altruism, as a moral principle, in philosophy. Conversely, if contingent reinforcers or a believed network of determining factors are shown not to be operative, then the question of status for the given behaviour is again thrown open and, temporarily at least, the given behaviour may again be subsumed under the philosophical category, altruism.

Of course, as deeper insights are gained into the relationships existing between the supposed initiator, the receiver and the environment in which the interaction takes place, the original classification of a behaviour as altruism may be altered to egoism.

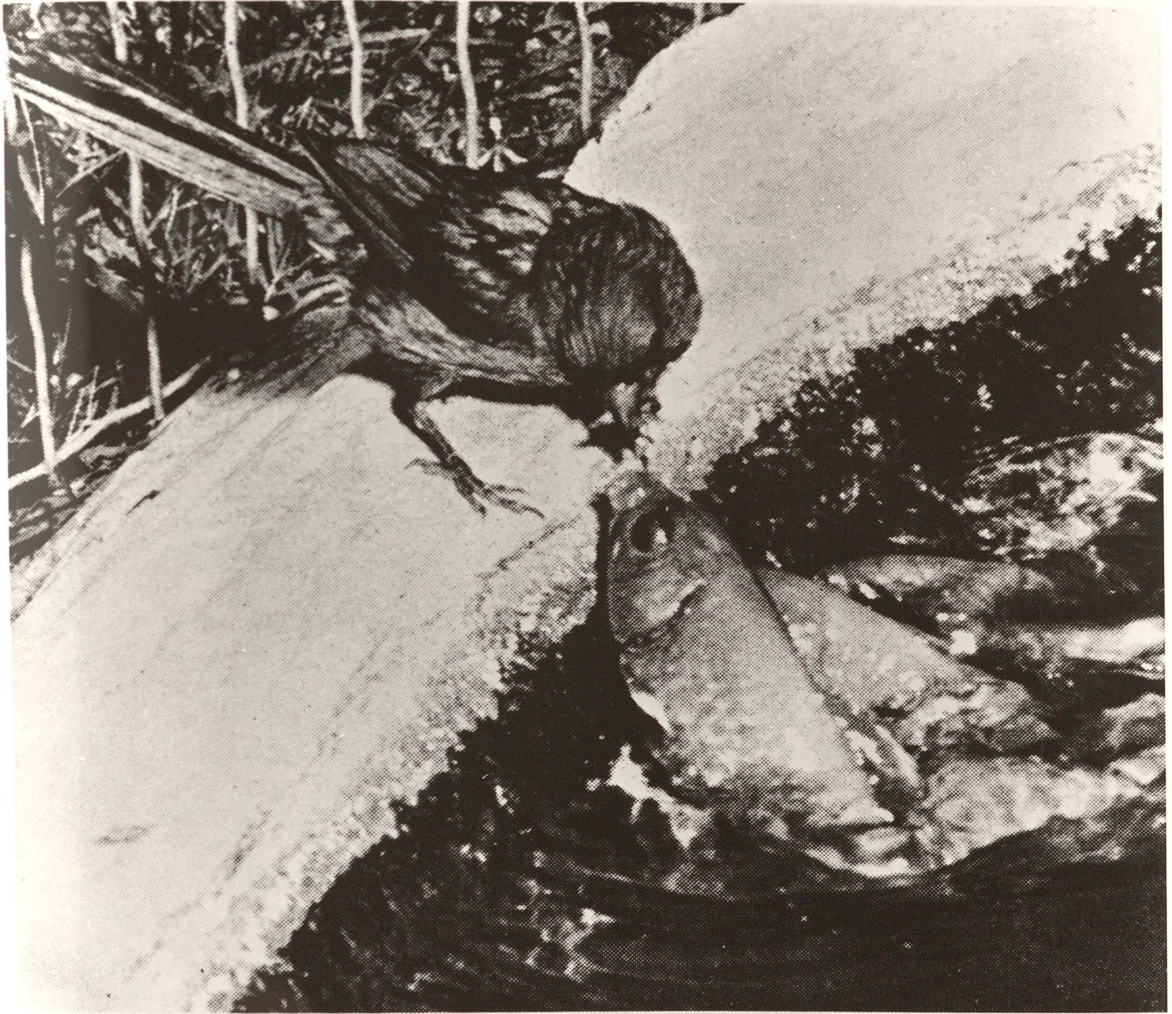


Fig.2 *"Operational altruism"* (after Tinbergen 1965).

VII. CAN AN ABSENCE OF BEHAVIOUR BE ALTRUISM?

In morality as in law, absences of behaviour are often treated as if they were behaviour. These absences or non-responses are typically negligent and wrong where there is held to be a duty to act (e.g. the prescribed duties mentioned in the N.E. Crimes Act of 1961 Sections 151, 157, 160).

In this general line Eberhard (1972) considered altruistic behaviour in wasps "... the failure to steal prey from nest mates ..." (p.1390). Darlington (1972) also made an interesting case for such altruism using dual and tri-determinant models which show that a given behaviour in the individual's repertoire may under some conditions be self-serving, whereas at other times the same behaviour may be beneficial to others. Specifically, he considered pecking orders which seem to involve, almost paradoxically, giving up at least temporarily the opportunity to reproduce. He stated "... gene Ap, is present in all individuals and determines that they form dominance-sequences, while positions in a sequence are determined by secondary, partly nongenetic factors, including perhaps differences in age, nutrition, disease, or early learning. Gene Ap has selective value and is maintained among effectively reproducing tops [leaders], while loss of altruistic bottoms [subordinates], which do little or no reproducing in any case (because of their inferior secondary characteristics), has little or no selective effect on the incidence of gene Ap." (p.294). With this reasoning, Darlington felt that the mechanisms ensuring territoriality, for example, may lead to starvation in poor times in poor areas, but would at the same time prevent competition in survival areas leading to the subsequent demise of the entire population.

Masserman (1968) gave rather similar evidence for altruism when discussing the significance of animal experiments for the comparative and clinical approaches to biodynamic therapy:

" 'Altruism': Some macaques continued to starve for days rather than pull a lever to secure readily available food if they had learned that this also subjected another macaque to an electric shock. Such 'succoring' behavior was apparently less dependent upon the relative age, size or sex of the two animals than on (a) their individual 'character' and (b) whether or not they had been mutually well-adjusted cagemates for a period of 3-6 months." (p. 255).

One of the philosophical problems of science associated with calling behavioural suppression, response inhibition or simply a non-response a response seems to lie in its measurability or, rather, lack of it. The famous dicta ascribed to E.L. Thorndike state that "If a thing exists, it exists in some amount" and "If it exists in some amount, it can be measured." (Cronbach, 1969, p.24). If a monkey gives food to a starving, begging, "other" monkey, we can measure the amount of food and use this amount in comparison to the total food intake or availability of food for the "altruistic" monkey in order to get an idea of the degree of altruism shown. However, if a monkey that regularly bites another, abruptly ceases from doing so, the problem of quantifying the so-called positive behaviour immediately becomes apparent. If, for example, it takes a split second to slash another and this occurs several times a day, will it be considered several occurrences of altruism or simply depression if no slashes occur? Is the altruism in the Masserman study a function of hours of deprivation? And, do the hours of the third day constitute an arithmetic or geometric progression over the altruism of day one? If one sent

guns to a people living in forested areas so they could acquire needed food, altruism could be measured in terms of the number sent. But if one refused to send guns to a people wishing to engage in a civil war, then how could one measure the amount of altruism? When categorizing an absence of behaviour as behaviour, one is of necessity involved with intent which more properly lies in the realm of the philosophy of psychology rather than the science of psychology.

VIII. IS THE EXISTENCE OF OTHER'S "NEED" OR "DISTRESS" NECESSARY TO ELICIT ALTRUISM, OR DOES IT OCCASIONALLY "OVERFLOW"?

Berkowitz (1968) asked the question this way: "What kind of individual would evoke the strongest reciprocity tendencies from the subject?" (p.49). And Krebs (1970) stated that "In almost all of the reported studies on altruism, altruistic behavior was elicited by a dependent other." (p.277). Nicoll and Meites (1959) found that the lactation responses of mother rats could be maintained during a 70-day period (instead of the usual 20-day) by replacement of the initial litter, with an equal number of 4-day-old foster pups, at 10-day intervals. Lorenz (1971) suggested that in humans certain stimuli from the small child elicit the parental care drive. He also stated that Tinbergen and Sietz's law of heterogeneous summation (the sum of the individual efficacies of the constituent characters equals the quantitative efficacy of every eliciting model, e.g. child, animal, doll or other) is operative here. Specifically the following characteristics were thought to be involved:

1. relatively large head
2. predominance of the brain capsule
3. large and low lying eyes
4. short, thick extremities
5. a springy elastic consistency
6. bulging cheek region
7. clumsy movements
8. and, according to Eibl-Eibesfeldt (1970, p.431),
a rounded body shape. (See figure 3)

It would seem that the situation of need or distress in others as perceived by observers as well as by a possible initiator of helping action would be, a priori, necessary for the action to be included under the laymen's category of altruism. However, if this a priori condition is added to the other conditions laymen have for altruism (Leeds 1963, Krebs 1970) (see p. 12), some may be caught in a conceptual bind. For if altruism is thought to be elicited or evoked, it may not logically be considered voluntarily emitted. And, if it is not voluntary, it is not altruism, at least not according to the generally agreed upon conditions for the term.

It would be pertinent here to discuss four possible ways of viewing altruism and need.

1. If need is perceived by the possible initiator (a relatively "free agent") and does not elicit altruism,
 - (a) altruism does not exist in the hypothesized initiator, or
 - (b) the possible initiator's "drive state" has not yet acquired an internal state of tension strong enough to impel the initiator to respond or behave adequately.
2. Need and altruism may be viewed
 - (a) from a causal view of science, i.e. need causes

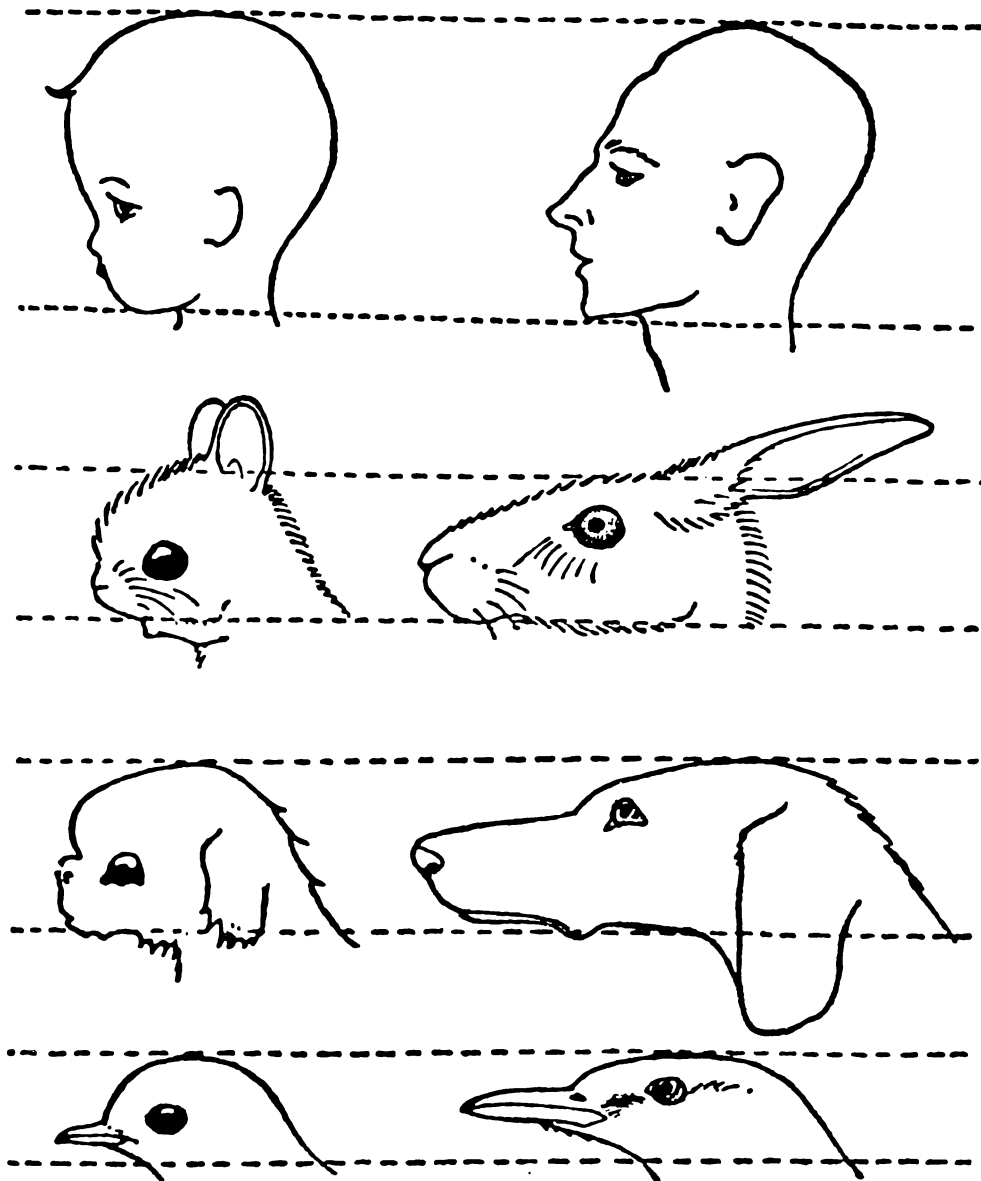


Fig.3 The releasing schema for human parental care responses. left: head proportions perceived as 'loveable' (child, jerboa, Pekinese dog, robin). right: related heads which do not elicit the parental drive (man, hare, hound, golden oriole). K. Lorenz (1971, p.155).

altruism to appear, or

- (b) from a correlational "Humean" view of science, where we may consider explanation to be the creation of a deterministic mental set about the correlation between need and altruism.

3. The correlation between altruism and need states may be definitional. And, as such, the eliciting or causal relationships must then be shown to have validity. We could have an "altruistic personality" (e.g. compulsive social groomer) randomly distributing "goodies" (grooming). When these "goodies" are distributed where others in need receive them the entire operation might reasonably then be identified by external observers as altruism (need present - help given), due to internal factors rather than external eliciting or evoking "causes". For possible initiators who do not perceive a need state and yet feel impelled to behave altruistically, we might consider "in vacuo" behaviour or "overflow" activities with reference to, say, Lorenz's imperfect (Hinde, 1956, p. 321) but interesting "Hydraulic model". Krebs (1971) felt that "Unsolicited food sharing offers more convincing support for altruism because it does not involve a noxious stimulus, but its underlying motives are also unclear." (p.412). In other words altruism apparently ought to "overflow ". However, logically it cannot "overflow" for then it would not be identified as altruism (need present - help given)!

Lehrman (1961) in discussing parental behaviour said that "Both in birds and in mammals, the establishment and maintenance of relations between the parent and the young (or eggs) is a process, or series of processes, of great complexity, involving a reciprocal interaction between, on the one hand, hormonal effects on behavior,

and on the other, the effects of external stimuli (including those arising from the behaviour of the animal and of its species-mates) on the patterns of hormone secretion." (p.1344). Hormonal effects may in fact reduce the discriminatory stimulus thresholds for altruistic behaviours.

Kilgour (1973, personal communication) stated that operational altruism in Romney sheep (sometimes called mismothering) may, in part, be defined as the picking up and mothering of another's lamb. He summarised (1971) two of the relevant variables as follows:

- "(a) The ewe, 3 to 4 hours before birth, is primed physiologically and ready to lick up and become attached to her lamb which is soon to be born.
- (b) If the other lambs freshly born are close by, such ewes will be strongly attracted to them. Smell appears to be critical." (p.202).

Eibl-Eibesfeldt (1970) seemed to be thinking of reduced stimulus thresholds in humans when he stated that "In Pekinese dogs breeders seem to have produced a perfect substitute object for the unfulfilled mothering reaction of older ladies." (p.432).

Krebs (1970) reported that "many studies have supported the notion that public transgression, whether intentional or unintentional, whether immoral or only situationally unfortunate, leads to reparative altruism." (p.267). Such transgressions appear to reduce stimulus thresholds for the discharge of altruistic behaviours. Another method for reducing these thresholds was related to success (ibid.) "... although none of the relevant experiments supplied unequivocal evidence, they all found indications that altruistic responses on behalf of dependent others are more probable after success than after failure, or after a neutral experience."

Perhaps the need or distress criterion in this context is too narrow. One might wish to benefit others, to make them "even happier". If anything, the recipient would be "signalling" happiness: so the altruistic behaviour is not then "elicited" as it might be by, e.g., crying offspring.

4. Altruism as the removal of noxious stimuli. Rice & Gainer (1962) operationally defined altruism as the "... behavior of one animal that relieves another animal's distress." (p.123). They placed forty albino rats individually in a compartment equipped with a bar which, when pressed, lowered either a styrofoam block or a "distressed" rat to the floor of an adjoining compartment, thus apparently relieving the suspended animal's "distress". Distress here being defined, operationally, by the rat exhibiting visual and auditory signs of discomfort such as squealing and convulsive wriggling. They found that the albino rats pressed a bar significantly more frequently when it lowered the struggling, distressed rat than when the bar lowered the plastic block.

According to Krebs (1970) "Rice (1965) also found that rats (but not guinea pigs) would press a bar to remove a companion from a tank of water." (p.261). Krebs questions, however, the attribution of altruism to these cases. He suggests (ibid.) that "It is possible that the rat's reaction was a function of the presence of another rat or the noxiousness of the screams of the distressed rats." Lavery & Foley (1963) also suggested that altruism as found by Rice & Gainer (1962) is not altruism, but merely the reaction to a noxious stimulus. They felt, in their experiment comparing the effects of white noise with squeals, that bar pressing can hardly be "... interpreted as altruistic since, in that case, both situations with squeals - either live or

recorded - should yield more frequent bar pressing than the white noise." (p. 173).

Krebs (1971) considered that "A final study (Nissen & Crawford, 1936) supplied unequivocal evidence that chimpanzees share food with one another. It did not, however, show that food sharing was based on altruistic motivations. The solicited food sharing might have been directed at the termination of a noxious begging response, in much the same way as the bar-press responses of the Lavery & Foley (1963) rats (c.f. Krebs, 1970, p.261)" (p.412). Nissen & Crawford (1936) had this to say about their study: "Responsiveness to begging may be (1) a response, probably related to reactions given in answer to call for help and appeals for sympathy, which gets rid of the presumably unpleasant stimulus of begging by the partner, or (2) an exchange with delayed reward ..." (p.416).

Krebs (1970) concluded that "All considered then, no real support for the existence of altruism in rats has been supplied." (p.261). This appears, however, to be an intuitive rather than deductive conclusion.

According to Webster's New World Dictionary (1953) noxious means "harmful to health or morals; unwholesome.-SYN. See pernicious." (p. 1006). In looking at several aspects of the word noxious it would seem as difficult a concept to "pin down" as altruism itself. If we consider that need must be perceived, then the modalities by which this information is obtained might be fruitfully examined. Labelling the incoming stimulus as noxious still does not tell us much about the nature of the outgoing response. Or, indeed, which response out of the behavioural repertoire will be used. It was one of these responses which the Rice & Gainer

(1962) study designated altruism.

Certainly a mother may upon hearing her baby crying in another room show signs of distress and tension, jump up, go to the baby, breast-feed it, and put it gently to sleep. Regardless of whether the discriminatory stimuli leading to the behaviour may be thought of as noxious or not, this for most of us would be an example of maternal behaviour. "The female turkey recognises her chick only by its calls and will brood a stuffed polecat that is fitted with a loudspeaker uttering the call of newborn turkeys. She will kill her own young if she is deaf and cannot hear their calls." (Schleidt, Schleidt and Magg, 1960).

Lorenz (1960), discussing visual discriminative stimuli and the reaction of Jackdaws, said that "Even when I took the babies from the nest and presented them to their parents on the palm of my hand, it left them quite unmoved. But the very day that the small feathers on the nestling burst through their quills, changing their colour into black, there followed a furious attack by the parents on my outstretched hand." (p.161).

Eimerl and DeVore (1966) also considered that, in monkeys (in this case langurs) "Once the infant's coat changes colour - from dark to light - the attitude of the other females changes. They still come to its aid if it is mistreated, perhaps by a too-vigorously playful older infant, but they no longer want to hold it." (p.89).

If, for the sake of simplicity, we assume that noxious was meant to be just another term for aversive stimuli, then we might ask what drive or movement is not, in some sense, so impelled. It seems that the two sources of auditory stimulation mentioned by Lavery and Foley (1963), squeals and white noise, are noxious

in differing degrees and will probably be attended to differentially. The question, however, arises as to why, then, the assumption is made that "noxious" stimuli connected to altruistic responses (squeals) should take precedence over those connected with egoistic responses (white noise). This assumption seems to be implicit in the criticisms presented above by Lavery & Foley (1963) and extended by Krebs (1970). Several possible routes are open to a rat mother presented with her squealing pups for removal of the "noxious" stimulation. She may for example abandon them, kill them or mother them. In the Rice & Gainer (1962) experiment rats could also as Krebs (1970) pointed out, crouch in fear. In other words, Krebs' conclusion as to the existence or not of altruism in rats and other infrahuman mammals, based on the studies cited, seems to be somewhat premature. This confusion in the research again seems to have its origins in the definitional issues which prevent further research from being interpreted meaningfully. Mykytowycz & Dudzinski (1972) for example, felt that "considering this objection of Lavery & Foley (1963) to Rice & Gainer (1962) it is difficult to decide whether the behaviour of male rabbits (which benefits the young) should be termed altruism or regarded merely as a reaction to the aggressive attitude of the females." (p. 117). They leave the question, as do so many other researchers, just hanging ...

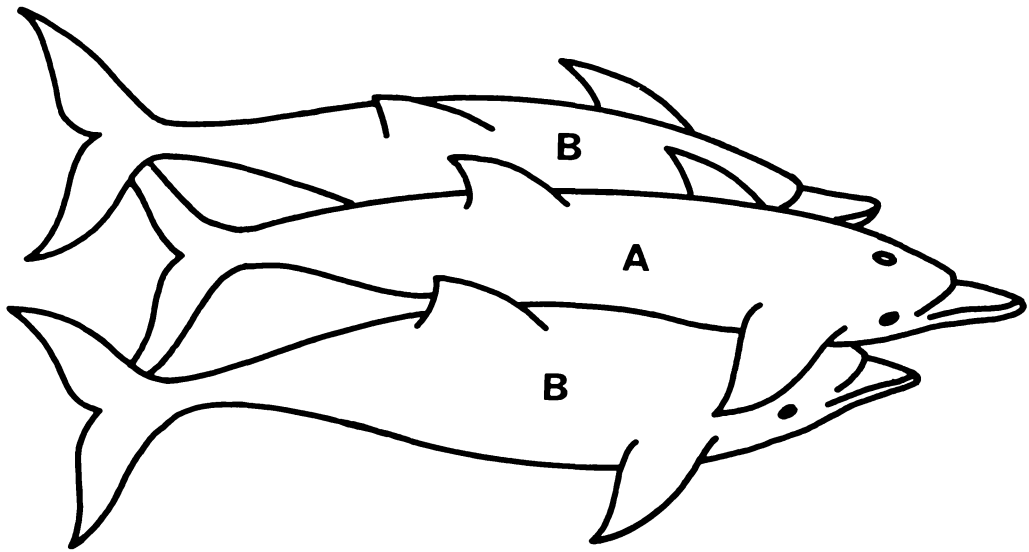


Fig. 4 Positions of the "assisting" pair of dolphins (B) in relation to the injured individual (A), (after Briggs 1956).

IX. IS ALTRUISM INNATE OR LEARNED?

An important dichotomy which researchers have considered is the innate versus learned nature of altruism.

The proponents of learning seem to have left little room for genetic factors in their definitions or usages of altruism. For example, according to Dewey (1959) "A correct theory of motivation shows that both self-love and altruism are acquired dispositions, not original ingredients in our psychological make-up, and that each of them may be either morally good or morally reprehensible." (p.324). In a general review of the field Sarason (1972) felt able to state, rather all encompassingly, that "Learning theorists view altruistic behavior as a product of modelling, conditioning, discrimination training, and rewards for self-sacrifice." (p.405).

Two studies that could be related to altruism's status as an intrinsically appropriate reinforcer may illuminate the matter a bit further. Tipton & Browning (1972) found that "verbal reward for an altruistic act did not positively influence a S to behave altruistically in another situation immediately following, but, to the contrary, it decreased the likelihood of this occurring." (p.322.) This would seem to suggest a drive state satisfied. This brings to mind the maxim "Do a good turn daily"! which has a frequency limitation implicit in it. This was also a rather surprising result, in that the investigation was designed to look at reward contra punishment in relation to altruism. Many researchers have worked with the problem of shaping altruistic behaviour with rewards, but few have considered whether or not altruism itself might be rewarding. Weiss, Buchanan, Altstatt & Lombardo (1971) did consider this problem, however, and felt able to state that "... our

research demonstrates that instrumental behavior can be learned and maintained solely through the rewarding function of altruism." (p.1263).

These two studies seem to indicate that altruism could be either a primary reinforcer or may, from another theoretical framework, be considered intrinsically motivating. People's willingness to pay to see "heart-rending" movies may possibly also be related to such a drive.

In the literature, there appears to be a fairly high correlation between interest in the innate aspects and the "causal" aspects of behaviour. In other words, those who interest themselves in understanding altruistic behaviour or predispositions for it, seem to be also interested in the innate explanation (see Chapter IV). On the other hand, those who wish to control or increase altruism seem to find they can "handle" altruism more easily if it is considered to be a learned behaviour (e.g. Goldiamond, 1968, Sarason, 1972).

X. IS REWARD A CONCOMITANT OF ALTRUISM?

The question of reinforcers for altruism also poses a problem. For example, Bryan and Test (1967) defined altruistic behaviour as "... those acts wherein individuals share or sacrifice a presumed positive reinforcer for no apparent social or material gain." (p. 400). According to Wilson (1971) "Altruism is self-destructive behavior performed for the benefit of others." (p.321). Hebb (1971) similarly considered that "The primary problem [regarding altruism] is whether there is purposive behaviour in which one animal helps another at some cost to himself

(in material wealth, such as food, or in the expenditure of energy), when the behavior has not been induced by reward or by threat of punishment." (p.409). And, Macaulay and Berkowitz (1970) defined altruism as "... behavior carried out to benefit another without anticipation of rewards from external sources." (p.3). Goldiamond (1968) in a similar vein suggested that some people when arguing about the import of behaviourism for altruism might just simply say "But when it comes to conscience, morality, altruism and regard for others, behaviorism falls short. These behaviors - which make us human - cannot be related to a system of overt and manipulable consequences." (p.32). The average person concerned with altruism probably just does not include behaviour which benefits another and yet gains rewards for the initiator of that behaviour in his category of altruism. However, this class of behaviours then could be considered to provide behaviours within the organism's repertoire which may then be used altruistically when need situations arise. The behavioural scientist is faced with the dilemma, pointed out by Krebs (1970), as to whether or not self-sacrificial behaviour can, in fact, continue in the absence of positive reinforcement. This would require proof of the null hypothesis which is, by definition, impossible. The more scientists look at altruistic behaviours the more clearly altruism as a category will be delineated by the removal of behaviours which are contingent on reward or avoidance of aversive effects. However, this search for complete delineation of altruism will be one without end.

Purported altruism in many contexts seems really to involve physiological or materialistic gains to the receiver in return

for intrinsic rewards to the giver or initiator of the behaviour. Intrinsic or metaphysical rewards for an individual in this context are considered in relation to internalised value or moral systems, i.e. "Black Box" variables (See Appendix B "The Good Samaritan"). Genetic factors probably also play their role in "rewarding" "suitable" "here and now" behaviour in the "here-after" (See Chapter IV).

XI. IS RECIPROCAL ALTRUISM A CONTRADICTION IN TERMS?

Reciprocal relationships may provide a background of behaviours in an animal's repertoire which may be used when opportunities for altruistic behaviour arise. However, to the extent that relationships are reciprocal, they are not considered altruistic. (See Chapter IV for a more thorough discussion).

XII. WHAT GENETIC RELATIONSHIP SHOULD THE GIVER HAVE TO THE RECIPIENT FOR THE GIVING TO BE CONSIDERED ALTRUISTIC? OR, WHAT IS THE MEANING OF "OTHERS"?

All genetic relationships between the giver and potential recipients are accepted for the purposes of increasing the understanding of the extensity of this relationship as a variable for the intensity of altruism exhibited. (See Chapters IV, V).

The following guidelines, developed from the discussions of the issues raised on p.10, formed a working base for this study:

- I. In the spirit of Comte, altruism is not considered to be reserved as a "higher human" quality. (see p.11).
- II. The implications of purposive behaviour regarding altruism are as follows:
 - (a) Lowered thresholds of stimulus sensitivity
 - (b) increases in general arousal level
 - (c) going through the memory "bank" to find modes of action that have been successful in the past for attaining a given goal
 - (d) rank ordering and using one of these modes as the situation requires
 - (e) and all this is done against a background drive which Tolman (1959, p. 102) calls the drive against effort and uncertainty and/or that for little effort and for certainty. (see p.19).
- III. Scientifically, altruism is considered in terms of the behaviour observed. Philosophically, altruism is considered in terms of the intention of the behaviour. (see p.23).
- IV. Altruism is almost coeval with egoism and certainly almost as old as life itself. (see p.25).
- V. According to the circumstances, altruism may be considered to be either a moral principle or a behavioural category, or both. (see p.27).
- VI. Altruism as a behaviour may be investigated scientifically, and be thereby more clearly delineated. As a moral principle implying choice and no reward to the donor, it

must be turned over to the philosophers. (see p.29).

- VII. Altruism as an absence of behaviour may be considered not measurably present. (see p.34).
- VIII. A perceived "need" state may be considered as information rather than as an irresistible elicitor. (see p.36).
- IX. It is reasonable to consider altruism as either a primary reinforcer or as being intrinsically motivating. Such innate predisposing properties are likely to lend themselves to modification through learning in some of the more complex species. (see p.46).
- X. No tangible extrinsic rewards should be forthcoming to the individual, in his lifetime, if his actions are to be considered altruistic. (see p.47).
- XI. In the immediate (life of the individual) form, reciprocal altruism is a contradiction in terms. However, it may be considered an antecedent condition for "true" altruism to appear. (see p.49).
- XII. All genetic relationships of the giver with the recipient are considered relevant data investigating altruism. It may turn out to be pertinent for an understanding of the extensity and intensity of altruistic behaviours. This will be taken up later in an evolutionary context. (see p.49).

DEFINING ALTRUISM

If in the assignment of data to a class or category (such as altruism) we circumscribe only one relationship, the characteristics of the original observations will be retained, and may be communicated directly, without loss of information. In other words, we may more easily reconstruct a mental image similar to the original. If the class or category circumscribes two or more relationships, some loss of information is incurred; but then the principles so derived may be useful in creating mental sets which will help in understanding new situations.. In other words, some loss of specific information is balanced by a gain in psychological economy.

But, if the category chosen is large or inclusive in relation to the total range of a set of possible observations, this loss of specific information may be so appreciable that the original categorization is defeated in its purpose of communication (Ferguson, 1966, p.28).

Grice & Strawson (1956) suggested that there are several ways by which a category or distinction may be criticized. It can be criticized:

- A. for not being a sharp distinction i.e. for admitting cases which do not fall clearly on either side of it.
- B. due to the ambiguity of the terms from which it is customarily drawn.
- C. due to confusion i.e. different meanings which are habitually conflated.
- D. because it is not useful. A distinction can be said to be:

1. useless for certain purposes, or
2. useless altogether.

Altruism includes a number of behaviours that are more generally thought of as species-specific or rather universal within a species. Such behaviours would have bio-genetically a rather "normal" status.

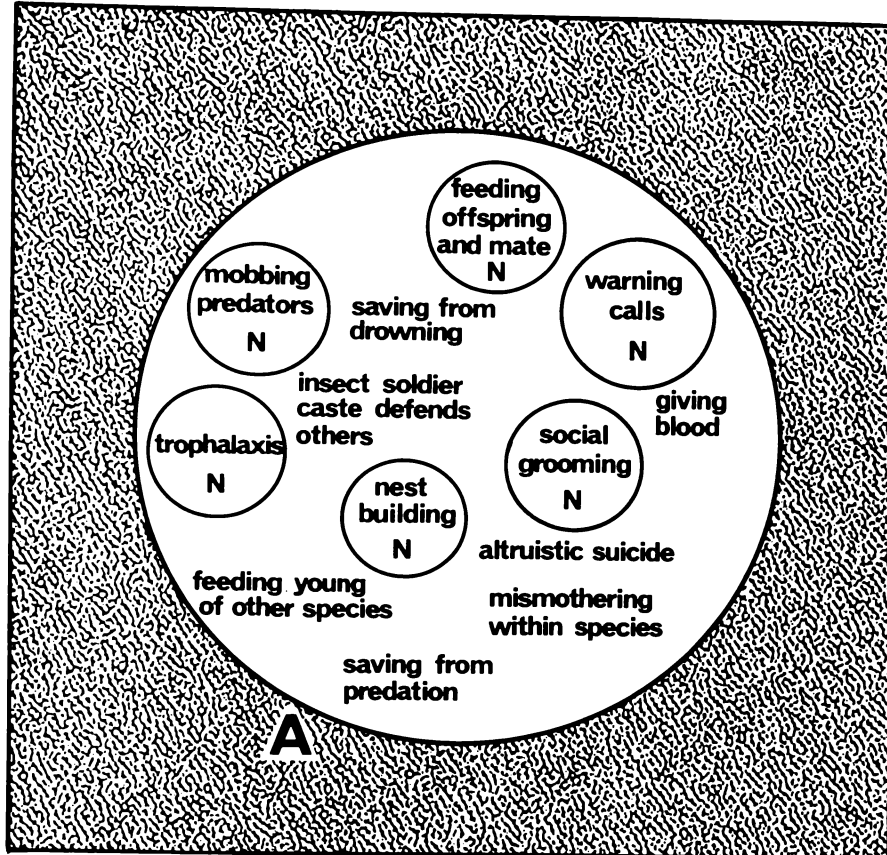
In that it is likely that the usage of the term altruism generally is reserved for unusual or "abnormal" situations, such as droughts, floods, drownings, and starvation etc., a reassessment of the sub-categories of altruism may be required. We could under these conditions consider that a number of the sub-categories might no longer be described as altruistic when they reached the criteria required for "normal" status. They could then be considered as possible predisposing or antecedent elements for altruism in less usual circumstances.

Altruism may be considered both an essential basic (in our understanding) category and a residual (in our usage) category.

Dividing the world of behaviour into two sections, between egoism (to self) and altruism (to others) would seem to include too much of the behavioural world for altruism to be useful. But, when used as a residual category, altruism both conveys information and serves to give us a gain in psychological economy. (see Fig. 5).

Let us consider two definitions for altruism simultaneously, one philosophical and the other scientific. This may help avoid some of the pitfalls pointed out by Grice & Strawson (1956) and listed above, and at the same time draw together the guidelines developed from the discussions emanating from the issues raised on p. 10.

W



A

W = directed activity which benefits oneself (egoism) others (altruism), both (reciprocity) and inanimate objects

A = { $a/a \in W$ and a is an altruistic act or behaviour which benefits other individuals more than one-self }

Fig 5. The Universe of Altruism minus "normal" (N) altruism (those behaviours basic for understanding altruism & its evolution) leaves the residual altruism of everyday usage.

Altruism (philosophical) is here defined as "voluntary" purposive activity likely to benefit others more than oneself when that activity has not been motivated by reward." Criteria for such an altruistic act are that:

- (a) it is a social behaviour directed towards others
- (b) benefit is taken to mean increases in physiological well-being and/or materialistic comfort.

Benefit could also be taken generally to mean drive reduction for the recipient. This would include, theoretically, the giving of intangible benefits (e.g. ideas, advice, songs, etc.) to the recipient. However, as no references to intangible benefits were noted in the literature, it is assumed that this more global view of altruism is by convention excluded.

Altruism (scientific) is defined as purposive activity likely to benefit others more than oneself. The criteria for an altruistic act are the same as above.

If when examining altruism (scientific) either a network of determining factors can be experimentally shown to be operative for a given behaviour, or contingent reinforcers found, that behaviour may be considered to not belong to the category delineated by altruism (philosophical) and subsumed under morality.

If, upon examining a given behaviour which has been excluded from altruism (philosophical) but can still be included in altruism (scientific), the believed network of determining factors or contingent reinforcers is experimentally shown in fact not to be operative, then the question of its permanent status as altruism (philosophical) is again thrown open. And, temporarily at least, the given behaviour may once more be subsumed under the category altruism (philosophical).

A scientist attempting to uncover the dynamics behind altruism (philosophical) may find that the subject matter diminishes with the success of his research. However, increased understanding of altruism (scientific) may help us to increase the incidence of such behaviours in the world around us.

C H A P T E R I I I

AN ALTRUISTIC BEHAVIOUR REASSESSED

Behaviour initially classed as altruism (philosophical) may on closer scrutiny be removed from that particular category by identifying conditions which would either predispose or reinforce the behaviour. This could still leave the behaviour in question in the altruism (scientific) category. However, should closer examination reveal that the behaviour also does not satisfy the criteria for altruism (scientific), it may be returned to the category egoism. A behaviour initially thought to benefit another at cost to the donator may prove to primarily benefit the donator and only secondarily the supposed other.

Heinz & Gysel (1970) categorised Ring-necked pheasant male vocalizations as alarm, flight, crow, hiss, antagonistic and pecked. They list the following categories for female vocalization: squeak, flight, pecked, precopulatory, distress, brood caution and brood gathering. The particular call of interest here is the flight call present in the repertoire of both sexes. Heinz & Gysel (1970), reporting on the physical characteristics of the male flight calls, point out that they are generally shorter in length than the "alarm" call. The harmonic structure, however, is similar with the fundamental at 1000 cycles per second or less. The female flight call is a higher pitched sound and is loudest between 2500 and 5000 cycles per second. On disturbing a hen with a brood one may hear this call as the hen takes off in flight (Heinz & Gysel, 1970). Casual observation of a pair of pheasants found that they would frequently crouch in nearby bushes and then suddenly with a great

startling squawk the brightly coloured male would lift his wings and move some 50 or more metres. The female would either scoot from bush to bush or also take flight but without squawking. It would be hunters who have imagined the call to be a warning or altruistic call as they could get a good bead on their quarry and bring in another dead male pheasant whereas the cryptically coloured female, initially unnoticed by them, would make her escape. The differential survival value of cryptic colouration between two species of pheasants found in New Zealand was shown in studies carried out by Westerskov (1963b). If in sexually dimorphic species initially differential survival rates exist, then it is but a short step to imagine there might also arise within such species genetically-linked behavioural modifications in the more heavily predated sex which may alleviate this differential.

That the squawk should be given by the male suggested an alternative to an altruism (philosophical) explanation. Maybe the call was, in fact, reserved to the brightly coloured males and served the primary function of scaring-startling or "freezing" predatory enemies in their tracks while the male flew away.

The hypothesis in this experiment, therefore, was that the sexually dimorphic, brightly coloured pheasant males would give the flight call significantly more frequently than the cryptically coloured females when startled into "true" flight.

SUBJECTS

The subjects were 40 male and 20 female Ring-necked pheasants (*Phasianus colchicus*) housed in separate outdoor paddocks according to sex and number at the Hilldale Game Farm, Hamilton, New Zealand. The ratio of males to females at Hilldale was 3 : 1. The age of

subjects was 29 weeks $\pm$ 2. Full maturity is considered to have been reached by 32 to 36 weeks. The total pheasant population from which subjects were drawn was 4250. They were raised from eggs and fed high protein special Game Bird Mix. Although considered genetically pure, the possibility exists for some slight mixture or cross in the total population with English Blackneck (*P. colchicus colchicus*), Mongolian (*P. colchicus mongolicus*) and Chinese Ringneck (*P. colchicus torquatus*) pheasants. It was not considered by the owner that any crosses occurred in the subject population. All the birds carried the phenotypic white collar markings. However, Westerskov (1963b) points out the difficulty in discerning black-neck from ring-neck pheasants among the wild stock now established in New Zealand. He states that "White collars persist in populations of otherwise black-neck-looking cocks as the white collar is dominant, pure black-necks being recessive in all crosses involving ring-necks" (Westerskov, 1963b, p.239).

These pheasants came from home reared eggs although the original stock was imported into Australia from England 100 years ago. As it is illegal to shoot pheasant hens in the Waikato region of New Zealand many more pheasant cocks are demanded to satisfy the shooters' market. This uneven ratio in a bird frequently known to exhibit harem behaviour is thus partially explained.

There were no number identification rings on the subjects, nor was there any individual data on the subjects available. The subjects were fed by hand generally and were used to seeing visitors (some 10,000 per year) at the game farm.

OBSERVATIONAL FIELD

The observational field consisted of fifteen open air paddocks enclosed with chicken wire netting to a general height of eight feet and covering half an acre in thirteen of the paddocks, the fourteenth covering three quarters of an acre and the last one and a quarter acres. Five of the half acre paddocks housed females, the other ten paddocks housed males. The general form of the paddocks was a rather long rectangular shape (see Fig. 6). Food was placed in three hoppers in each paddock and drinking water was available in every paddock. Shelter existed in two paddocks. Camellia and grass were the main plants growing in the paddocks. Roughly three pheasants per paddock per year break their necks in the overhead netting which is one of many factors which may contribute to the decreasing possibilities for stock that has been cage-raised for many generations to survive in the wild.

PROCEDURE

On 12 June 1973 (temperature 13.2°C with three quarter cloud cover) between 1400 and 1600 hours two observers moved together through each of fifteen paddocks. After quietly herding the birds into one end of the runway-shaped paddocks, one observer would single out a bird at random and by approaching rapidly and flailing the air with outstretched arms induce the subject to run-fly to the other end of the paddock. True flight was required of each subject and was identified by a flight covering not less than fifteen feet. Vocalizations were noted and reported to an assistant who recorded the observations. The assistant (also a graduate student in psychology at Waikato University) remained outside the paddock where things were relatively calm. Individual subjects were selected on the basis of their being easily identified (in

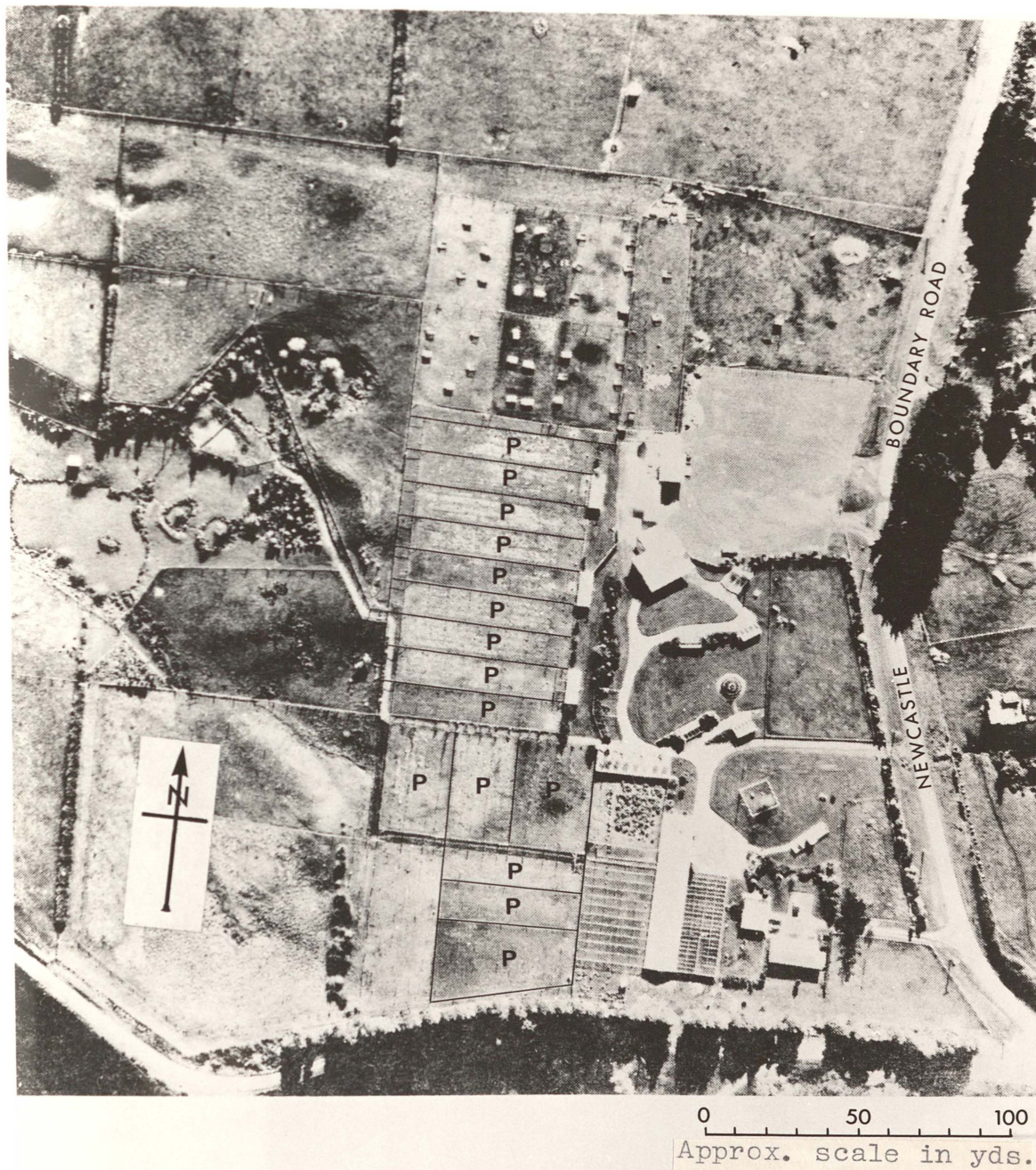


Fig.6 Aerial view of Hilldale Game Farm at Hamilton, N.Z. showing pheasant pens, (P). (Courtesy of Mr M. Powell).

terms of preventing duplication of subjects) and their position in the pen. Two birds were selected from one pen, six from another pen and four from each of the remaining eighteen pens. This selection procedure was used to prevent duplication of subjects.

DISCUSSION AND RESULTS

The hypothesis that the brightly coloured cock birds would be more likely to give the flight call than the hen birds was supported by the results of this study (see Table IV).

Table IV

Distribution of Pheasants According
to Sex and Vocalization

	Squawked or Squeaked	No Sound	Total
Males	15	25	40
Females	2	18	20
Total	17	43	60

$$\underline{\chi^2} \text{ corrected for continuity} = 3.70$$

$$\underline{df} = 1, p < .05$$

Vocal threat is important in many animals that fight with their mouths (Guthrie, 1970). Using the mouth for fighting - that is, pecking - is one of the main behaviours used to establish or reinforce relationships occurring between cock pheasants as a result of agonistic encounters. Vocalizations as part of the intimidation ritual have been well documented by Heinz & Gysel (1970). They point out that caution should be taken not to place undue emphasis and meaning on anthropomorphic call designations such as "alarm" used in the research literature.

Many good reasons for giving warning signals are given by Trivers (1971). He feels that "Warning calls are selected for because they aid the bird giving the call. It is disadvantageous for a bird to have a predator eat a nearby conspecific because the predator may then be more likely to eat him. This may happen because the predator will

- (i) be sustained by the meal,
- (ii) be more likely to form a specific search image of the prey species,
- (iii) be more likely to learn the habits of the prey species and perfect his predatory techniques on it,
- (iv) be more likely to frequent the area in which the birds live, or
- (v) be more likely to learn useful information about the area in which the birds live." (Trivers, 1971, p.44).

However, these reasons are as valid for females as well as males. In monomorphic species both sexes may or may not give "warning" calls, as both are under relatively similar selection pressures. In dimorphic species, however, one or the other partner is likely to be harder pressed by nature to survive. Such calls then may be more readily developed in the sex under the greater predation perils. In this connection it is important to remember that the categorization implied by the terms monomorphic and dimorphic represents in reality two points on a scale rather than two sections of a clear dichotomy.

It is suggested here that if the call is primarily for the bird making the call, then the effect may be even more immediate than the indirect ways suggested. Anyone who has suddenly come upon a pheasant in the bush is well aware of the success of the male flight call in producing a temporary "startle reflex" or

paralyzing reaction in the observer whilst the male flies off into cover.

This "benzai" effect (Guthrie, 1970) by the cock pheasant gives an egoistic reason for the call's existence on the first level supported on the second level by the five egoistic lines suggested by Trivers (1971) above.

The female apparently gives her flight call mainly in connection with brood care (Heinz & Gysel, 1970) and so her behaviour, if it is tied to the caring situation, may indeed be altruistic.

The offspring are likely to have a selection pressure to attend to the noises both parents make in regard to predators. A call given for self-preserving reasons by the cock bird could very well function as a warning cry for the offspring without this being its intended function. However, this does not really fit into Darlington's (1972) concept of dual determinant systems discussed in more detail in Chapter II, p. 34.

In the discussion of the relationship between other's need and altruism (p.39, point three), it was suggested that external observers may define a behaviour as altruistic when in fact the relationship is due to random or other factors rather than eliciting or evoking causes presented by the stimuli of conspecifics. However, as well as possibly distributing benefits to others, the behaviour of the donators seems in this instance to positively affect his own survival. This behaviour, therefore, should be regarded as essentially egoistic.

Accordingly, this research study re-analyses one of the warning calls (the flight call) in male pheasants and suggests that it be removed from the altruistic category. This exercise

helps to emphasize that the definition of altruism (scientific) presented in Chapter II does have the power of discrimination demanded by Grice & Strawson (1956) for philosophically sound definitions.

C H A P T E R I V

STRENGTHENING MODELS FOR THE DELINEATION AND ESTABLISHMENT OF ALTRUISM

In agreement with Cohen (1972) one could state that definitions of altruism only specify what it is. Once altruism is defined (see Chapter II), the problem to be resolved is the possibility for its establishment and maintenance. It seems plausible to consider that there may be inherited dispositions to behave in ways which, although detrimental to the survival of the individual exhibiting the behaviour, would favour the survival of other members of its species (Allee, 1966; Aronfreed, 1968). Examples of the pervasiveness and strength of inherited dispositions to behave egoistically are found in some species of the Cuculidae (cuckoos) and Icteridae (cowbirds). These species clearly do not learn parental caretaking roles from their foster parents (Hamilton and Orians, 1965). They also apparently do not imprint for mating with foster parent types (Eibl-Eibesfeldt, 1970). Altruistic behaviour is difficult to explain, as an evolutionary phenomenon, on the basis of individual selection because of the known cases of extreme altruism shown by group members - such as in the co-operative breeding found among some avian species (Brown, 1970; Skutch, 1961). Galt (1940) seemed to suggest that altruism may even precede egoism.

Allee (1966, p.914H) felt that "... the social relations of man need reinterpreting from the point of view that altruism did not arise entirely as a unique human attribute without biological antecedents". Some of the main lines of evidence cited to support this conclusion were:

1. For many species, if a population is reduced in size below a critical point, it is in danger of dying out (through, for example, the lethal effects of inbreeding).
2. Many species are able to change an unfavourable environment to such an extent that, though some may be killed, others can then survive when they could not have done so in the "uncolonized" environment.
3. Sex may be considered the original to other behaviour. Sex may have grown out of certain proto-co-operations of asexual organisms.
4. Colonial Protozoa could hardly have arisen from solitary forms unless colonies of cells that remained attached to each other had shown survival values greater than those exhibited when the cells were scattered isolates.
5. The evolution of Metazoans from Protozoa was probably based on similar relationships. Each advance in complexity of metazoan individuals came from the natural selection of an increased ability in natural co-operation on the part of the evolving stock.
6. The rate of evolution is still more rapid when a large widely distributed species has relatively small breeding colonies that are not completely isolated from one another.

Holmes (1945, p.109) felt that "Animal societies everywhere are mutual benefit associations, and the altruistic instincts

which make for social solidarity and effective co-operation would be favoured by natural selection as well as variations that aid the individual per se. Instincts leading to unselfish behaviour are just as basic, therefore, as any other manifestation of life."

The classical genetic model for natural selection does not seem sufficient to explain altruistic acts by an individual at the cost of decreasing reproductive capabilities (Dobzhansky, 1968; Haldane, 1966; Lewontin, 1970). For some, one method of resolving the dilemma caused by this model regarding the origin of social behaviour would be to abandon it (Kalmus, 1969). The dilemma is easily appreciated when considering the selection of a recessive allele (a) which causes its bearer to provide, at cost (C), benefits (B) to other members of its Mendelian population. The dominant allele (A) causes its bearer to refrain from such behaviour. (Formulae used throughout this chapter have had minor substitutions made in the interests of consistency as well as continuity in dealing with altruism.) Under random mating we would have the Hardy-Weinberg (1966) equilibrium formula zygote frequencies of:

$$\begin{array}{l} p^2 \text{ of AA} \\ 2pq \text{ of Aa} \\ q^2 \text{ of aa} \end{array}$$

After selection, these frequencies become:

$$\begin{array}{ll} p^2(1+q^2B) & \text{of AA} \\ 2pq(1+q^2B) & \text{of Aa} \\ q^2(1+q^2B)(1-C) & \text{of aa} \end{array}$$

The increase in each frequency by the factor $(1 + q^2B)$ is based on the assumption that the amount of benefit is directly proportional to the concentration of altruists (aa) in the

population. This concentration must inevitably decrease, however, because of the factor $(1-C)$ by which the homozygous recessives are reduced each generation (after Williams, 1966). The dilemma of the classical model under random mating suggests that the importance of altruism to the theory of evolution is its implication for the existence of kin selection. The change from solitary to social behaviour probably occurred in family or kin groups and originated from parental behaviour (Dobzhansky, 1968; Maynard-Smith, 1964; Wilson, 1971).

The protective impulse of the parental instinct is the only truly altruistic factor in human nature according to McDougall (1931). Consequently, an animal sacrificing its life for its offspring would clearly also be altruistic (i.e. giving benefit to others at cost to oneself). Altruistic behaviours would probably be more prevalent among animals already having an extended period of parental care-taking (e.g. social insects, birds with altricial young, and mammals). Although altruism would commonly be considered in connection with the behavioural repertoire of the organism, some consider altruism on the genetic or allelic level. They believe behaviour which takes the life of the individual but saves relatives who are more likely to possess and pass on as many, if not more, of a given allele to be in fact "genetically egoistic" (Haldane, 1966; Trivers, 1971).

In order to explain a few of the many instances of altruism observed in animal populations Trivers (1971) invoked reciprocity. Gouldner (1960) saw mutuality of gratification as a general principle without which he felt no social system, relationship or set of actions would be stable.

Reciprocal giving requires the identification and exclusion of "cheaters" if giving is to increase within a population. Trivers (1971) set up a model to show how non-random dispensation of benefit could occur. With slight modifications this model states that the net benefit accruing to a typical donor must exceed that accruing to a typical non-donor. That is,

$$(1/q^2) (\sum B_k - C_j) > (1/p^2) \sum B_m$$

where (B_k) is the benefit to the initiator of the k th beneficial act performed toward him, C_j is the cost of the j th beneficial act by the initiator, B_m is the benefit of the m th beneficial act to the non-donor, where p is the frequency in the population of non-donors and q is the frequency of donors. This type of social behaviour would not have to depend on all acts being controlled by the same allele at a given locus, as long as for each donor-allele the net average benefit to the donor exceeded the average benefit to a non-donor (i.e. B_m is kept small). Such a model helps to explain reciprocal acts exchanged between inter- as well as intra-species members. Trivers used his model for a deeper examination of the dynamics behind such social interactions as warning calls in birds, symbiotic cleaner relationships in fish, and humans saving one another from drowning. Some have felt, however, that reciprocal altruism is a contradiction in terms because the probabilities of benefits are mutual (Darlington, 1972; Krebs, 1970).

In order to differentiate between altruism and reciprocity it is suggested here that we consider the following. A carried out beneficial act (B) may be considered unity. The sum total of past interactions with the recipient is represented by (n) .

Factors which affect the recipient's carrying out towards the original donor a similar act also affect the original donor's expectation (E) of the probability of return for his efforts (B_k). As this approaches zero, so does the original behaviour resemble altruism. As the expectation of return approaches unity so does it resemble reciprocity and, finally, if it exceeds unity it may be considered egoism. Expectations may be said to exist for the initiating animal (x) in relation to each other animal in a given group. In other words, the same actions will be altruistic when directed towards animal (y), but reciprocal when directed towards (z) and egoistic when directed towards (w).

$$E_x(B_k) = \frac{\sum_{i=1}^n \left[\frac{B_{y \rightarrow x}}{B_{x \rightarrow y}} \right]_i}{n}$$

$$\begin{array}{ccc} 0 \leq E_x(B_k) \leq 1 & & 1 < E_x(B_k) \\ \text{Altruism} & \text{Reciprocity} & \text{Egoism} \end{array}$$

Examples of interrupting or interfering factors which could cause differentiation to occur in the amount of benefit given and received would be status in a dominance hierarchy, sex, age, disturbances to the group from predators, death or injury, feeding time, etc. It seems that such factors would also be rather intimately connected with the dimension of time unless we limit this concept to simultaneous behaviours, such as the social grooming observed in horses standing head-to-tail brushing flies away from each other's noses with their tails or bite-scratching at the base of each other's necks (Fraser, 1974). Reciprocal relationships would or could provide a background of antecedent conditions for the occurrence of "true altruism". However, to the extent that relationships are reciprocal, they are not altruistic.

Another method to get around the problem of establishing altruism in mendelian populations suggests that a social individual who succeeds in finding at least one social partner within a given number of trials is assigned a fitness greater than one (relative to the fitness of an asocial, taken to be fixed at one), while a social individual failing to find a partner is assigned a fitness less than one (Boorman and Levitt, 1972; Boorman, 1974). This model, however, falls into the reciprocal altruism class, and begs the initial criterion for altruism that benefit must be contributed at some cost.

What kinds of genetic relationships between the giver and the recipient should be included in order for the behaviour to be categorized under the heading altruism? A difficult word in the definition of altruism is "others". Some have felt that the term altruism is only applicable to an organism performing an act benefiting another not closely related genetically (Haldane, 1966; Trivers, 1971). Mates would probably have to be excluded along with the genetically related group as in many situations a contribution to one's species' gene pool could not be ensured without a mate. When its application is limited in this way, the clearest occurrence of altruism would probably be considered to be that shown between species. For example, people caring for injured or sick animals, dogs saving children from burning houses, conservationists trying to save a species rapidly going extinct and dolphins saving people in danger of drowning (Alpers, 1963; Hebb, 1971). Mothering the young of another species would probably also be included here (Fabricius, 1964; Lorenz, 1970; Skutch, 1961; Tinbergen, 1965).

Some restrict altruism to those "... behaviours by which some individuals benefit others of the same species without benefiting themselves" (Darlington, 1972, p.293). Following this view one might consider as most altruistic those behaviours dealing with intraspecies "others" having the greatest social and/or genetic distance from oneself and therefore the least possibility of return. Put another way, altruism might be thought to be most clearly shown when exhibited toward "hated" out-group, or "enemy", intra-species members.

The care given by parents to offspring, which is highly unlikely to be returned, is actually easily understood in that parent-altruists in each generation have benefited by care received from their parents. Darlington (1972) called this "serial altruism". The individual "sacrifices"; consequently, the species (kin group) is "rewarded". Berkowitz (1968) would probably consider "serial altruism" a type of reciprocity in which "... the individual provides rewards to another in relation to benefits he has received or anticipates, but the person to whom the rewards are given is not necessarily the same one who has benefited him in the past or who will maximise his outcomes in the future." (p.48). However, though a behaviour qualifying as "serial altruism" may be thought by some to be genetically egoistic or reciprocal, it must here be considered altruistic, unless it can be shown that the individual would be likely to benefit during the remainder of its lifetime.

The idea of serial altruism fits in with Williams' (1966) conception that altruism can occur regularly only under one of two conditions:

1. Natural selection of alternative alleles, based ultimately on the mean reproductive success of their

carriers. This will favour altruistic interactions when they involve related individuals. For example, in some avian species offspring from the first brood of the season assist in the rearing of later broods (Skutch's innubile helpers, 1961).

2. Whenever there are behavioural mechanisms under condition 1. there will inevitably be times when such aid is provided "by mistake" to unrelated individuals. (See Welch & Kilgour, 1970, on "mismoothering".)

Statistically correlated gene effects help us to understand selection for altruistic and against selfish behaviour: "...a trait which directly increases reproductive output may not survive if it is correlated with having ruthless relatives, and a trait which directly lowers reproductive output may sweep through a population if it is correlated with having helpful relatives." (Stern, 1970, p. 53).

Hamilton (1963, 1964) proposed that in order for altruistic genes to increase in a population the benefit (K) to the recipients must be greater than the inverse of the Wright coefficient of relationship (r). However, the sum of the inbreeding coefficients (Wright, 1966) for the individuals involved could probably also be used as efficiently for describing the relationship. That is, .50 for parents, offspring and siblings; .25 for grandparents, grandchildren and half-siblings; .125 for cousins and so on down to .00 for all recipients whose relationship with the altruist can be considered to be negligibly small. Hamilton's formula

$$K > 1/r$$

extended the classical genetic theory covering parental care, still having the generation as the time unit of progress. Consequently

it was reasoned that animals in some circumstances would more likely volunteer their lives, if in so doing they save at least two siblings or offspring, who are then able to reach reproductive maturity.

Support for Hamilton's formula has been found among social insects (Hamilton, 1964; Wilson, 1971) and altricial birds (Wood, 1975). Among several of the social insects (Hymenoptera) the sibling relationship of many of the members of a colony is genetically greater than the relationship to offspring. This is due to parthenogenetic reproduction whereby males are produced from unfertilized female workers or queens. They are therefore haploid and in turn contribute little genetic variance to their offspring. As the genetic variance originates mainly in the queen the coefficients of relationship among siblings descended from sexual unions is approximately .75. This would indicate, according to Hamilton's formula, that siblings would be more involved in one another's well-being than in producing offspring. However, this would have its logical lower limit, in any given colony-type species, at one reproducing "queen", otherwise extinction. The average coefficient for the entire colony would depend on the number of drones impregnating the queen. This average would be somewhere between .25 (the coefficient existing between two half-siblings) and .75 (Hamilton, 1972).

It is in such colonies that one may observe altruistic suicide. For example, a honey bee worker when defending the hive uses its barbed sting. This tends to remain embedded when the bee pulls away from its victim, causing part of the bee's viscera to be torn out and the defender herself to be fatally injured (Sakagami and Akahira, 1960).

Half-sibling coefficients of relationship (averaging about .25) would be expected in those groups of animals having either "harems" or widespread female promiscuity, as found in several mammalian orders, such as Artiodactyla (Box, 1973) and Primates (Crook, 1970). Espinas (1877) suggested a connection between harems or promiscuity and prosocial behaviour nearly a century ago. Such groups not infrequently have different roles for members based on such characteristics as sex, age, lactation, caretaking of young and strength. One class may be found to be more likely to defend others, e.g. young adult males defending young and their lactating mothers (Eibl-Eibesfeldt, 1970; Jay, 1965).

Further down the scale represented by coefficients of relationship, we come to stronger pair-bonding as in gibbons and semangs. Strong pair-bonding precludes harem building or promiscuity and consequently avoids inbreeding (Aberle et al, 1963; Kortmulder, 1968; Livingstone, 1969). Comparisons between some standard number of individuals (e.g. 30) living nearest to each other would probably show that animals living in monogamy have coefficients of relationship that are considerably smaller than those obtained from similar numbers of individuals living in polygamous and/or promiscuous societies. Depending, then, on breeding patterns and number of offspring, groups may, at least theoretically, be considered to exist on a continuum down to where genetic relationships between altruists and recipients are negligibly small.

Some modifications of Hamilton's (1963) formula are presented here to increase its accuracy and usefulness. Lewontin (1970) thought that the (K) in Hamilton's formula (above) represented a ratio. It is suggested here that this ratio is (B/C) where (B) is benefit to the recipient(s) and (C) is cost to the altruist.

Following this line, benefit (B) to the recipient(s) must be greater than the cost (C) to the altruist over the sum of the coefficients of relationship (r) existing between the altruist and the recipient(s). Hamilton's formula would lead us to conclude that altruism may occur with equal probability towards parents and grandparents as towards offspring and grandchildren. To rectify this it is suggested that a potential genetic contribution factor (G) be incorporated. Factor (G) would be obtained by dividing the potential genetic contribution of the recipient(s) by that of the altruist. Benefit is considered in relation to the proportion of total potential genetic contribution by the recipient which has been "saved". Cost is measured in the proportion of total potential genetic contribution which is lost to the altruist. The revised formula then is:

$$B > \frac{C}{\sum_{i=1}^N r_i G_i}$$

If it is assumed that an average offspring has a full complement of potential offspring, whereas an average parent has only one-half the potential, then benefit (B) of saving an offspring to reproductive maturity at cost (C) to the altruist, death (i.e. loss of the remaining potential genetic contribution), gives the formula the following value:

$$1 > \frac{.50}{.50(2)}$$

$$1 > .50$$

From the point of view of evolution a parent sacrificing itself for an offspring who is then able to reach reproductive maturity would indeed be considered sound. That is, provided

risk situations occurred randomly and in inverse proportion to the average number of litters typical for the species in question. However, it would not be practical for a mature offspring to save a parent at cost death when parents are likely to have fewer potential offspring. For example, if it takes twenty per cent of an animal's total life span to mature to a reproductive adult and the average litter is born halfway through the adult period (i.e. after sixty percent of life has passed) and while the young of that litter are maturing another twenty per cent of life passes, then only one-quarter of the total potential genetic contribution remains to be made by a parent in relation to the total possessed by its newly matured offspring. These conditions would give the formula the following value:

$$.25 \nabla \frac{1}{(.50)(.25)}$$

$$.25 \nabla 8$$

which suggests that altruism would not be "fixed" genetically in this direction at such a cost to the altruist. Social insects are an interesting exception here in that the parent "queen" lives longer to produce more offspring than do most of her progeny. However, drones are quickly dispatched when they have completed a season and their usefulness to coming generations is at an end.

This addition to Hamilton's formula helps explain the preponderance of parental care in the animal world as opposed to geriatric care. It also suggests that older parents may be more altruistically disposed toward offspring than younger parents.

Lewontin (1970) widened the applicability of Hamilton's formula. He assumed (N) individuals, with a benefit (K) conferred on the *i*th individual in a population whose relationship to the

altruist is r_i . $(^B/C)$ is here substituted for (K) . He felt that the condition for increase of the gene is

$$\text{cov} \left[(^B/C)_i r_i \right] > (1/N) - (\overline{^B/C}) \bar{r}$$

which gave the result that if the average benefit is sufficiently high, the gene may be fixed even if close relatives are favoured less than distant relatives ($\text{cov } (^B/C)_i r_i$ negative). As so little quantitative data has been collected to test sample values of this formula, it is difficult to assess where the potential genetic contribution factor should be incorporated. However, it is suggested that a modification of this nature would increase the formula's generalizability for use when more data has been collected.

Just where mates fit into this world of kin selected biological altruism is still rather unclear.

The wide diversity in terms of a definitional axiom for the word "others" is clearly disruptive for scientific communication about variables relevant to altruism. It would seem viable to choose one altruistic relationship as basic (e.g., parent-offspring) and consider other relationships in terms of degree or strength when compared back to the standard relationship. If we graphed such a situation, the x-axis could give an indication of genetic relationship between altruist and recipient(s) times the relative potential genetic contribution factor. The y-axis could then be measured in terms of injury and considered a risk scale with death as the uppermost point. The y-axis could also be measured in terms of energy expended (on a caloric scale) or given (as in the case with foodstuffs) in relation to the total amount available to the organism. Both scales (risk and caloric) would

need clear illustration of their connection whether direct or indirect, with the potential genetic contribution factor.

(See Fig. 7).

In relating Fig. 7 to Sorokin's dimensions on altruistic love discussed in Chapter II (p.30), we could consider the x-axis to be an extensity, duration or purity scale, and the y-axis an intensity scale.

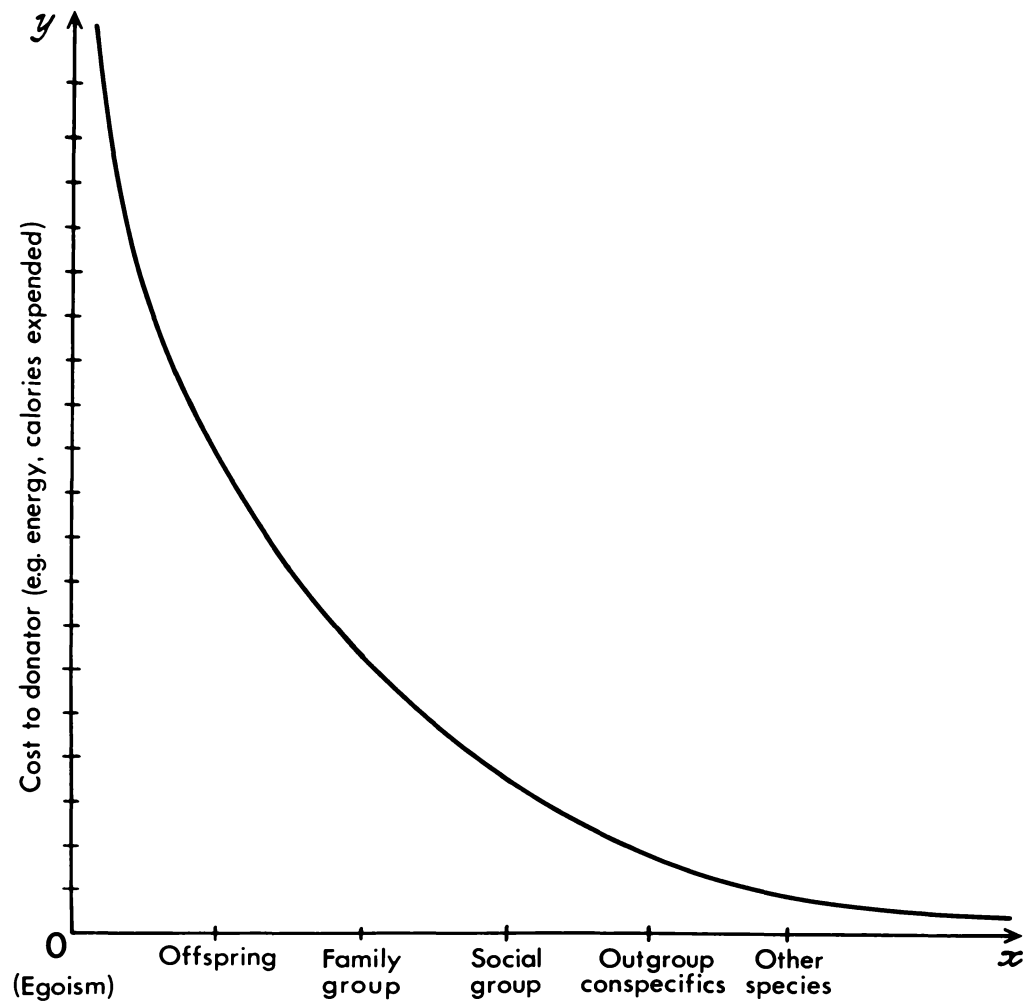


Fig. 7 The Altruism-Energy Graph hypothesizes a correlation between cost for the donator and the genetic coefficients of relationship, existing between donator and receiver. Cost to the donator could be measured directly in terms of decreases in reproductive capacity, or indirectly through energy expended, or amount (e.g. food) given in relation to the total amount available to the donator.

The y axis, instead of being measured in terms of individual cost, could represent the psychological expenditure of the total animal kingdom in these directions and may be measured by the number of species showing altruistic behaviours towards increasingly, genetically, distant classes of "others".

C H A P T E R V

AN INVESTIGATION INTO THE GENETIC ANTECEDENTS OF ALTRUISM

A natural development of the line of thought contained in Chapter IV asks: how can we test a genetic theory for altruism which to date seems to be substantiated only by data on insects in the relatively more complex world of the warm-blooded vertebrates. Birds as a class are well suited for such investigations (Brown, 1970). Most birds care for their young, which certainly takes a lot more energy, and entails a greater risk for parents than would a more self-centred line of action. Darlington (1972) has suggested that such behaviour might be termed "serial altruism".

As the number of eggs in a clutch is approximately constant for a species within a given area, and as closely related birds usually lay about the same number of eggs (Lack, 1968), the "genetic investment" of clutch size at a given point in time suggested itself as an excellent means of testing Hamilton's formula. Altricial or nidicolous birds seemed ideal subjects, particularly as most are helpless and dependent on the care shown by others. The helpless period extends from about three to five weeks, depending on the species. The aves order Passeriformes contains some 67 Families encompassing more than 5,000 species. Van Tyne and Berger (1966) considered the Families of this order close enough, morphologically and evolutionally, to state that "... if we rigidly maintained the same standards as we work through the birds of the world, setting up family groups from the ostriches and rheas down to the modern songbirds, we would probably place all passerine birds (or at least the songbirds in the suborder Passeres) in one family" (p.377).

The Passeriformes family groups vary enough in average clutch size (from one in the Menuridae to nine in the Paridae) to possibly serve as an index against which greater amounts of prosocial behaviour may be correlated. The number of family groups within the order Passeriformes also lends itself more readily to a satisfactory statistical research design than do the other avian orders.

EXPERIMENT I

Hamilton's (1963) formula (see Chapter IV) would suggest that in an avian order where the number of primary caretakers for altricial young varies, a relationship may be found between this variable and clutch size. It was hypothesized that Aves Families belonging to the order Passeriformes and having only one caretaker will have a significantly smaller average clutch size than those Families having two parental caretakers.

Method

(a) Subjects: 67 Families of the aves order Passeriformes.

(b) Procedure: Van Tyne and Berger's (1966) reference tables were used as the main source of information on parental caretaking and for statements about clutch range. Clutch averages were derived from the clutch range, according to the conventions suggested by Lack (1947, p.346). The Families were divided into two categories, female only caretaking groups, and both parents caretaking. One group of six Families had some species with female only and some with both caretaking. These Families were split into two, and the six were consequently treated as twelve discrete ethofamilies. This division of Families is analogous to Emerson's (1956) division of morphologically similar species (termed ethospecies) according to behavioural criteria.

Design and Results

The mean clutch size for the Families of the order Passeriformes was found to be 3.65 with a standard deviation of 1.39. The point biserial correlation was obtained between the number of primary caretakers and clutch size, and then converted to t (Ferguson, 1966). There were nine Families with one caretaker, having an average clutch size of 2.89, and 57 Families with two caretakers, having an average clutch size of 3.80 ($t = 1.80$, $df = 64$, $p < .025$).

Discussion

Many conditions affect clutch size (Lack, 1968; Von Haartman, 1971). When the average clutch size in a Passeriformes Family becomes greater than 2.0, it would appear that the genetic return is great enough to bring two caretakers to the scene. Of the nine Families or ethofamilies with one caretaker, six had clutch averages of two eggs or less. Of the 57 Families or ethofamilies having two caretakers, 52 had clutch averages greater than two eggs. Yapp (1970) apparently felt that a hypothesis suggesting smaller clutch sizes in species where only one sex fed the young than those in related species where both sexes fed them was not valid, because examples were known where this was not so. This hypothesis, however, does not appear to have previously been subjected to statistical analysis. Small passerine birds such as those belonging to the Families Paridae and Sittidae (encompassing circa 82 species) manage to raise on the average more than eight young per pair. This indicates that a single caretaker could, in fact, take care of a brood, of up to four young, or three considering heat loss (Von Haartman, 1971), with no help. A caretaker runs a greater risk to self, from predators, in coming to a relatively

fixed point (the nest) over an extended period of time (Skutch, 1949). Of course, one caretaker is invariable as there would be no survival in altricial birds if there were no caretakers present. However, if there is an additional caretaker, the survival chances of the clutch are certainly enhanced. A mutation on a given allele for parental care in the additional parent is more likely to be fixed in the population when there are at least two offspring, one of which, statistically speaking, will carry the helpful allele into the succeeding generation. And, if a large population of alleles at various gene loci are needed for full-blown behaviours to be established, then difficulty in maintaining such behaviours, in the gene pool, when broods are smaller than two would be apparent. Lack (1968) suggested an absence of variation in clutch size with pair-bonding. He used closely related species to test this hypothesis and found no significant correlation. A difficulty here is that evolution or devolution affecting the pair-bond relationship may not have had the required time to also effect a change in the clutch size. But, when comparing Families, which as evolutionary units are still reasonably close, variations may in fact be observed. Another difficulty was his expectancy for the clutch size of species with two parental caretakers to be double the clutch size of species with only a single caretaker. Hamilton's formula suggests rather that a critical point for an additional caretaker may in fact be the survival of at least two offspring. As clutch sizes are only an index to the number of offspring surviving to reproductive maturity, a clutch size somewhat larger than two would probably be critical for the facilitation of, in this case, male caretaking behaviour. It should be emphasized here that a correlational not a causal relationship is inferred.

The "genetic investment" of larger clutches is not considered to cause greater prosocial behaviour, but rather to provide better conditions for its appearance.

The only other avian order where the young in all the constituent Families are nidicolous and which varied in the number of primary caretakers was the Apodiformes (encompassing three Families). The Trochilidae Family (318 species) has an average clutch of less than two eggs and the young are cared for by the female alone. The Hemiprocnidae Family (three species) plus one species from the Trochilidae Family, have an average clutch of less than two eggs but the young are cared for by both parents. The Apodidae Family (76 species) has an average clutch of 3.5 eggs and the young are cared for by both parents (Van Tyne and Berger, 1966).

EXPERIMENT II

Skutch (1961) described and listed helping activities found in the ornithological literature, presenting what he considered to be a reasonable idea of the range and variety of helpfulness among birds as well as the groups and circumstances in which helpers are most likely to be found. He defined a helper as "... a bird which assists in the nesting of an individual other than its mate, or feeds or otherwise attends a bird of whatever age which is neither its mate nor its dependent offspring." (Skutch, 1961, p.198). The only member of the order Apodiformes to appear on Skutch's list of helpers was *Chaetura pelagica* with a clutch average of 4.5 from the Apodidae Family.

It was hypothesized that the species of altruistic birds, from the order Passeriformes, mentioned on Skutch's list plus

those ten found in the course of research for these studies, would be found to have come from Families having greater clutch sizes than those Families in which no altruism had been recorded. This hypothesis was tested for both intraspecies altruists (A) and interspecies altruists (B).

Method

(a) Subjects: Out of Skutch's list of more than 130 helping species, nearly a hundred were Passeriformes and therefore suitable for this study. Information on the clutch size of the Vangidae was added according to Thomson (1964). Those eight Families whose clutch size and/or parental care was not described were placed in a neutral category. The Family Dulidae, not used in Experiment I, was added as it appeared on Skutch's list. The additional information which added ten species also added three more Families to the altruistic Families. The Acanthisittidae (New Zealand Wrens) have as a Family group, according to Van Tyne and Berger (1966, p.498), 2 to 5 eggs per clutch or an average of 3.5 for the four species. However, according to Falla, Sibson and Turbott (1966), one species (*Xenicus Lyalli*) has been extinct since 1894 (no clutch size recorded), one species (*Acanthisitta chloris*) showed helping behaviour and had a clutch range of (4-5), and two species (*Xenicus longpipes* and *Xenicus gilviventris*) do not seem to have been observed helping others. Their range was (2-3). One Australian species (*Pteropodocys maxima*) of the Campephagidae, according to Hindwood (1966), is known to show helping behaviours. However, he considered it to be an aberrant member of its Family in this respect? Its clutch range seems to be (2-3), with 3 being usual, according to Gould and Rutgers (1967). The Neosittidae were included with the altruists according to the information in

Van Tyne and Berger (1966). (See Table V and Appendix C).

Design and Results

The Families were divided according to whether or not they had been known to show altruistic behaviour. The data took the form of a table comprised of R rows and two columns. The point biserial correlation was obtained, then converted to t (Ferguson, 1966). There were 34 non-intraspecies (A) altruistic Families having an average clutch size of 3.09, and 27 Families containing intraspecies (A) altruists and having an average clutch size of 4.46 ($t = 4.32$, $df = 59$, $p < .0005$). There were 47 non-inter-species (B) altruistic Families having an average clutch size of 3.32, and 14 Families containing interspecies (B) altruists and having an average clutch size of 5.00 ($t = 4.51$, $df = 59$, $p < .0005$).

EXPERIMENT III

It was hypothesized that the Families of Passeriformes (both intra and interspecies altruists) used in Experiment II and recorded as having more than one species showing helping behaviours would have clutch sizes greater than those Families having only one species mentioned.

Design and Results

The data took the form of a table comprised of R rows and two columns. The point biserial correlation was obtained, then converted to t (Ferguson, 1966). There were 12 Families with one altruistic species having an average clutch size of 3.83, and 18 Families with two or more altruistic species having an average clutch size of 4.81 ($t = 1.84$, $df = 28$, $p < .05$).

Table V The Ten Passeriformes Species which
were Added to Skutch's List of Helpers

Family	Genus Species	Clutch Average	Range	Reference
1. Icteridae	Euphagus cyanocephalus	5	U.S.A.	Bent, 1948
2. Acanthisittidae	Acanthisitta chloris	4.5	N.Z.	Falla et al, 1966
3. Sylviidae	Mohoua albicilla	3	N.Z.	Falla et al, 1966
4. Sylviidae	Mohoua ochrocephala	3.5	N.Z.	Falla et al, 1966
5. Neosittidae	Neositta pileata	3	Aust.	Hindwood, 1966
6. Neosittidae	Neositta chrysoptera	3	Aust.	Firth, 1969
7. Campephagidae	Pteropodocys maxima	2.75	Aust.	Hindwood, 1966
8. Malurinae	Malurus melanotis	3.5	Aust.	Hindwood, 1966
9. Grallinidae	Struthidae cinerea	6.5	Aust.	Chisholm, 1958; Gould and Rutgers, 1967
10. Artamidae	Artamus insignis	3*	New Ireland	Gould and Rutgers, 1967

* As the information on species' clutch size could not
be found the average for the Family was substituted

EXPERIMENT IV

It was hypothesized that the Passeriformes species listed by Skutch (1961), plus the ten additional altruistic species mentioned in Experiment II, would not have clutch sizes different from the Families from which they were drawn. The clutch sizes for two species from the Family Corvidae could not be found and as seven species were already included from this Family, these two were deleted. Also deleted were one polioptilinae, one artamidae and one furnariidae, which was considered unfortunate as there were no other members from their Families in the sample. It is not felt that this significantly affected the acceptance or rejection of the hypothesis.

Design and Results

The data from the altruistic species were paired with data from their Families. The combined data took the form of a table comprised of R rows and two columns. The point biserial correlation was obtained, then converted to t (Ferguson, 1966). This procedure yielded a t value of .56 ($df = 206$) which was non-significant and the retention of the null hypothesis was supported.

EXPERIMENT V

It was hypothesized that the altruistic species used in Experiment IV which were interspecific helpers would have greater clutch sizes than intraspecific helpers.

Design and Results

The data took the form of a table comprised of R rows and two columns (inter vs intra). The point biserial correlation relationship was obtained, then converted to t (Ferguson, 1966). If species would normally have appeared in both groups, they

were placed only among the interspecific helpers. There were 73 intraspecific helping species having an average clutch size of 4.33, and 34 interspecific helping species having an average clutch size of 5.05 ($\underline{t} = 2.18$, $\underline{df} = 105$, $\underline{p} < .025$).

EXPERIMENT VI

It was hypothesized that the helpers used in Experiment V and having more than one recorded instance of helping, would have a greater clutch size than those with only one recorded instance. Instances of helping were counted by considering the individual helping as 1, regardless of the number of recipients (2 helpers were counted as two instances, etc.).

The data took the form of a table comprised of R rows and two columns (one vs more instances). The point biserial correlation was obtained, then converted to t (Ferguson, 1966). There were 18 intraspecific (A) helping species with one instance of helping observed and having an average clutch size of 3.65, and 55 intraspecific (A) helping species with more than one instance of helping observed and having an average clutch size of 4.56 ($\underline{t} = 2.20$, $\underline{df} = 71$, $\underline{p} < .025$). There were 18 interspecific (B) helping species with one instance of helping observed and having an average clutch size of 4.60, and 16 interspecific (B) helping species with more than one instance of helping observed and having an average clutch size of 5.56 ($\underline{t} = 1.73$, $\underline{df} = 32$, $\underline{p} < .05$).

EXPERIMENT VII

It was hypothesized that the data from Experiments I and II (A) would evince a trend towards increasing clutch sizes with increasing degrees of prosocial behaviour.

Procedure

61 Families plus the six ethofamilies were used only once to form discrete groups. If Families would normally have appeared in more than one group they were placed in the group having the most prosocial behaviour - that is, intraspecific cells followed by male and female, etc. Table VI shows the data used for the chi square test applied to this 2 x 3 contingency table ($\chi^2 = 8.5688$, $df = 2$, $p < .01$).

Due to the fact that a division within the intraspecies altruists between Families where only one altruistic species had been observed and Families where more than one altruistic species had been observed created cell frequencies which were below those required, for chi square a separate analysis was run using the point biserial correlation. The data took the form of a table comprising R rows and two columns (one instance vs more instances). The correlations obtained were then converted to t (Ferguson, 1966). The Dulidae Family was excluded from these calculations as there is only one species in this Family. There were nine Families with one altruistic species having an average clutch size of 3.67, and 17 Families with more than one altruistic species having an average clutch size of 4.91 ($t = 2.04$, $df = 24$, $p < .05$).

EXPERIMENT VIII

It was hypothesized that the data from Experiments I and II(A) and II(B) would evince a trend towards increasing clutch sizes with increasing degrees of prosocial behaviour.

Procedure

The 61 Families (plus six ethofamilies) were used only once to form discrete groups. If Families would normally have appeared

Table VI Data Used for Chi Square Analysis in Experiment VII

Caretaker	Families Classified By Clutch Size			Average Clutch Size
	0-3.0	3.1-9.0	Total	
Female	6	3	9	2.89
Male and female	17	14	31	3.23
Intraspecies altruists	6	21	27	4.48
Total	29	38	67	

$$\chi^2 = 8.5688, \text{ df} = 2, p < .01$$

in more than one group, they were placed in the group having the most prosocial behaviour. That is, the interspecific cells were filled first followed by the intraspecific, etc. The procedure resulted in a clutch average drop from 3.80 for the two caretaker group (Experiment I) and from 4.46 for the intra-species altruist group (Experiment II). Table VII shows the data used for the chi square test applied to this 2 x 4 contingency table ($\chi^2 = 13.8623$, $df = 3$, $p < .01$).

EXPERIMENT IX

It was hypothesized that the data from Experiments V, and VI(A) and VI(B) would evince a trend towards increasing clutch sizes with increasing degrees of prosocial behaviour. Table VIII shows the data used for the chi square test applied to this contingency table ($\chi^2 = 7.6459$, $df = 3$, $p < .05$).

DISCUSSION EXPERIMENTS II - IX

In various Families of Passeriformes, the average clutch size of related species is about twice as large in mid-Europe as in equatorial Africa (Lack, 1968). Within a species the average difference in clutch size for the passerines found in both England and southern Spain is about .40 of an egg. Clutch sizes tend to be larger at greater latitudes as well as at higher altitudes. This is all more or less according to Hesse's Rule that "Birds which live in the cooler parts of the range of the species lay more eggs per clutch than the races in the warmer parts of the range" (Hesse, 1922, quoted by Von Haartman, 1971). These findings are, however, contested by those of Hussell (1972) in his study of Arctic passerines.

Table VII Data Used for Chi Square Analysis in Experiment VIII

Caretaker	Families Classified By Clutch Size			Average Clutch Size
	0-3.0	3.1-9.0	Total	
Female	6	3	9	2.89
Male and female	17	11	28	3.14
Intraspecies altruists	5	11	16	3.90
Interspecies altruists	1	13	14	5.00
Total	29	38	67	

$$\chi^2 = 13.8623, \text{ df} = 3, p < .01$$

Table VIII Data Used for Chi Square Analysis in Experiment IX

Caretaker	Species Classified By Clutch Size			Average Clutch Size
	0-4.0	4.1-11.0	Total	
Intraspecific altruists observed once	13	5	18	3.65
Intraspecific altruists observed more than once	24	31	55	4.56
Interspecific altruists observed once	6	12	18	4.60
Interspecific altruists observed more than once	5	11	16	5.56
Total	48	59	107	

$$\chi^2 = 7.6459, \text{ df} = 3, p < .05$$

If Lack's findings and Hesse's Rule hold, we would expect to find most of the observations on altruistic species further from the equator or in mountain tracts. This does indeed seem to be the case. The significant results of Experiments I to IX may be confounded by the fact that the main body of recording ornithologists also live in at least northern latitudes (i.e. North America and Europe) if not in mountainous tracts, and it is probable that a greater number of trained observers would be more likely to discover and record "unusual" altruistic behaviours than would the fewer observers in the rest of the world. However, due to the rather large proportion of Australian, African, Central and South American species in the sample, it may not turn out to be the important factor it first appears to be. None of the eight Families having a clutch average of two or less (encompassing 504 species in Experiment II) was recorded as exhibiting altruistic behaviours, whereas all of the six Families having a clutch average of five and a half or greater (encompassing 266 species) were recorded as having altruists among them.

That observations have occurred more than once (Experiment VI) or in more species than one (Experiment III) within a given Family suggests that such behaviours may be more soundly established elements in their repertoire.

Experiment IV checks the Family clutch data in Van Tyne and Berger (1966) against the clutch averages found for the various species on Skutch's list as well as the additional ten listed in Experiment V. No significant differences were detected.

Outspecies altruism (Experiments V and VIII) is most interesting in this context, as obviously little if any genetic "feedback" can occur, unless the species in question has a tendency

towards mutual helping. Only three of the 34 species showing inter-species altruism came from Families where no species were also listed for intraspecific helping activities, and two of these three had only one instance of helping recorded

During 30 years of scientific bird watching in Central America, Skutch (1961) only observed two (!) instances of inter-species helping as opposed to no less than 55 instances of intraspecific helping involving 18 species. As Skutch (1961) points out, the large percentage of interspecies contra intraspecies altruism that gets recorded is probably due to the fact that it normally demands sustained and careful observation to identify the number of individual caretakers of the same species that are attending a nest, whereas interspecific helpers are more likely to be noticed and reported by the casual bird watcher.

Large clutches demand more caretaking and it was assumed that birds most prone to caregiving would also most easily be "triggered" by various similar stimuli in the environment. In some situations the young of other species may prove to be super-optimal stimulators eliciting "mismoothering" (Fabricius, 1964; Lorenz, 1971; Tinbergen, 1966). However, a precondition for a behaviour to "mis-fire" is of course that it exists in the first place. It will probably be found that nest parasites such as the Cuckoo and the Cowbird pick for their hosts just such "altruists"; that is, birds with higher clutch averages (e.g. the Sylviidae and Motacillidae) (Hamilton and Orians, 1965).

Campbell (1972) felt that as opposed to the genetically determined behavioural dispositions of the social insects, in man "The behavioural dispositions which produce complex social interdependence and self-sacrificial altruism must instead be products of culturally evolved indoctrination, which has had to

counter self-serving genetic tendencies" (p.21). However, we seem to have around us a considerable array of prosocial behaviours among warm-blooded vertebrates. It would be logical to imagine that if we can explain the occurrences of prosocial behaviour among the social insects on the basis of evolution, then a similar genetic argument may clarify our understanding of prosociality in more complex life forms.

The coefficient of relationship is possibly more easily recognised (by population geneticists) as the sum of the inbreeding coefficients for the two individuals involved. Interestingly enough, inbreeding, although vital for the establishment of altruism, could lead to a loss in genetic potentialities for the adjustments demanded by a changing external environment. We might see this as an exchanging of genetic adaptiveness for a genetically "fixed" social adaptiveness.

Research into mammalian societies may possibly uncover similar relationships. For example, these may be investigated by comparing the frequency of caring behaviours (e.g., social grooming) occurring within age classifications with that occurring between different age groups. Assuming that in a given mammalian society all the offspring of any one season have the same sire, the greater the difference in age between group members, the more likely it is that a given alpha male has been supplanted and the group members concerned have had different sires. It follows that, for the group as a whole, the coefficient of relationship between members will be inversely related to their difference in age. This reduction in the coefficient of relationship is augmented by the fact that the coefficients of relationship of successive alpha

males will also be negatively related to their age differences. It is expected that as age difference increases and the genetic relationship correspondingly decreases, the amount of caring behaviour exhibited will also be less.

C H A P T E R V I

AN INVESTIGATION INTO ALTRUISTIC BONDING

We have specified what altruism is (Chapter II) and looked at models for establishing it in genetic populations (Chapter IV) and then examined aspects of it in the warm-blooded avian social world (Chapter V). The next step is to look for a behaviour in mammalian social groups which may also be either subsumed under the title altruism or which may provide antecedent conditions for its appearance at a later stage.

An aspect growing out of Chapter II which seemed to merit further investigation concerned the possibility of a critical period for maternal bonding to lambs. A critical period as a basis for altruism would, of course, limit the concept in two dimensions. If such a period existed it would be classified as a "normal" (see p. 53) behaviour. Also, clear eliciting or antecedent conditions would keep the behaviour out of the altruism (philosophical) category, although it could still be safely subsumed under the altruism (scientific) category (see p. 55).

Critical periods like imprinting generally take place only during a specific sensitive time in the development of the organism (Eibl-Eibesfeldt, 1970), possibly due to conflicting drives states maturing at different but close periods in time. (Hess, 1962). In Romney sheep the "... ewe, 3 to 4 hours before birth is primed physiologically and ready to lick up and become attached to her lamb which is soon to be born." (Kilgour, 1971, p.202). (See also Chapter II, p.40). Partially due to this time lag, it is estimated that approximately ten per cent of lambs could be paired with incorrect mothers under high density

lowland lambing practices on New Zealand farms.

Hight & Jury (1970) found that of 7727 lambs born during the period of their study, 17.8 per cent died between birth and weaning. In single-born lambs, only 15.1 per cent of deaths were attributed to starvation whereas 41.7 per cent of the multiple-born lambs were thus classified. The six causes of lamb mortality listed were dystokia (32.3 per cent), starvation (26.5 per cent), infections (11.6 per cent), uterine deaths (10.3 per cent), abnormalities (1.4 per cent) and misadventure (3.7 per cent). Important non-infectious causes of lamb mortality included physiological starvation due to poor mothering and lack of milk (Alexander & Peterson, 1961).

Poor mothering it was thought may be connected to variables surrounding the critical period. The importance of the first few hours after birth for the establishment and strengthening of epimeletic bonds from the ewe to the lamb emphasised by Kilgour (1970, 1971) suggested that a mothering factor in primiparous ewes might exist which could affect subsequent success, as measured by reduced lamb mortality, of these ewes in raising their twins. If so, possibly some ewes could from their first season have extra lambs fostered on to them during the critical period. These super-mothers could be used each season to take up the "orphaned" lambs with a resultant economic benefit to agriculture.

Therefore, the hypothesis postulated in this experiment was that primiparous ewes having twins would have a lower lamb mortality record for twins born during the second lambing season than ewes having only single lambs on their first lambing.

SUBJECTS AND OBSERVATIONAL FIELD

The data presented are derived from the lambing records of 5077 ewes grazed at the 2000 acre Whatawhata Hill Country Research Station over the period 1954 - 1967, where first cross (F_1), second-cross (F_2), and third-cross (F_3) Border Leicester x Romney ewes were mated to first-cross Border Leicester x Romney rams.

PROCEDURE

The relevant data from Hight & Jury's (1969) study regarding the procedure for the initial data collection stated that:

"All sheep were grazed together from birth, except when they were rotationally grazed over the mating period. The mature ewe flock was used, as in most commercial enterprises, to assist with land development. Ewes were first mated to lamb at 2 years of age ... Lambing usually commenced in the third week of August, ... Early lambing ewes were preferentially fed together on pasture for a short period before lambing commenced ... Multiple-born lambs were grazed with those born or reared as singles from birth... No culling on reproductive performance was practised. All rams were mass mated, and therefore full pedigrees are not available.

Lambs, whether dead or alive, were weighed and identified with numbered brass ear tags within 24 hr of birth, and their sex, birth rank, dam number, and birth date recorded. In later years numbered neck tags were attached to all ewes before lambing to facilitate the recording of lambing data. Weaning was in late November or early December, the average age at weaning varying from 80 - 85 days over the 9 years of the trial. Only those lambs present at weaning or lamb shearing in December were recorded as "weaned" and included in calculations of lambs weaned per ewe present at lambing or lamb survival rates."

(Hight & Jury, 1969, p. 643)

In the procedure for testing the present hypothesis all ewes whose primiparous experience was a single offspring and which in the following lambing season came down with twins were extracted to form one experimental group. The data on twin lambs were used to put them into one of two groups:

1. Died prior to weaning, and
2. Survival to weaning. (See tables IX and X).

All ewes whose primiparous experience was twins and which in the following lambing season came down with twins, were extracted to form the second experimental group. The twin data of this group was split along the same criteria as the first experimental group. The results were then tested with a chi square for significance using the correction for continuity (Siegel, 1956, p.110).

Where there were triplets one of the three in six out of the seven cases died before weaning which could tend to support the original hypothesis. However, triplet data was removed due to its paucity in the research records, and the remaining twins were treated as if they did not have a further sibling.

One of the questions which Tinbergen (1968) suggests as distinguishing the ethological view of behaviour asks "In what ways does this phenomenon (behaviour) influence the survival, the success of the animal?" (p.2). The non-significant results above (see Table X) suggest that, contrary to the initial thinking, it may in fact be maladaptive from the ethological viewpoint for parents to bond or establish expectancies for a given number of offspring, especially when that number is dependent upon the apparently low frequency occurrence of multiple births during the primiparous experience.

Although the results of this study did not support the original hypothesis and give further insights into altruism they did have a particular value in the stimulation they provided to look for differences in sex ratios for the various generations of crosses between breeds of sheep. (See Appendix D).

Table IX Mortality Table for Lambs of
Twins-Twins and Single-Twins
Ewes

Cause of Death	Lambs from Twins-Twins Ewes	Lambs from Single-Twins Ewes
Exposure	1	1
Starvation	5	12
Misadventure	0	4
Undiagnosed	3	25
No post mortem	3	11
Infection	2	2
Total	14	55

Table X Proportions of Deaths to Survivals
for Lambs of Twins-Twins and
Single-Twins Ewes

	Lambs Survived to Weaning	Lambs Died	Total
Single-twins ewes (178)	301	55	356
Twins-twins ewes (53)	92	14	106
Total	393	69	462

χ^2 corrected for continuity = .0142 n.s.

C H A P T E R V I I

INVESTIGATIONS CONCERNING SOCIAL GROOMING AS AN ANTECEDENT BEHAVIOUR OF ALTRUISM

INTRODUCTION

The desire to use the formula developed in Chapter IV (p.71) to delineate a subset of altruists from egoists led to the investigation of social grooming as an antecedent behaviour of altruism. Social grooming apparently occurs in most of the mammalian and avian species so far investigated by zoologists. Indeed, amongst mammals the commonest form of friendly behaviour is social grooming (Ewer, 1968). It is also known to occur among the social insects. For example, when a bee desires to be cleaned by worker bees she performs a grooming dance, during which she shakes her body and stamps her legs (Dimond, 1970). Grooming is one of the keys to a rather interesting symbiotic relationship occurring between the giant cowbird (*Scaphidura orizivora*) and various avian species belonging to the icterid family in Panama. The nestlings of the icterids suffer heavy mortality from botflies (*Philornis*), but they are protected from these when a giant cowbird also lays an egg in the nest. The young cowbird preens its host's nestlings (which it does not eject, as the cuckoo does) and removes the flies (Smith, 1968).

Laboratory mice can only remove the ectoparasitic mite (*Myobia musculi*) by oral grooming which means that an individually housed mouse cannot control serious mite infestation on its own head and shoulders, (Fraser & Waddell, 1974). Grooming is also apparently a quite important social behaviour for laboratory rats, for it occurs rather early in the ontogeny of their repertoire, i.e. at or about the thirteenth day (Dimond, 1970).

Quantitative data on social grooming is rarely recorded but where it does get recorded it appears to be a relatively low-incident behaviour when compared with the time spent eating or resting. For example, social grooming actions have a frequency in patas of roughly one per hour according to Chance & Jolly (1970). And Poirier's (1970) study on langurs found that mutual grooming bouts ranged from under one minute to 23 minutes in length, with approximately 50 per cent of these lasting one minute. Only 134 bouts of social grooming were recorded and these occurred at the rate of one grooming interaction per 9.3 hours of observation for the eight monkeys being studied. The determining factors of social grooming among rhesus macaques, patas and other sub-human primates were considered to be age and dominance-status (Chance & Jolly, 1970). The same determining factors were found for social grooming in baboons (Carthy, 1965) and langurs (Poirier, 1970).

The Waikato dairy region has the highest density of dairy cows in New Zealand (Hancock, 1954). In fact, "Within a radius of 50 miles, the densest animal population on pasture on the face of the earth" (City of Hamilton, 1974, p.27). As very little is known about cow social grooming, investigations into this behaviour appeared to provide an ideal opportunity for combining a theoretical search for a hypothetical construct with an exploration of possible practical importance in the dairy world. Also, the foremost institution for scientific studies on farm animals in New Zealand, the Ruakura Agricultural Research Centre, made available a substantial population of research subjects. It was located just across the street from the University of Waikato (see Fig. 11). This institution also has a continuing programme in the study of farm animal behaviour.

According to Fraser (1974), mutual grooming is one of the two most common simple reflexes seen in healthy cattle. In spite of

the fact that cows (*Bos taurus*) have been domesticated some 5000 years (Price & Nevens, 1966) very little is known of the variables affecting or correlated with their social grooming. In a summary of the knowledge to date, Hafez (1969) devotes a total of six sentences to social grooming out of more than sixty pages covering other aspects of cattle behaviour. This summary suggests:

1. That in 95 per cent of the cases only the head, neck and shoulders of the herd mate were licked (Brownlee, 1950).
2. That licking interactions have been found to involve animals less than three rank positions apart on the social scale; most commonly, a subordinate animal would lick its immediate superior (Schloeth, 1962).

Findings from more recent sources suggest:

3. That cows high on the rank order received more grooming (Samraus, 1969).
4. That daily social rhythms in cattle are determined by feeding periods (Samraus, 1969).
5. That calves indulge in self-grooming for up to 52 minutes per day and adult cattle lick themselves on as many as 152 occasions per day (Roy, Shillam and Palmer, 1955). Unfortunately no similar estimations were forthcoming about social grooming.

The main value of social grooming for the recipient is seen in that it helps cleanse the hair of mud, faeces, urine and ectoparasites, consequently reducing the risk of disease (Fraser, 1974). Hafez (1962) speculates that the licking of salt or some other desirable chemical compound from the neighbouring animal induces social grooming in the groomer. Such speculations as these are based on what may be termed the "nutritional hypothesis".

Samraus (1969, p.810), however, felt that "... whereas the motives of the passive licking partner appear to be clear-cut (e.g. irritating stimuli), no sufficient explanation could be found for the motivation of the active partner."

Three distinct stages were involved in distilling altruism from social grooming. The first stage was designed to give better descriptive information of herd parameters with relation to social grooming. The second stage examined the correlations between individual characteristics and the giving and/or receiving of social grooming. The third stage used the formula developed in Chapter V to delineate from the group of social groomers two subsets, the altruistic and the egoistic. These were then checked to find factors which might predispose an individual towards altruism by looking at the same characteristics as those used to gain insight into social grooming in the second stage. A second part of this third stage looked into the term "others" and the tendency of identical twins to behave similarly. The efficacy of the "nutritional hypothesis" as a reason for social grooming was discussed in the light of the findings from both the second and third stages.

PILOT STUDY

A pilot study was run on two different days with two different herds early in 1973. The first observation was carried out on 8 March 1973 between 0900 and 1200 hours and, after a break for lunch, continuing from 1330 to 1530 hours at which time milking occurred. The weather was warm and the day generally overcast (20.2°C , light moderate winds). The herd consisted of 179 cows comprising Ayrshires, Friesians, Jerseys, Jersey x

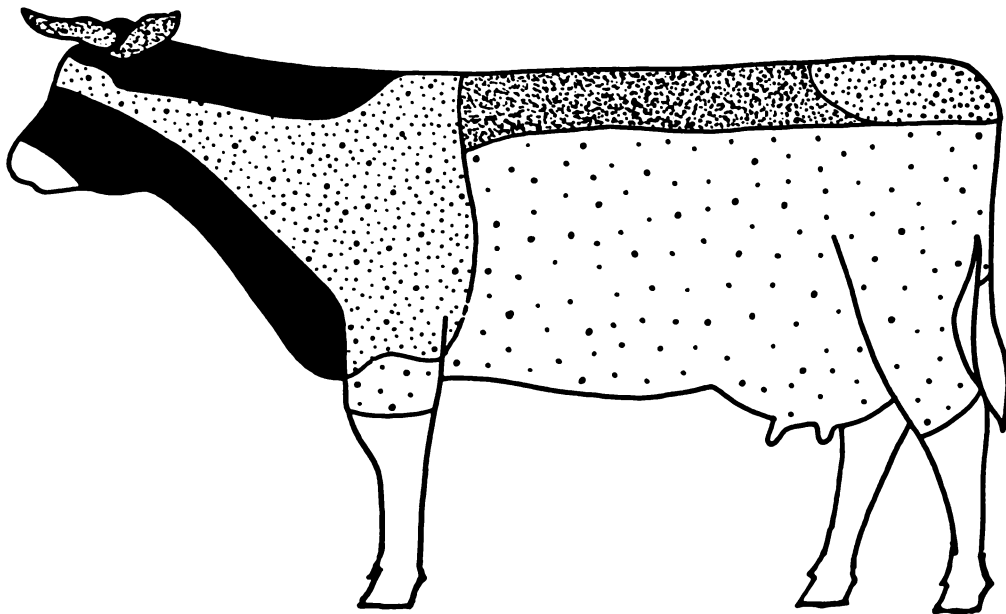
Friesians, as well as Jersey x Ayrshires. Human observers were able to walk relatively freely among the dairy cows without unduly stressing them, as evidenced by the fact that many cows lay resting and ruminating. A turn of the head was about as much notice from the cows as one lone observer rated. Therefore, blinds were not considered necessary and social grooming could be recorded satisfactorily. Lying down was taken to be an index of lack of stress in the herd generally. Milking time thoroughly disrupted the patterns of social behaviour and ended the observational period. This could also have been due to the use of dogs to herd the cows into the milking sheds.

In order for licking to be considered grooming, it was necessary for it to begin around the head and forequarters. It could then proceed to the anal region but it was not considered grooming if licking was confined to the anal region. This decision seems to be in agreement with Sambraus' (1969) observations (see Fig. 8).

Social grooming may be a behaviour of very low incidence (when related to the observation time necessary to get a sufficient behavioural sample) as only 15 minutes of the observed behaviour in this initial pilot study could be so described. Herd details made available by Young (1973) helped particularly in identifying individual cows. However, the paddock size was too large (four acres) and there were too many cows (179) to be able to observe them adequately.

Some cows had nose rings with spikes on them to keep them from suckling others. Such rings, it was thought, might affect social grooming.

On 10 March 1973, another warm overcast day (23.9°C, fine), an observational period was held between 1030 and 1145 hours on a



GROOMING FREQUENCY

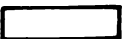
	High
	Frequent
	Average
	Seldom
	Never

Fig. 8 *Mutual Grooming: Patterns in dairy cows.*
(after Sambraus 1969).

Ruakura herd comprising 20 cows. No social grooming was recorded but peak social grooming times for this herd were considered by Ruakura observers to be roughly 1000 to 1130 hours and 1600 to 1830 hours.

RESEARCH QUESTIONS AND HYPOTHESES

First Stage - Herd 1 and Herd 2

The general paucity of descriptive information on social grooming in dairy cows in the scientific literature suggested the need for research into several areas concerning general herd parameters:

1. How much of a cow day is spent grooming
 - (a) Twin?
 - (b) Non-twins?
2. What per cent of total grooming time is exchanged within twin pairs?
3. How long is the average interaction with
 - (a) Twin?
 - (b) Non-twins?
4. What is the average number of inter actions a day per cow with
 - (a) Twin?
 - (b) Non-twins?
5. What is the daylight or diurnal herd social grooming cycle?

Second Stage - Herd 1 Hypotheses

1. That groomer's age, body weight, milk weight and milking order would correlate positively with the number of non-twins groomed and the time spent grooming non-twins.
2. That a cow's age, body weight, milk weight and milking order would correlate positively with the number of non-twins it received grooming from and the amount of time

that cow received grooming from non-twins.

3. That age, body weight, milk weight and milking order would correlate positively with the amount of time twins spent grooming or being groomed by each other.
4. That breed would be correlated with the dependent variables given in Hypotheses 1, 2 and 3 above.
5. That the experiment on reinforcement schedules in progress at the same time would be correlated with the number of other non-twin cows grooming was given to or received from.
6. That the experiment on reinforcement schedules in progress at the same time would be correlated with the amount of time grooming was given to or received from other non-twin cows.
7. That the experiment on reinforcement schedules in progress at the same time would be correlated with the amount of time a cow gave or received grooming from its twin.
8. That spiked nose rings affect social grooming rank.

Second Stage - Herd 2 Hypotheses

9. That groomer's body weight would correlate positively with the number of heifers groomed and with the time spent grooming non-twins by a given heifer.
10. That a heifer's body weight would correlate positively with the number of heifers that groomed it and the amount of time that heifer was groomed by non-twins.
11. That body weight would correlate positively with the amount of time twins spent grooming or being groomed by each other.

12. That breed would be correlated with the dependent variables given in Hypotheses 9, 10 and 11.

Second Stage - Herd 1 and 2 Hypotheses

13. That the amount of grooming given by one member of a twin pair is correlated positively with the amount given by the other member of the pair.
14. That the amount of grooming received by one member of a twin pair is correlated positively with the amount received by the other member of the pair.

SUBJECTS

Two herds of identical twin cows from Dairy I at the Ruakura Animal Research Centre in New Zealand were used in this study. These twin subjects were generally obtained as calves by advertisement throughout New Zealand and came to Ruakura at four to seven days of age. Herd 1 contained 104 cows. 100 of these formed twin pairs where both twins were present in the herd. The twins of the remaining four cows had been removed from the herd because they were dry that season. Herd 2 contained 40 twin yearling heifers.

All cows had previously been ear-marked and branded with a three or four digit number which identified the individual and simultaneously indicated the year of birth. The numbers of identical twins followed one another; for example, 319 and 320 would be a pair of twins (see Fig. 13a). The initial 3.. is the code number indicating cows two years old during 1973. Seventeen cows in Herd 1 had nose rings, some of which had also been embellished with spikes to prevent suckling. Generally, if one twin required a nose ring the other was also so supplied. Tails

of all subjects were docked (see Fig. 9) which is the current practice in New Zealand. Rich pasturage gives a rich loose manure which if the tail is not docked may be spattered by the tail on farmers during milking. The treatments and marking mentioned above were all carried out according to the standard practice at Ruakura for dairy stock research subjects.

An experiment on variable schedules of reinforcement in the milking shed was also in progress using the same subjects. Different coloured collars were used to designate treatment groups. These collars also aided in the identification of subjects across an open paddock (see Figs. 9, 13a and 13b). Subjects in Herd 1 were milked twice a day, once at 0500 - 0630 hours and again at 1500 - 1630 hours. No dogs were used. The gates were opened and the cows generally walked themselves to the milking yards. They were sprinkle-washed during their wait in the yard just before milking. Food for both herds consisted of maize, silage, grass and meal concentrate consisting of one-third barley, one-third maize and one-third linseed. Anti-bloat substances were added to the drinking water. Care and culling by the Dairy I staff was not considered at the outset of this study to be systematically related to social grooming as displayed by the individual cows within the herd. The reason for this is that the staff had little information on the herd parameters with regard to social grooming which could bias their behaviour towards these cows.

OBSERVATIONAL FIELD

The main paddocks used by the Dairy I staff for the cows during the observational period were 7, 8C, 10, 10A, 10B, 10D, 25, 25A and 25B (see Fig. 10). This was all according to the standard farming routine including paddock rotation used at



Fig.9 *Typical mid-morning period, some cows lying down chewing their cud, some grazing, and some involved in social grooming. (Courtesy Macqueen Ruakura A.R.C.)*

Dairy I. Paddocks were generally flat with few if any trees and stock could generally be viewed at all times. However, cows could get behind one another and this may have meant that a few instances of social grooming went unseen. Each paddock was supplied with a circular cement water trough. Barbed wire fencing separated the paddocks, interspersed with electrified lines.

EQUIPMENT

Observers wore broad-brimmed hats and long-sleeved shirts for sun protection, and each observer or observer pair carried:

Two pens, two stopwatches, and one wristwatch

A clip board equipped with rubber bands (to prevent the paper from flapping as this was found to disturb the cows)

Identification pages which listed cow number, collar colour, breed and, for some, coat colour and/or distinguishing markings

Observation sheets used to record data.

Initially, a pair of 8 x 40 binoculars were used, but after two days of observations a 3 x wide angle monocular was substituted as this was handier to use and more suitable for the distances.

Information recorded in the observational periods was entered into summary or collation notebooks which kept a record for each cow in the herd (a sample page is included in Appendix N).

Out of a total of four stopwatches, only one had separate knobs for starting, stopping and returning to zero. Separate knobs are to be preferred for this work as a pause is difficult to differentiate from a stop and when several pairs are grooming simultaneously the mental calculations can be trying.

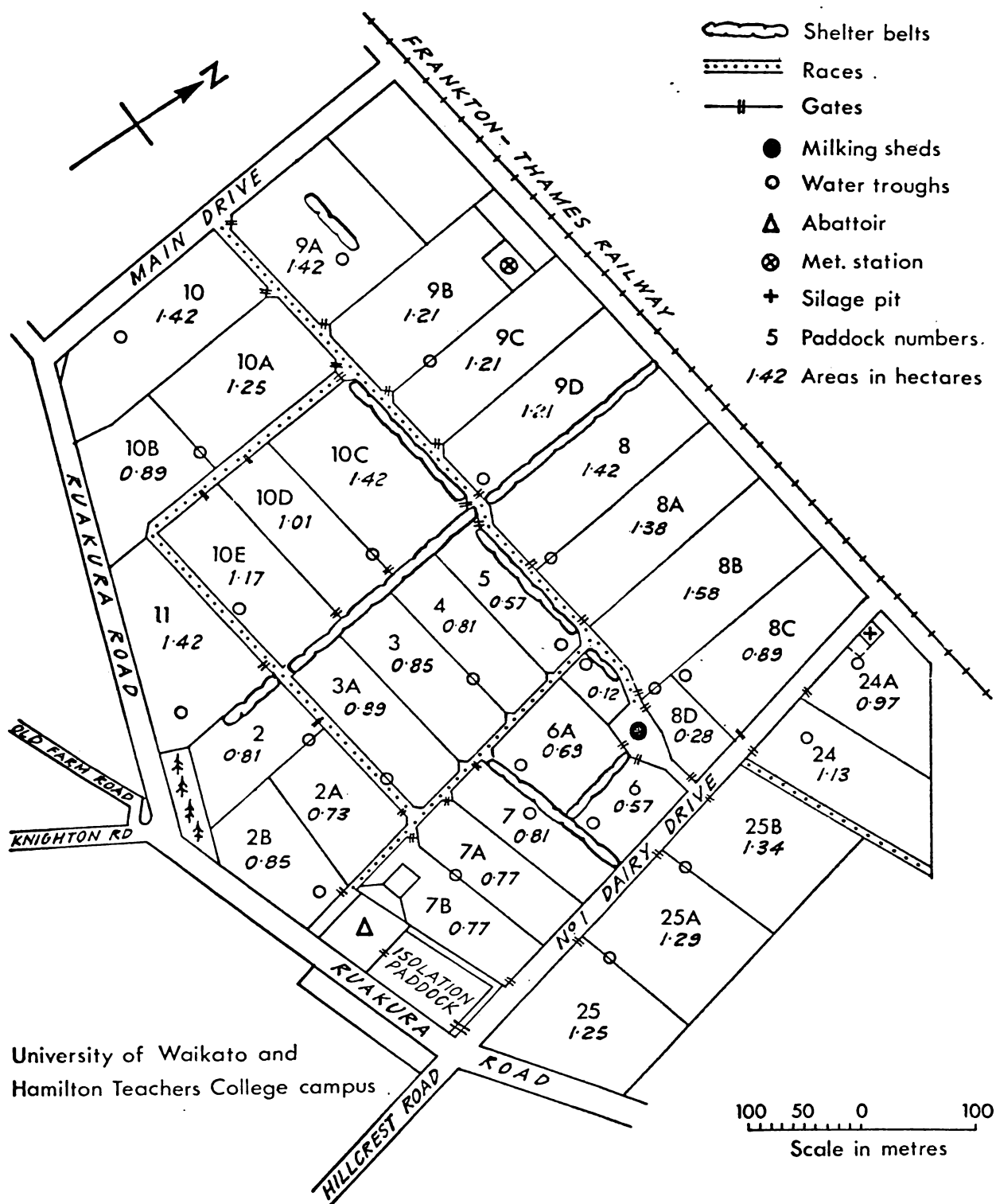


Fig.10 Plan of paddock layout for No. 1 Dairy at the Ruakura Agricultural Research Centre.

PROCEDURE

Sunny warm days with good light were chosen.

As suggested by experience gained from the earlier pilot study, no attempt was made to conceal the observers from the cows being observed. During test sessions the observers moved through the paddock and mixed with the cows easily. The cows were clearly aware of the observers.

When social grooming was noticed a stopwatch was started (after 60 seconds of grooming, the observer moved so that he was close enough to be able to identify the cows involved). Identification was usually double checked by the observer. When two observers worked together, one recorded and the other checked numbers and called back the information at a relatively normal voice level.

Observations were collected for two hours between about 1600 and 1800 hours every day during the twenty-four days over the eleven week summer period covered by the study (4 December 1973 - 16 February 1974; see Table XI). At least two hours of observations were collected prior to 1300 hours on fourteen different days. During the last five days of the study continuous observation was maintained from after morning milking circa 0700 hours until 1930 hours, about sunset. Cut-off points were not related to observations but to external pressures on the observers.

Observers were rotated from herd to herd. Time of day was irregularly recorded along with grooming interactions and comments were added when necessary. Standardized observation sheets used to record data were prepared. The cow exhibiting social grooming and the cow being groomed were both identified and the time, i.e. length of interaction, was recorded. Collation notebooks

Table XI Summary of Observational Periods of Social Grooming in Cows

	Date Dec. 73 - Feb. 74	Time	Observers*	No. Cows Grooming	Total Seconds	No. Cows Receiving	Temperature Range °C	
							High	Low
Herd 1	4 Dec.	1600-1800	GV, MW	24	2,430	26	22.5	14.3
	5 Dec.	1615-1805	PC, GV, EW, MW	27	3,120	28	24.6	11.5
	6 Dec.	1600-1800	MW	10	1,170	11	24.2	11.1
	9 Dec.	1640-1830	MW	19	2,580	20	24.8	13.5
	10 Dec.	1600-1800	MW	22	2,285	31	25.8	9.0
	11 Dec.	1600-1800	MW	8	450	9	27.6	9.5
	22 Jan.	1600-1830	EW, MW	11	1,220	13	24.0	15.7
	28 Jan.	1700-1845	MW	15	2,585	18	25.7	13.1
	29 Jan.	0900-1100	MW	16	1,960	23	27.2	11.4
	29 Jan.	1615-1815	MW	7	380	7	27.2	11.4
	30 Jan.	0900-1100	MW	24	3,505	27	25.7	10.2
	30 Jan.	1615-1815	MW	16	2,180	17	25.7	10.2
	31 Jan.	0915-1115	MW	8	845	11	28.9	13.9
	31 Jan.	1600-1800	MW	0	0	0	28.9	13.9
	1 Feb.	0915-1115	MW	5	695	7	30.8	17.0
	1 Feb.	1645-1845	MW	15	1,165	15	30.8	17.0
	2 Feb.	1000-1215	MW	11	2,050	14	35.7	14.6
	4 Feb.	1700-1930	MW, SW	24	2,700	26	24.8	17.4
	5 Feb.	1145-1300	MW	11	1,590	15	28.9	17.1
	5 Feb.	1700-1830	MW	5	195	5	28.9	17.1
	8 Feb.	0900-1300	MW	5	390	5	28.8	16.4
	8 Feb.	1630-1845	MW	9	800	9	28.8	16.4
	9 Feb.	0900-1100	MW	3	510	3	30.1	17.5
	9 Feb.	1630-1830	MW	9	645	10	30.1	17.5
	10 Feb.	1630-1930	MW	9	335	9	30.2	19.0
	11 Feb.	0830-1200	MW	7	1,010	11	29.8	17.1
	11 Feb.	1700-1830	MW	5	120	5	29.8	17.1

cont. next page

Table XI cont.

	Date Dec.73 - Feb.74	Time	Observers*	No. Cows Grooming	Total Seconds	No. Cows Receiving	Temperature Range °C	
							High	Low
Herd 1	12 Feb.	0700-1300	JM,KR,MW	19	1,995	21	28.3	16.6
	12 Feb.	1300-1910	JM,MW	14	3,115	15	28.3	16.6
	13 Feb.	0700-1300	GJ,JM	30	5,070	38	27.4	19.7
	13 Feb.	1300-1915	GJ,JM	28	3,990	29	27.4	19.7
	14 Feb.	0730-1300	JM,MW	20	4,455	25	28.0	17.6
	14 Feb.	1300-1915	GB,MW	16	1,555	18	28.0	17.6
	15 Feb.	0700-1300	GB,GJ	17	2,770	17	29.4	19.7
	15 Feb.	1300-1930	GB,JM	30	4,095	32	29.4	19.7
	16 Feb.	0700-1300	GB,MW	27	6,355	35	28.3	20.0
	16 Feb.	1300-1940	JM,MW	49	9,485	46	28.3	20.0
Herd 2	12 Feb.	0700-1300	DB,GJ,EW	6	155	6	28.3	16.6
	12 Feb.	1300-1915	DB,GJ	16	2,290	18	28.3	16.6
	13 Feb.	0700-1300	DB,MW	7	305	7	27.4	19.7
	13 Feb.	1300-1915	MW	9	1,795	12	27.4	19.7
	14 Feb.	0730-1300	GJ	10	555	10	28.0	17.6
	14 Feb.	1300-1915	GJ,JM	16	2,455	22	28.0	17.6
	15 Feb.	0700-1300	MW	10	1,835	12	29.4	19.7
	15 Feb.	1300-1930	MW	25	3,660	26	29.4	19.7
	16 Feb.	0700-1300	GJ,EW	19	1,850	17	28.3	20.0
	16 Feb.	1300-1935	GB,GJ	22	3,855	27	28.3	20.0

* DB - Donna Booth GB - Graham Blanks PC - Peter Copeman GJ - Gunnar Johnsson
 JM - John McKee KR - Kay Ryan GV - Glynis Vercoe EW - Eva Wood
 MW - Mark Wood SW - Sterling Wood

were brought up to date each evening.

The sample of social grooming taken was that which was observed during the observational periods on the days chosen at the times chosen. As this was exploratory research, where observers had little information or feedback relating to individual cow differences, no systematic observer biases with regard to the characteristics of the cows under investigation were considered to have occurred. An interaction was considered to be all of the social grooming given by one cow to another. By definition there were only two opportunities for a given cow to groom a given other cow, either before 1300 hours or after. The incidents occurring between a pair of cows before 1300 hours were added together and designated one interaction. A similar consolidation was used for incidents after 1300 hours. This data artefact was considered necessary due to the difficulty of deciding in the field whether or not a given interaction had in fact ceased and when a new interaction might be considered to begin. In other words, a social grooming interaction is measured more specifically in terms of time spent licking.

Body weights were recorded weekly throughout the observational period by the staff of Dairy I using Donald's hydraulic scales. Milk weight was recorded daily by Dairy I staff and the records of the seven weeks when the main observations on social grooming were made were used to obtain an average score of milk production. (See Appendix O).

Observations were made while the cows were being milked in the rotary milking shed (Figs 11 and 12) to establish a milking order. This facilitated discrete and accurate ratings. The motorised gate behind the cows moved, keeping a rather constant

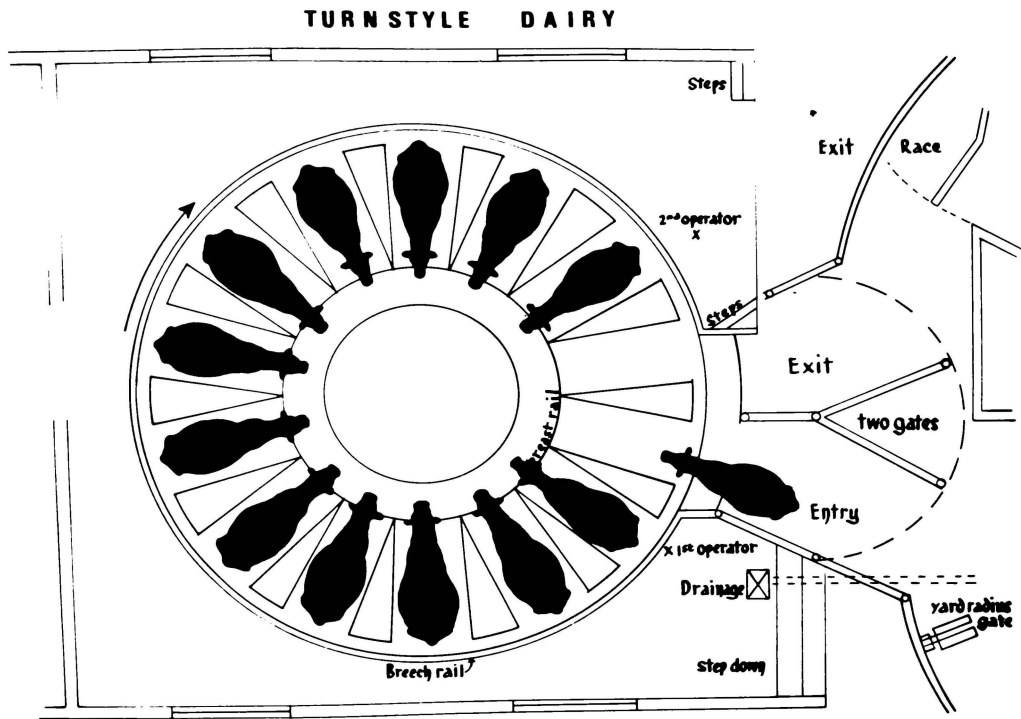


Fig. 11 Milking shed where the single file milking orders were established, at No.1 Dairy (courtesy of Ruakura A.R.C.)



Fig.12 Rotary milking shed, showing the single file entry and exit, allowing for clear data collection milking order.

flow of cows through the milking shed. Milking order was recorded five times in a two-week period when all of the cows in Herd 1 were milked using one platform, a procedure which necessitated single file entry.

Breed was noted according to Dairy I records (see Appendix P for summary statistics). In considering the variable breed for analysis, two points were important.

1. Ayrshire x Jersey and (AxJ) x J were not included, as there were too few of them.
2. The rest of the cows were given a number which represented the numbers of eighths of Friesian blood. In other words, 0 for Jerseys, 2 for (JxF) x J, 4 for J x F, 6 for (JxF) x F, 8 for Friesians. One cow (JxF) x F x F was also assigned a 7.

Suckling in the herds was noted and regarded as a special category of behaviour distinct from social grooming.

Collar colour referred to reinforcement schedules, where numbers were assigned according to the information obtained from Dairy I, the most effective schedule in relation to milking order was given the highest number and so on down five steps with a control group between steps two and four. (see Appendix I).

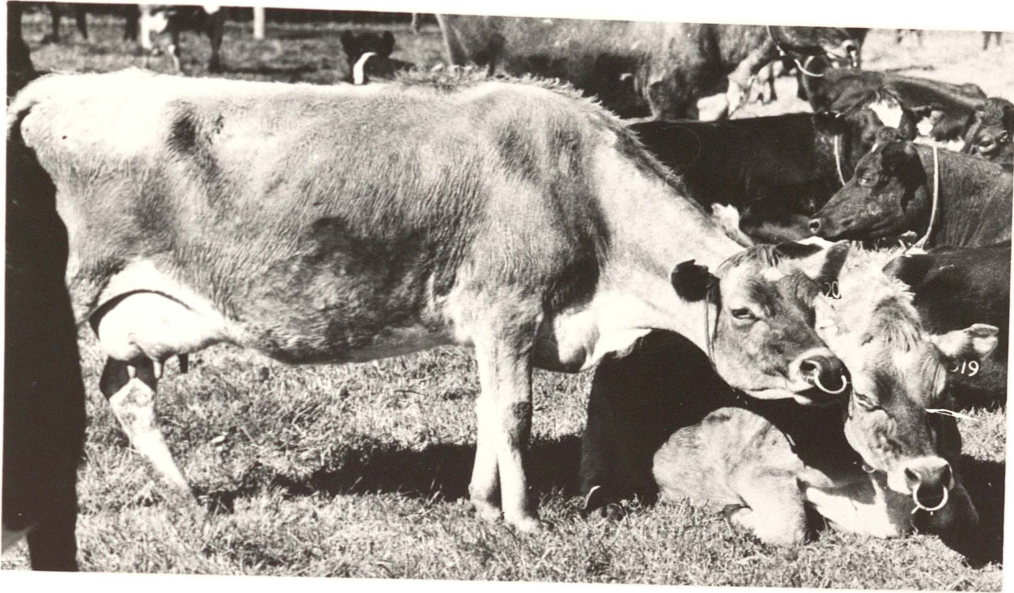


Fig.13a Showing twin 320 grooming twin 319. Both have nose rings embellished with spikes. (Courtesy Macqueen Ruakura A.R.C.)

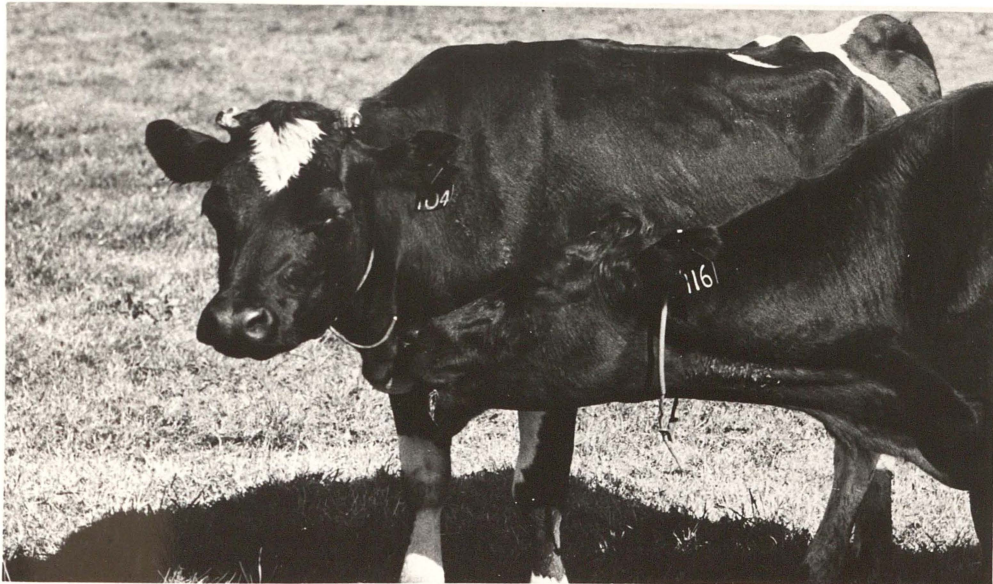


Fig.13b Shows grooming between four year olds not genetically related but belonging to the same "class". (Courtesy Macqueen Ruakura A.R.C.)

DATA ANALYSIS AND RESULTS

First Stage - Herd 1 and Herd 2

The first research question involved simply a tally of time plus establishment of confidence intervals (according to Ferguson, 1971, p.138). The remaining research questions involved elementary arithmetic computation.

The results of this analysis are given in Table XII, where it is pointed out that the discrepancy between the total for twins and non-twins is due to the fact that four cows whose twins were not in Herd 1 were excluded from the calculations.

In Herd 1 an average of 82 seconds per cow per day were spent grooming, 56 seconds grooming twins and 28 seconds grooming non-twins. In Herd 2, the corresponding figures were 94 seconds in total, 56 seconds for twins and 38 seconds for non-twins.

The percentage of total grooming time exchanged between pairs was 65.45 per cent for Herd 1 twins and 59.56 per cent for Herd 2 twins. In Herd 1 the average length of an interaction per cow with all other cows was 134 seconds, that with twins 183 seconds and that with non-twins 89 seconds. In Herd 2, the corresponding figures were 96 seconds with all other heifers, 153 seconds with twins and 62 seconds with non-twins.

The average number of interactions in Herd 1 a day per cow with all other cows was .62, with twins .31 and with non-twins .32. In Herd 2 the corresponding figures were .98 with all other heifers, .36 with twins and .62 with non-twins.

The daylight or diurnal herd social grooming cycle for Herd 1 showed a mid-morning peak occurring between 0900 and 1000 hours, and another peak between 1730 and 1930 hours. These appeared to be related to the milking times and subsequent grazing periods

Table XII Grooming Parameters Taken During Intensive Consecutive
Observation 12-16 February 1974*

	Herd 1 (104 cows)		Herd 2 (40 heifers)	
	Non-twin	Twin [‡]	Non-twin	Twin
(1) Total Grooming seconds	14,815	28,070 [‡]	7,585	18,755 [‡]
(2) Average seconds per subject per day	28	56	38	56
(3) Average seconds per interaction	89	183	62	153
(4) Total interactions	167	153	123	73
(5) Average interactions per subject per day	.32	.31	.62	.36
(6) Range of per cent of subject day spent grooming others	.00 - 1.15	.00 - 1.15	.00 - .47	.00 - .63
(7) Average per cent of subject day spent grooming others	.06	.13	.09	.12
(8) 99% confidence intervals of (7)	.03 - .10	.09 - .18	.04 - .13	.07 - .18

* Total observation time - 61 hours 20 minutes

‡ Four cows whose twins were not in the herd were excluded from the calculations, leaving 100 subjects

‡ Percentage of total grooming time exchanged within twin pairs:
Herd 1 - 65.45 Herd 2 - 59.56

which were followed by bouts of social grooming. The lack of milking periods for the non-lactating heifers in Herd 2 affected the daylight social grooming cycle which showed a mid-morning heat of the day quiescent period building up to a mid-afternoon to evening peak of grooming activity. (See Figs 14 and 15 and Appendices E, F, G and H). These figures required a slight modification in the histograms (i.e. transformation to density of the Y-axis) due to the time period used for milking (one and one-half hours) in Herd 1. This modification was carried out according to the conventions suggested by Huntsberger (1963). The distribution of the total time spent in the social grooming of others for the cows in Herd 1 is given in Fig. 16, where sixteen cows gave no grooming responses whatsoever and two gave more than seventy-five minutes of grooming to other herd members.

Second Stage - Herd 1 Hypotheses

In the second stage the basic information on herd parameters gathered in the first stage was tested by using Spearman's coefficient of rank correlation. Significance levels for the correlation coefficients obtained were then checked in Ferguson (1971, p. 450).

Hypothesis 1 stated that the independent variables age, body weight, milk weight and milking order would be found to correlate positively with the number of non-twins groomed. However, the only variables which reached an acceptable significance level were age ($p < .0005$) and body weight ($p < .025$) (see Table XIII). This hypothesis also suggested that a positive correlation would be found between the independent variables mentioned above and the total number of seconds of grooming given to non-twins. The only

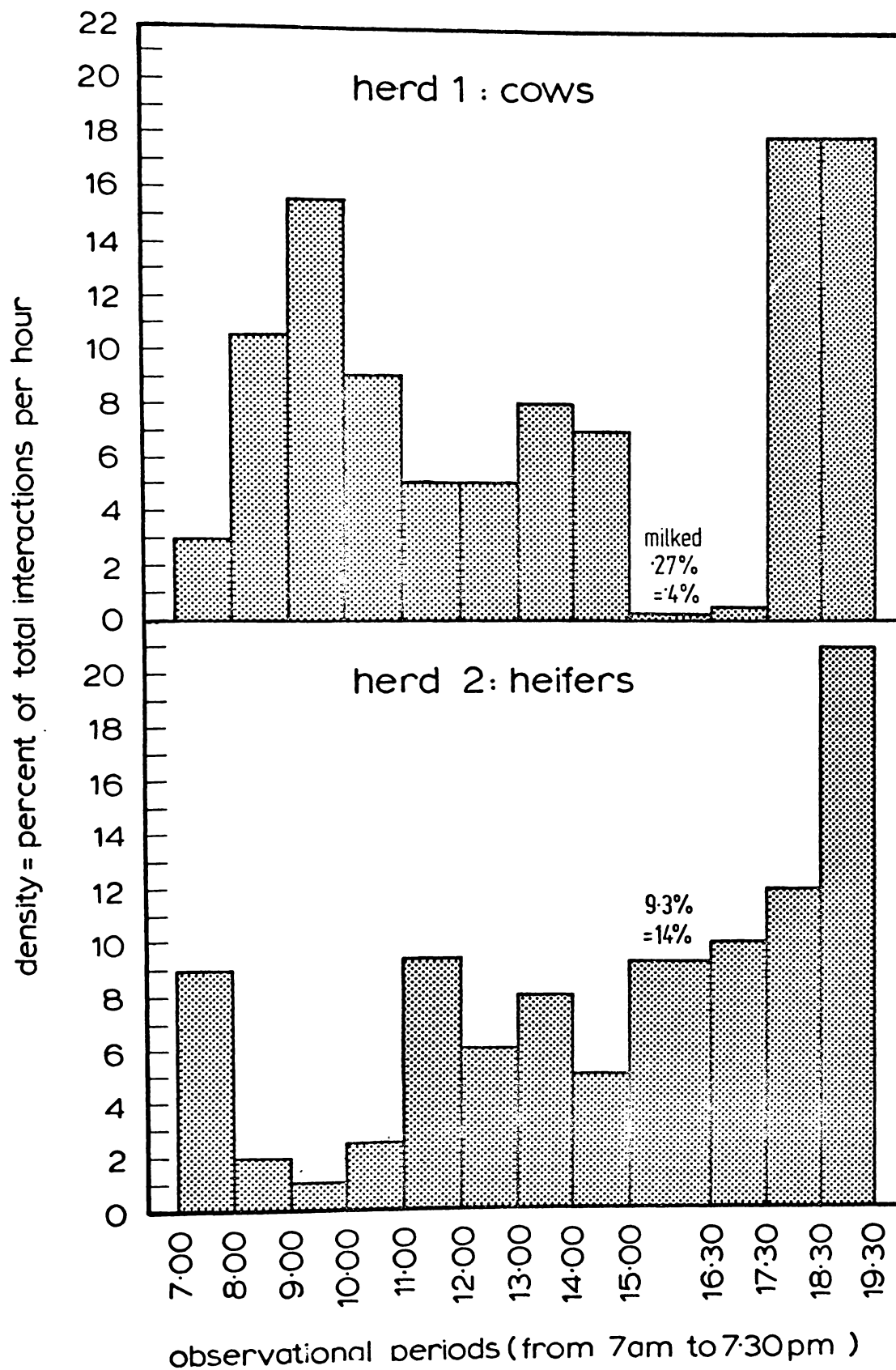


Fig. 14 Bar graphs showing the diurnal grooming rhythms for the cows from two herds at Ruakura Agricultural Research Centre (in interactions per hour).

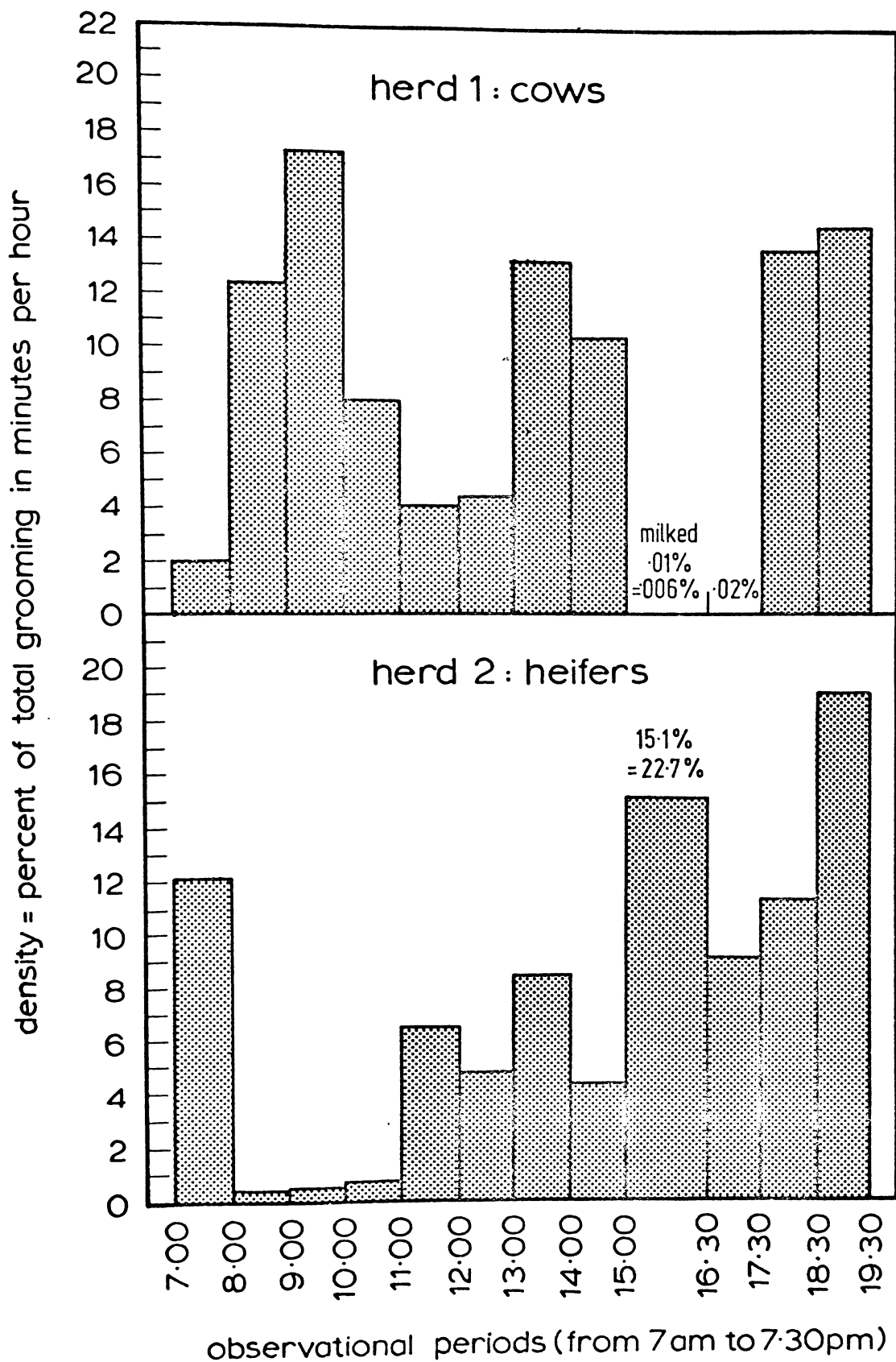


Fig. 15. Bar graphs showing the diurnal grooming rhythms for the cows from two herds at Ruakura Agricultural Research Centre (in minutes per hour).

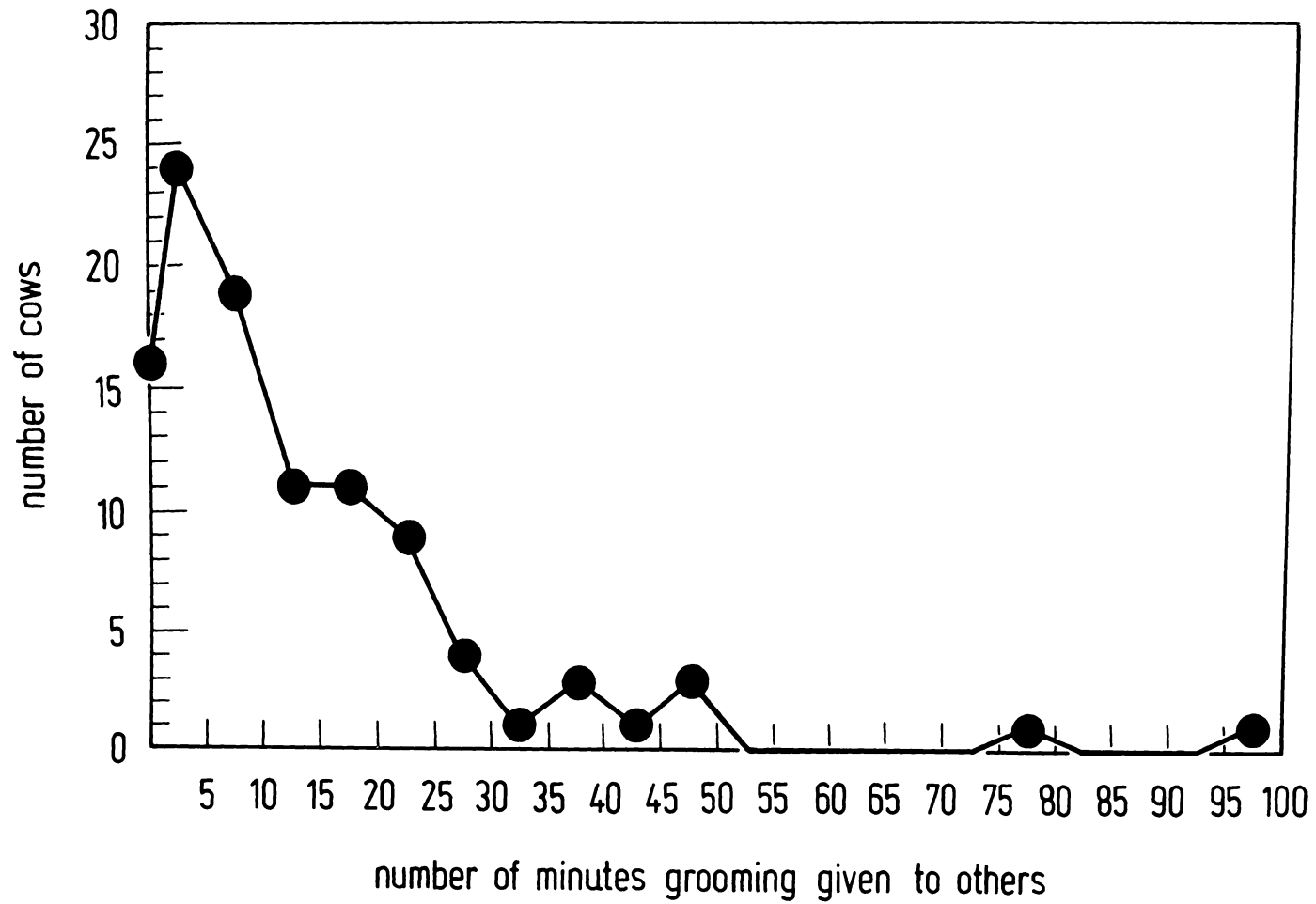


Fig.16. Frequency polygon showing distribution of total time spent in social grooming for the cows of Herd 1.

variables which reached an acceptable significance level were again age ($p < .0005$) and body weight ($p < .025$) (see Table XIV).

Of the independent variables age, body weight, milk weight and milking order which it was hypothesised would be found to correlate positively with the number of non-twins a cow received grooming from (Hypothesis 2), the variables which reached an acceptable significance level were age ($p < .0005$), body weight ($p < .025$), milk weight ($p < .025$) and milking order ($p < .005$) (see Table XV). This hypothesis also suggested that a positive correlation would be found between the independent variables mentioned above and the amount of time that a cow received grooming from non-twins. The same variables again reached an acceptable significance level - age ($p < .005$), body weight ($p < .05$), milk weight ($p < .025$) and milking order ($p < .005$) (see Table XVI).

Hypothesis 3 suggested that the independent variables age, body weight, milk weight and milking order would be found to correlate positively with the amount of time twins spent grooming or being groomed by each other. The only variable which reached an acceptable significance level was milking order, both for the amount of time cows spent grooming their twin ($p < .05$) and for the amount of time cows received grooming from their twins ($p < .05$) (see Table XVII).

Breed was not found to be significantly related to any of the dependent variables (Hypothesis 4). Therefore, the null hypothesis was retained.

The experiment on reinforcement schedules in progress at the same time (represented by collar colour) did not prove to be significantly related to either the number of non-twins groomed (see Table XIII) or the number of non-twins from which grooming

was received (see Table XV). Hypothesis 5 was therefore not supported.

Hypothesis 6 also concerned the experiment on reinforcement schedules in progress at the same time (represented by collar colour). These reinforcement schedules did not prove to be significantly related to the amount of time grooming was given to or received from non-twins (see Tables XIV and XVI).

The results generated by Hypothesis 7 showed that the experiment on reinforcement schedules in progress at the same time (represented by collar colour) did not prove to be significantly related to the amount of time grooming was given to twins (see Table XVII), but did prove to be significantly related to the amount of time grooming was received from twins ($p < .02$).

Hypothesis 8, that spiked nose rings affect social grooming rank, was tested by using the Mann-Whitney U test for two independent samples. This was a two-tailed hypothesis as it was felt that nose rings could identify good social groomers or on the other hand prevent social grooming from occurring at all. The results from this test proved to be quite non-significant.

Hypotheses 9, 10 and 11, which concerned Herd 2 and suggested that body weight would be positively related to the giving and receiving of social grooming between either non-twins or twin, was not supported. Neither was Hypothesis 12 supported, which suggested that breed would also be significantly related to the independent variables (see Tables XIII, XIV, XV, XVI and XVII).

Hypotheses 13 and 14, that grooming and being groomed are twin-linked, was tested by using Spearman's co-efficient of rank correlation which investigated the probability of both members of a twin pair having similar grooming ranks. The 50 twin pairs in

Table XIII Correlation Coefficients for Number of Non-twins Groomed

	Independent Variables	Number of Non-twins Groomed	Significance Level
Herd 1 (104 cows)	Breed *	.171	n.s.
	Age	.360	$p < .0005$
	Body weight	.225	$p < .025$
	Milk weight	.117	n.s.
	Milking order	.096	n.s.
	Collar colour	.091	n.s.
Herd 2 (40 heifers)	Breed	.202	n.s.
	Body weight	.106	n.s.

* Only 100 cows were used in obtaining this correlation as both the Ayrshire x Jerseys and (AxJ) xJ were removed from the herd.

Table XIV Correlation Coefficients for Total Seconds of Non-twin Grooming

	Independent Variables	Number of Seconds	Significance Level
Herd 1 (104 cows)	Breed*	.145	n.s.
	Age	.363	$p < .0005$
	Body Weight	.195	$p < .025$
	Milk weight	.098	n.s.
	Milking order	.143	n.s.
	Collar colour	.129	n.s.
Herd 2 (40 heifers)	Breed	.165	n.s.
	Body weight	.174	n.s.

Table XV Correlation Coefficients for Number of Non-twins from which herd members received grooming

	Independent Variables	Number of Non-twins Received from	Significance Level
Herd 1 (104 cows)	Breed *	.125	n.s.
	Age	.349	$p < .0005$
	Body weight	.227	$p < .025$
	Milk weight	.212	$p < .025$
	Milking order	.261	$p < .005$
	Collar colour	.077	n.s.
Herd 2 (40 heifers)	Breed	.261	n.s.
	Body weight	.218	n.s.

* Only 100 cows were used in obtaining this correlation as both the Ayrshire x Jerseys and (AxJ) x J were removed from the herd.

Table XVI Correlation Coefficients for Total Seconds of Grooming Received from Non-twins

	Independent Variables	Number of Seconds	Significance Level
Herd 1 (104 cows)	Breed *	.131	n.s.
	Age	.286	$p < .005$
	Body weight	.185	$p < .05$
	Milk weight	.214	$p < .025$
	Milking order	.283	$p < .005$
	Collar colour	.008	n.s.
Herd 2 (40 heifers)	Breed	.257	n.s.
	Body weight	.154	n.s.

Table XVII Correlation coefficients between Independent Variables and Seconds of grooming given to and received from twin.

	Independent Variables	Seconds Grooming Twin	Significance Level	Seconds Received From Twin	Significance Level
Herd 1 (100 cows)	Breed*	-.047	n.s.	-.047	n.s.
	Age	-.004	n.s.	-.004	n.s.
	Body Weight	-.061	n.s.	-.061	n.s.
	Milk weight	.036	n.s.	.094	n.s.
	Milking order	.224	$p < .05$	.257	$p < .02$
	Collar colour	.193	n.s.	.245	$p < .02$
Herd 2 (40 heifers)	Breed	.050	n.s.	.050	n.s.
	Body weight	.193	n.s.	.215	n.s.

* Only 96 cows were used in obtaining this correlation as both the Ayrshire x Jerseys and (AxJ) x J and the four singles were removed from the herd.

Herd 1 and 20 twin pairs in Herd 2 formed the two subject populations used in this analysis. Grooming appeared to be twin-linked insofar as it had a correlation of 0.71 for number of cows and 0.69 for number of seconds in Herd 1. These yielded significance levels of $p < .001$ and $p < .001$. A similar analysis looking at the classification of those receiving grooming yielded coefficients of correlation of 0.52 for number of cows and 0.58 for number of seconds. The Herd 2 results agreed with the above findings but at lower significance levels due, it is imagined, to lower subject numbers and shorter observational period. These levels were, however, still significant $p < .05$ for the number of heifers grooming was given to and for the number of seconds grooming was received from other heifers.

Hypothesis 2 that age, body weight, milk weight and milking order would correlate positively with the number of non-twins from which a cow received grooming, was checked using Pearson's product moment correlation. This check with a parametric test found similar correlations (age .353, body weight .289, milk weight .250 and milking order .297) that were also significant to similar levels as the Spearman rank correlations. Consequently it was felt justified to continue with an analysis of regression (see Table XVIIIa) which gave two factors as being clearly important, age and milking order. A similar analysis where amount of time cows received grooming from non-twins was also carried out. This showed Pearson product moment correlations (age .371, body weight .242, milk weight .202 and milking order .260) which when subjected to an analysis of regression again found age and milking order to be the most important factors (see Table XVIIIb).

Table XVIIIa Summary Table for Stepwise Regression with Number of Cows
(excluding twin) from which a cow received Grooming as the
Dependent Variable and Age, Body Weight, Milk weight and
Milking order as the Independent Variables

Independent Variables	Coefficient of Correlation (R)	R^2	Increase in R^2	F Value
Age	0.3527	0.1244	0.1244	14.4949
Milking order	0.4198	0.1762	0.0518	6.7538
Body weight	0.4351	0.1893	0.0131	1.6144
F-level or Tolerance insufficient for further computation				

Table XVIIIb Summary Table for Stepwise Regression with amount of time a
cow received grooming from other cows (excluding twin) as the
Dependent Variable and Age, Body Weight, Milk weight and Milking
Order as Independent Variables

Independent Variables	Coefficient of Correlation (R)	R^2	Increase in R^2	F Value
Age	0.3709	0.1375	0.1375	16.2657
Milking order	0.4148	0.1721	0.0345	4.2127
F-level or Tolerance insufficient for further computation				

DISCUSSION - FIRST STAGE

It has been reported that time spent grooming or being groomed has a more important connection with the social significance of grooming than does frequency (number of interactions) (Chance & Jolly, 1970). Interaction as a unit for measuring frequency proved difficult to define. Even licking generally requires the tongue to be withdrawn into the mouth between licks. Where a cow turned her head away, then back and licked again, the decision to call it a continuation of social grooming rather than a new interaction seemed to be merely a matter of choice.

Samraus (1969) mentions 316 interactions of social grooming without giving a clear definition of what an interaction delineates. In order to give a clear definition, the convention used in this study was that of calling all grooming interactions occurring from one cow to another prior to 1300 hours one interaction and those after 1300 hours another interaction. This allowed for only two possible interactions per cow per day and cut down on a possible serious source of error in inter-observer reliability. It was felt that the reliability of judgments was further increased by discussions about criteria with the observers before and during the day's research was in progress and by mixing observers and herds according to a randomized schedule set out by the principal observer. The time schedules for observations given in Table XI have the initials of the people who were working most of the period recorded. However, off-duty observers covered the staggered lunch breaks so that everyone had a one and a half hour lunch break without occasioning a break in observations.

As the study concentrated on daylight activities the grooming that may occur during the evening was not taken into account.

Systematic differences in grooming patterns in the dark would be an interesting avenue for further research, given night time viewing equipment (e.g. infrared sighting equipment) that would not change the conditions for the cows observed.

Descriptive data about herd grooming parameters is scarce in the bovine literature. Therefore the first section of this study was designed to increase the amount of descriptive data available on cows social grooming in terms of frequency, length of time and diurnal grooming cycles.

The generalizability across herds from this data is somewhat impaired by the small number of herds, one herd of cows and one of heifers. However, the recorded quantitative data about these herds, added to that which was already known, may help to create a more substantial base for an in-depth study of the subject.

The two main parent breeds of the subjects in this study were Holstein-Friesian and Jersey. The Holstein-Friesian breed has been selected for dairy qualities for about 2,000 years. Their high milk production has a relatively low butterfat content (Price & Nevens, 1966). Jersey cattle are rather smaller in size. The Jersey as a breed (probably French in origin) was recognized in 1763. Jersey milk production, although lower than Holstein-Friesian production, is quite rich in butterfat and animals of this breed are therefore in demand for crossing with other breeds to improve the quality of a herd's milk. What effect long breeding and inbreeding programmes have had on the social grooming frequencies of the original bovine stock is difficult to ascertain. Tinbergen (1965) discusses rather profound changes in the social sexual behaviour of domestic animals. Changes wrought by domestication could also conceivably occur in the incidence and/or quality of social grooming.

It was felt that the two herds studied here would be more likely to spend time in social grooming because they were composed of twin pairs. In general dairy herds would probably spend less time grooming than was spent in this study between twins and yet more than occurred between non-twins.

As the main purposes of the study were to see if a group of altruists and egoists could be reasonably clearly delineated and to investigate the role of "others", the presence of twins added a dimension to the work. It was felt that although this took the study a step further away from the usual herd situation with relation to social grooming, it added a step in theoretical depth in relation to altruism.

It so happened that the period during which this study was executed (December 1973 - February 1974) turned out to be one of the driest summers in sixty years. Few opportunities for observing in the rain presented themselves during this period. However, the casual observations made suggest that social grooming is not affected by rain. For this study, the weather could be therefore considered a constant. This dry period caused a serious setback, when, during the key observational period (12 February to 16 February), it was announced by the Dairy I staff that they were going to be forced to dry the herd off, as well as cull it, starting from 17 February. Consequently, the research team was disbanded.

It should be pointed out that a methodological assumption based on a mathematical relationship may have clashed with a genetic reality when numbers were given to the Jerseys, Friesians and crosses thereof. Numbers were assigned according to the mathematical probabilities of carrying genes from the original

stock. However, the actions of dominant and recessive characteristics, if related to social grooming, could serve to disrupt the requirement of an interval scale necessary for the Pearson product moment correlation. An additional problem was the extremely uneven distribution across the genetic categories.

DISCUSSION - SECOND STAGE

From the intercorrelations between the independent variables for Herd 1 shown in Table XIX one might expect a cluster to develop when these variables are correlated with non-twin social grooming. Body weight (which is frequently associated with higher status in cattle, Pouissou, 1972) and milk weight have the highest correlation on the table and both do correlate significantly with the amount of social grooming received. However, when looking at the time spent grooming, milk weight drops considerably in correlation, whereas body weight maintains a significant relationship with non-twin grooming.

Age correlates significantly with all the measures of social grooming and agrees with the findings of most of the studies investigating this relationship (Brantas, 1967/68; Carthy, 1965; Chance & Jolly, 1970; Poirier, 1970).

Milking order was used in this study as a measure of status. The concept of dominance as a unitary quality has received serious criticism. Kilgour (1957) separates dominance from leadership. A cow is considered to be dominant over another when she shows a superiority in fighting ability. Here it was thought to be most often observed in yards and other relatively enclosed places where physical proximity was closest. Leadership, on the other hand, was defined as "that animal which is in the advance position in movements of the herd" (Kilgour, 1957, p.53). Movement patterns are

Table XIX Herd 1 (104 cows) Pearson Product moment correlations between the Independent Variables

	Breed*	Age	Body Weight	Milk Weight	Milking Order	Collar Colour
Breed*	X	-.074	.508	.400	-.001	-.084
Age	-.074	X	.498	.360	.211	.178
Body weight	.508	.498	X	.661	.168	.017
Milk weight	.400	.360	.661	X	.312	-.063
Milking order	.001	.211	.168	.312	X	.166
Collar colour	-.084	.178	.017	-.063	.166	X

* Correlations are based on 100 cows as the Ayrshire crosses were removed for computational purposes.

occasioned in herds when going from paddock to milking yards and back again, and also in the shifts which occur during the daily grazing movements between paddocks. Milking order or bail order as it was called in Kilgour (1957) suggested that high dominance cows tend to take medial places in the milking order. The movements, however, to the bail by the herd were generally strung out, which may have helped to accentuate the difference in the bail order and dominance measures. According to Brantas (1967/68) "Willems and Lampo (1964) find a connection between the order of entrance into the milking stall and the age. However, they also prove that entrance-order is not identical with dominance order" (p.142). Syme (1972) believes that competitive orders should be established within the special demands of each situation rather than using the global term dominance.

As a backing gate was used to force cows into close proximity and ensure steady entry into the rotary milking shed (see Fig. 12), it was felt that the milking order observed in this study represented something between Kilgour's (1957) dominance and leadership categories. A later study may be able to get several measures of status and find out which one does in fact correlate best with the giving and/or receiving of social grooming.

In this study, milking order correlated significantly not only with the amount of grooming received from non-twins, but also with that exchanged between twins. The higher the status the more one receives. At first a startling conclusion. It makes, however, sound ethological sense. If an animal mother in the wild perceives that two offspring out of a litter of six are weak, then if she takes more care of them and they die, not only do they die but her energy investment, which could have gone to increase

the survival margin of the more successful offspring, also dies.

The Pearson product moment correlation in Herd 2 between the independent variables breed and body weight was .592 which was of a similar magnitude to the correlation found in Herd 1.

The intercorrelations between the dependent variables noted for both herds give a roughly similar picture. The number of cows grooming was given to correlates highly with the number of seconds given (.97 in Herd 1, .88 in Herd 2), and the number of cows grooming was received from correlates highly with the number of seconds received (.78 in Herd 1, .81 in Herd 2, see Appendix Q). This suggests that grooming relationships tend to have short optimal time periods for the establishment of social relations or the carrying out of the grooming movements. It was not, however, noted which partner terminated the greater number of interactions, the giver or the receiver. Giving and receiving between twins also correlated highly (.66 in Herd 1, .45 in Herd 2). Apparently cows recognize each other and do not just distribute grooming randomly. This reinforces the idea that one may use social grooming as an index of "friendliness" (Dimond, 1970; Ewer, 1968), between cows. This is important as behaviour leading to social stability in a herd must have a positive relationship with maximum milk production.

Stress factors are known to decrease milk yield (Brantas, 1967/68; Kilgour, 1969). This finding combined with one of the implications of this research suggests that if cows are culled on the basis of a drop in milk production, as often happens (see Appendix M), then in those cases where good social groomers are removed herd harmony may suffer, with a resultant loss in total herd milk production. Future research may be able to establish causal chains from the correlational ties which could have

pragmatic applications for the dairy farmer.

Culling out good groomers in some areas of the world can have disastrous results for cattle mortality. For example, Rich (1973) found in British Columbia that maternal grooming was a significant factor in the protection of calves from the Rocky Mountain wood tick, *Dermacentor andersoni*, which causes paralysis in up to 40 per cent of large herds, with severe death losses. The calves of poor grooming mothers had such great tick infestations that survival chances became remote.

The significant positive correlation between the number of seconds grooming was received from twins and collar colour, is rather difficult to interpret. The decision to treat the numbers assigned on the basis of reinforcement schedules as an interval scale may have been unwarranted.

THIRD STAGE

Hypotheses

1. That in Herd 1 cows would prefer grooming their twin to any other cow in the herd.
2. That in Herd 2 heifers would prefer grooming their twin to any other heifer in the herd.
3. That there would be a difference between Herd 1 and Herd 2 in the proportions that preferred to groom their twin versus any other in the herd.
4. That two year olds would differ from heifers in the proportions that preferred to groom their twin versus any other in the herd.
5. That in Herd 1 cows would be more likely to groom their own age group than other age groups, as

measured by both the number of seconds and number of cows groomed.

6. That in Herd 1 cows would be more likely to groom their own age group than the next nearest age group and the next age group than the furthest age group, as measured by both the number of seconds and number of cows groomed.
7. That in Herd 1 with increasing age cows would be more likely to groom other cows rather than grooming only their twin.
8. That in Herd 1 with increasing age cows would be more likely to prefer grooming another cow to grooming their twin.
9. That the altruism-egoism dichotomy would correlate significantly with age, body weight, milk weight and milking order which were shown to be factors in the giving and/or receiving of social grooming between non-twins.
10. That the altruism-egoism dichotomy would correlate significantly with the amount of time twins spent grooming and receiving grooming from each other.
11. That altruism is twin-linked.
12. That egoism is twin-linked.

Data and Results

Hypotheses 1 and 2 were tested with a one-sample chi square according to Siegel (1956, p.42). Herd 1 cows preferred grooming their twin to any other cow in the herd ($p < .001$, see Table XX) (Hypothesis 1), and Herd 2 heifers preferred grooming their twin to any other heifer in the herd ($p < .001$, see Table

XXI) (Hypothesis 2).

Hypotheses 3 and 4 were tested with a chi square after the data had been put in a 2 x 2 form and corrected for continuity. No significant difference was found between Herd 1 and Herd 2 in the proportions that preferred to groom their twin versus any other herd member (Hypothesis 3). However, the significance level ($p < .10$, see Table XXII) is recorded as it would have been significant had this been a one-tailed hypothesis. Hypothesis 4 was supported in that a significant difference was found between the proportion of two year olds in Herd 1 and the proportion of heifers in Herd 2 that preferred to groom their twin versus any other herd member ($p < .05$, see Table XXIII).

Hypotheses 5 and 6 were tested with a one-sample chi square according to Siegel (1956, p.42). To test Hypothesis 5 relating to age groups, the cows were divided into three age groups as follows:

- (1) 32 two year olds,
- (2) 35 three year olds, and
- (3) 37 four or more year olds.

It was hypothesized that Herd 1 cows would be more likely to groom their own age group than other age groups. Cows who gave an equal or no response were deleted from the group for the purposes of analysis. This explains the discrepancy in the total number of cows in Table XXIV and Table XXV. Herd 1 cows were more likely to groom their own age group than other age groups classified by seconds ($p < .01$, see Table XXIV) and when classified by number of cows groomed ($p < .001$, see Table XXV).

Hypothesis 6 suggested that Herd 1 cows would be more likely to groom their own age group rather than the next nearest age group, and the next age group rather than the furthest age group,

Table XX Preference in Herd 1 for Cows to Groom Twin rather than other cows

	Preferred Twin	Preferred Other Cow	Total
Number	(.86)	(85.14)	
of cows	67	19	86

$$\chi^2 = 5138.0075, \text{ df} = 1, p < .001$$

Table XXI Preference in Herd 2 for Heifers to Groom Twin rather than other Heifers

	Preferred Twin	Preferred Other Heifer	Total
Number of	(1.01)	(37.99)	
heifers	24	15	39

$$\chi^2 = 537.2196, \text{ df} = 1, p < .001$$

Table XXII Herd as a Factor in Choice of Preferred Grooming Partners

	Herd 1	Herd 2	Total
Chose twin most	67	24	91
Chose non-twin most	19	15	34
Total	86	39	125

$$\chi^2_{\text{corrected}} = 2.8507, \text{ df} = 1, p < .10 \text{ (n.s.)}$$

Table XXIII Two Year Olds versus Heifers in Choice of Preferred Grooming Partners

	Herd 1 Two Year Olds	Herd 2 Heifers	Total
Chose twin most	20	24	44
Chose non-twin most	2	15	17
Total	22	39	61

$$\chi^2_{\text{corrected}} = 4.6629, \text{ df} = 1, p < .05$$

Table XXIV Preference in Herd 1 (Measured in Seconds)
for Cows to Groom Own Age Group rather
than Other Age Groups

	Own Age Group	Other Age Groups	Total
Number	(22.62)	(44.38)	
of cows	34	33	67

$$\chi^2 = 8.6433, \text{ df} = 1, p < .01$$

Table XXV Preference in Herd 1 (Measured by Number of
Cows) for Cows to Groom Own Age Group
rather than Other Age Groups

	Own Age Group	Other Age Groups	Total
Number	(19.68)	(38.32)	
of cows	36	22	58

$$\chi^2 = 20.4842, \text{ df} = 1, p < .001$$

Table XXVI Preference in Herd 1 (Measured in Seconds)
for Cows to Groom Own Age Group rather than
Next and Furthest Age Groups

	Own Age Group	Next Age Group	Furthest Age Group	Total
Number	(14.80)	(14.96)	(14.24)	
of cows	30	8	6	44

$$\chi^2 = 23.6170, \text{ df} = 2, p < .001$$

Table XXVII Preference in Herd 1 (Measured by Number
of Cows) for Cows to Groom Own Age Group
rather than Next and Furthest Age Groups

	Own Age Group	Next Age Group	Furthest Age Group	Total
Number	(12.20)	(12.24)	(11.56)	
of cows	29	6	1	36

$$\chi^2 = 35.9621, \text{ df} = 2, p < .001$$

classified according to seconds and number of cows. The age groups were defined as for Hypotheses 5. However, only the choices of the oldest and the youngest groups were attended to as the middle age group could not be meaningfully used in this test as it did not have any group two steps away from it. The hypothesis was supported both in terms of the classification in seconds ($p < .001$, see Table XXVI) and when the cows were classified according to the number of cows groomed from any given age level ($p < .001$, see Table XXVII).

Hypotheses 7 and 8, concerning Herd 1, were tested with a chi square after the data had been divided into three groups as follows:

- (1) 32 two year olds,
- (2) 35 three year olds, and
- (3) 37 four or more year olds.

Cows that did not groom any other cows and cows that did not have their twin present in the herd were removed from the analysis, leaving 22 cows in group (1), 33 in group (2) and 31 in group (3), giving a total of 86 cows for the testing of these hypotheses. It was found that with increasing age cows were significantly more likely to groom other cows rather than grooming only their twin ($p < .05$, see Table XXVIII) (Hypothesis 7). It was also found that with increasing age cows were significantly more likely to prefer grooming another cow in the herd to grooming their twin ($p < .01$ see Table XXIX) (Hypothesis 8).

The altruism-egoism dichotomy was constructed in such a manner that giving and receiving would be likely to be highly correlated. These correlations are given in Table XXX.

Table XXVIII Herd 1 - Age as a Factor in Grooming
Twin Only versus Grooming Non-twins

	2 years	3 years	4+ years	Total
Twin	7	10	3	20
Non-twins	15	23	28	66
Total	22	33	31	86

$$\chi^2 = 5.0238, \text{ df} = 2, p < .05$$

Table XXIX Herd 1 - Age as a Factor in Cow's Choice
of Preferred Grooming Partner

	2 years	3 years	4+ years	Total
Chose twin most	20	28	19	67
Chose non-twin most	2	5	12	19
Total	22	33	31	86

$$\chi^2 = 8.0566, \text{ df} = 2, p < .01$$

Hypotheses 9 and 10 were tested using the Point Biserial correlation (egoism = 0, altruism = 1) which was then checked for levels of significance in Ferguson (1971, p.457). Hypothesis 9 suggested that the independent variables age, body weight, milk weight and milking order, which were shown to be significantly correlated with the giving and/or receiving of social grooming between non-twins, would also be significantly correlated with the altruism-egoism dichotomy. However, only age proved here to be significant, older cows being more likely to be altruists ($p < .01$, see Table XXXI). As suggested by Hypothesis 10, the altruism-egoism dichotomy correlated significantly with the amount of time twins spent grooming each other ($p < .05$) and the amount of time twins received grooming from each other ($p < .05$) (see Table XXXI).

Hypothesis 11, that altruism is twin-linked, was tested by using the binomial distribution

$$p(X \geq 6/n=8) = \sum_{X=6}^8 \binom{8}{X} (.14)^X (.86)^{8-X}$$

which was derived from the data in Appendix K (see Table XXXII) and looked at the probability of both members of a twin pair appearing in the altruistic group versus the probability of their not both appearing in the altruistic group. A total of 100 cows (50 twin pairs) was used in this analysis. This yielded a significance level of $p < .0002$.

Hypothesis 12, that egoism is twin-linked, was tested by using the binomial distribution

$$p(X \geq 5/n=14) = \sum_{X=5}^{14} \binom{14}{X} (.19)^X (.81)^{14-X}$$

which was derived from the data in Appendix K (see Table XXXIII), and looked at the probability of both members of a twin pair

Table XXX Herd 1 Point Biserial Correlations
of Altruism-Egoism with Measures
of Giving and Receiving Grooming

Given	Number of cows	.889	$p < .005$
	Seconds	.776	$p < .005$
Received	Number of cows	-.635	$p < .005$
	Seconds	-.563	$p < .005$

Table XXXI Herd 1 Point Biserial Correlations
between Altruism-Egoism and the
Independent Variables

15 Altruists, 20 Egoists	Breed	-.024	n.s.
	Age	.409	$p < .01$
	Body weight	.066	n.s.
	Milk weight	-.185	n.s.
	Milking order	-.047	n.s.
	Collar colour	-.048	n.s.
14 Altruists,*	Seconds groomed twin	.331	$p < .05$
19 Egoists*	Seconds received from twin	.335	$p < .05$

* singles not included

Table XXXII Herd 1 Altruists*

Cow Ear Tag Number	Age (1974)	Groomed/Received	
		Cows	Seconds
:(861	8	12/2	1880/270
:(862	8	15/7	2720/990
:(989	7	9/4	1440/245
(990	7	6/2	745/ 45
(017	6	6/3	360/125
(018	6	8/3	365/100
108	5	6/2	760/275
:(127	5	9/4	1185/225
:(128	5	8/1	1335/145
+ 133	5	13/3	2065/790
:(201	4	10/2	990/100
:(202	4	16/1	1090/ 55
234	4	13/3	675/ 90
:(307	3	17/0	3250/ 0
:(308	3	14/1	1675/125

* Altruists gave at least 330 seconds in interactions with at least four cows and received back less than $\frac{1}{2}$ of the amount they gave from less than $\frac{1}{2}$ the number of cows they groomed.

! These cows gave at least 900 seconds to at least seven cows and were therefore one or more standard deviations from the mean.

{ Signifies twin pair.

+ Single

Table XXXIII Egoists*

Cow Ear Tag Number	Age (1974)	Groomed/Received	
		Cows	Seconds
±(021	6	2/9	115/1000
(022	6	2/6	35/ 430
029	6	0/4	0/ 415
103	5	0/4	0/ 700
± 109	5	2/7	10/1020
{123	5	0/7	0/ 535
{124	5	0/8	0/ 445
+ 207	4	1/5	15/ 530
{211	4	2/4	105/ 460
(212	4	0/4	0/ 405
221	4	0/4	0/ 380
225	4	2/4	185/ 500
239	4	0/4	0/ 785
302	3	2/5	60/ 415
311	3	2/4	75/ 495
319	3	0/4	0/460
{329	3	2/5	255/1215
{330	3	0/5	0/ 535
{331	3	2/5	20/ 555
{332	3	2/4	115/ 370

* Egoists received at least 330 seconds in interactions with at least four cows and gave back less than $\frac{1}{2}$ of the amount they received to less than $\frac{1}{2}$ the number of cows from which they received grooming.

± These cows received at least 675 seconds from at least six cows and were therefore one or more standard deviations from the mean.

{ Signifies twin pair.

+ Single

appearing in the egoistic group versus the probability of their not both appearing in the egoistic group. Again, a total of 100 cows (50 twin pairs) was used in the analysis (four singles were excluded). This yielded a non-significant result of $p < .11$.

DISCUSSION - THIRD STAGE

The scale of "others" begins with twin pairs giving roughly two-thirds of their grooming time to each other and only one-third to the rest of the herd. This was highly significant for both herds. There was no significant difference noted between the herds. Neither was a significant difference found between Herd 1 and Herd 2 in the proportions that preferred to groom their twin to any other herd member. However, if a one-tailed question had been asked of the data - for example, will increased herd density decrease grooming partner preferences from the more distant "others" to twin - a significance level supporting H_1 would have been reached. Indeed, such reasoning may clarify the difference found between heifers and two year olds in this respect.

Research into the effects of population density and age structures in cows may provide clues as to methods for increasing social integration. It is only due to the fact that identical twin herds were used that such a relationship could be brought to light. Under more usual herd conditions, increased density may simply depress social grooming altogether. In this study only one member of Herd 2 ($N = 40$) did not groom as opposed to 16 in Herd 1 ($N = 104$).

The next step on the scale of "others" involved asking whether or not Herd 1 cows would prefer grooming their own age group to any other age groups. This significant finding led to another step where age groups could be broken down into three groups composed of roughly similar numbers. Here again, in a more accentuated form, a five-point scale emerged which appeared to delineate a spectrum of social distance inversely related to the amount of time social grooming was given to herd

members.

1. Self,
2. Twin,
3. Own age group,
4. Next age group, and
5. Furthest away age group.

Age, the most pervasive variable which correlated with social grooming, also turned out to be significantly related to the preference of grooming a non-twin to twin. A formula which was developed in Chapter V (see p.71) to differentiate altruism from reciprocity and egoism has an inherent weakness in its conception, in that benefit may be returned to the initiator via an alternative modality. The greater the number of possible modalities, the more complex the problem of deciphering the meaning of a given behavioural act. It was thought that the use of domesticated dairy cows would reduce the theoretical options by which benefits could be returned.

Using this formula for differentiation, it was possible to separate out two subgroups, the "altruists" and the "egoists". Altruists were defined as those which gave at least 330 seconds grooming to at least four cows and received back less than half of the amount they gave from less than half the number of cows they groomed. Egoists received at least 330 seconds from at least four cows and gave back less than half of the amount they received to less than half the number of cows from which they received grooming. Tables XXXII and XXXIII, which were drawn out of Appendix K, show the subgroups drawn.

The altruism-egoism dichotomy correlated highly with the measures of grooming given and received, as was expected in that

the dichotomy's structure was based on these measures. Age alone of the independent variables correlated significantly with giving.

The implications of the findings of this chapter suggest that the nutritional hypothesis for social grooming does not hold up, unless, for some reason, the nutritional gains from a twin differ from any gains received from non-twins. Unfortunately, since the nutritional hypothesis demands proof of the null hypothesis, it cannot be disproven. However, despite an extensive search of the literature no proven substances have been cited as being the mineral intake required for social grooming to occur. Two substances suggested for this role have been salt (Hafez, 1969) and vitamin D. Vitamin D₃ (cholecalciferol) is formed in the skin of animals by irradiation of provitamin 7-dehydrocholesterol (Jennings, 1970). In this connection it is widely known that exposure to sufficient summer sunshine makes the giving of the vitamin D to dairy cattle unnecessary (Jones, 1954). The evidence for the tentative conclusion that the nutritional hypothesis can not apply in the case of either salt or vitamin D is based on the following:

- (a) Cows licked more the older they were; also, they were licked more the older they were. Thus older cows both produce more of substance X on their skins and need more of it in their digestive systems.
- (b) The substance would have to be profusely produced on the skin and/or needed only in the minutest quantities as grooming interactions generally lasted less than one and a half minutes per day.
- (c) Cows high on the milking order (cum dominance order) would have to produce more of the substance as they get groomed more often.

A substance to fit these types of requirements has so far not been proposed and this author considers that, on the basis of this, research credulity is being stretched to believe that pro-social behaviour must be so motivated.

Of course, the altruistic behaviour a species exhibits must exist initially within the behavioural repertoire, where it probably serves to benefit the individual directly. Self grooming as an antecedent behaviour makes its appearance in calves where they spend up to 52 minutes a day cleaning themselves with their tongue (Roy, Shillam & Palmer 1955). Later it appears to expand and also become a social behaviour increasing group cohesion.

Another question raised by this study but which is as yet unresolved, is whether or not cows can discern members of other twin pairs as separate "personalities". A closer examination of dominance hierarchies, leadership patterns and milking order may provide future research clues into such recognition factors.

The nature of the herds precluded an exact analysis of genetically programmed or based behaviour because they were composed entirely of identical twins. If we had had a herd composed of fraternal twins as well, we could have used Dobzhansky's (1970) formula for heritability (h):

$$h = \frac{(r_I - r_F)}{(1 - r_F)} \quad (p.87)$$

where r_I is the correlation coefficient between the measurements of a trait observed in members of identical twin pairs and r_F is the coefficient obtained from fraternal twin pairs.

($h = 0$) indicates variations due to
environmental factors, and

($h = 1$) indicates purely genetic factors.

As it was, altruism proved to be identical-twin-linked to a high significance level. Twins enter the Ruskura herd when they are between four and seven days old and stay several years (oldest pair was eleven years old). It would seem that either they bond to each other at a "critical" period or there is something about genetic similarity which stimulates behavioural togetherness (as evidenced by the disproportionate amount of time twins spent grooming each other). A suggestion for workers in animal research which grows out of the frustration of not being able to neatly separate these hypotheses is that in living stock where identical twins are studied for an understanding of genetic variables, a control group of fraternal twins should also be studied.

Altruism (scientific) was distilled from an antecedent behaviour, social grooming. None of the conditions leading to the giving or receiving of grooming were linked to the altruism-egoism dichotomy except age. Neither age alone as a predisposing condition, nor the proposed nutritional hypothesis as a reinforcing event, seem sufficient to remove the behaviour studied from the category altruism (philosophical). The results of this chapter indicate that a pro-social behaviour, in this case social grooming, may form an antecedent or basis for the occurrence of altruistic actions within a herd of cows.

CHAPTER VIII

GENERAL SUMMARY AND CONCLUSIONS

Initially it was thought that the area of amicable responses in animals was not well studied in comparison with aggressive responses. A thorough literature survey shows that this is not fully correct. The early chapters indicate problems of definition and research methodology for the study of altruism. In order to partially resolve the problems of definition altruism was considered to be both a "normal" (in our understanding) and a residual (in our usage) category. The category altruism was then examined from two main vantage points: a philosophical and a scientific. Two definitions having similar criteria were developed covering these aspects. The criteria for altruism were considered to be:

- (a) That it is a social behaviour
- (b) That it is directed towards others
- (c) That benefit is taken to mean increases
in physiological well-being and/or material-
istic comfort.

Altruism (scientific) was defined as purposive activity likely to benefit others more than oneself, whereas altruism (philosophical) was defined as voluntary purposive activity likely to benefit others more than oneself when that activity has not been motivated by reward. According to the circumstances, altruism may be considered to be either a moral principle or a behavioural category or both. Altruism as a behaviour may be investigated scientifically, and be thereby more clearly delineated. As a moral principle implying choice and no reward to the donor,

it belongs to the field of ethics and must be turned over to the philosophers.

No tangible extrinsic rewards should be forthcoming to the individual in his lifetime, if his actions are to be classified as altruistic. Although the literature is unclear about the relationship of altruism to reciprocity it was felt here that in the immediate (life of the individual) form, reciprocal altruism is a contradiction in terms.

In order to differentiate between altruism and reciprocity the following were considered. A carried out beneficial act (B) is unity. The sum total of past interactions with the recipient is represented by (n). Factors which affect the recipient's carrying out towards the original donor a similar act also affect the original donor's expectation (E) of the probability of return for his efforts (B_k). As this approaches zero, so does the original behaviour resemble altruism. As the expectation of return approaches unity so does it resemble reciprocity and, finally, if it exceeds unity it may be considered egoism. Expectations may be said to exist for the initiating animal (x) in relation to each other animal in a given group. In other words, the same actions will be altruistic when directed towards animal (y), but reciprocal when directed towards (z) and egoistic when directed towards (w).

$$E_x(B_k) = \frac{\sum_{i=1}^n \left[\frac{B_{y \rightarrow x}}{B_{x \rightarrow y}} \right]_i}{n}$$

$$\begin{array}{ccc} 0 \leq E_x(B_k) \leq 1 & & 1 < E_x(B_k) \\ \text{Altruism} & \text{Reciprocity} & \text{Egoism} \end{array}$$

Altruism is almost coeval with egoism and certainly almost as old as life itself. It is therefore reasonable to

think of altruism as either a primary reinforcer or as being intrinsically motivating. These considerations led to investigations into several behaviours in the animal world. During an experiment using pheasants it was found that the brightly coloured males make significantly more loud calls than do cryptically coloured females. These calls are considered by some investigators to be warning calls. It is now felt they should be given an egoistic interpretation. Primarily the effect would be that of "freezing" predators while making a get-away, something in the nature of a "war hoop" rather than warning cry, although secondarily it seems to also serve that purpose, due possibly to a rather one-sided selection of the sound stimuli by offspring and used as a signal to take cover. The exclusion of a behaviour from the category altruism was considered to show some of the powers of discrimination to be gained by using the definitions developed in Chapter II.

The nutritional hypothesis, often proposed to explain the motivation for social grooming, was examined in dairy cows. As disproving this requires proof of the null hypothesis, which is impossible, an alternative route seemed to be to show that the existence of a nutritional substance having the characteristics implied by the studies on social grooming was most unlikely. This also meant that a behaviour which had been excluded from altruism (philosophical) because of the hypothesis could at least temporarily be reinstated.

Examination of some of the models for genetic antecedents to altruism was considered an important step leading to greater understanding of the biological bases of altruism. Improvements were made to Hamilton's (1963, 1964) formula

$K > 1/r$, where (K) is the benefit conferred and (r) is the Wright coefficient of relationship. The benefit (B) to the recipient(s) must be greater than the cost (C) to the altruist over the sum of the coefficients of relationship (r) existing between the altruist and the recipient(s). Hamilton's formula would lead us to conclude that altruism may occur with equal probability towards parents and grandparents as towards offspring and grandchildren. To rectify this, a potential genetic contribution factor (G) should be incorporated. Factor (G) would be obtained by dividing the potential genetic contribution of the recipient(s) by that of the altruist. Benefit is considered in relation to the proportion of total potential genetic contribution by the recipient which has been "saved". Cost is measured in the proportion of total potential genetic contribution which is lost to the altruist. The revised formula is:

$$B > \frac{C}{\sum_{i=1}^N r_i G_i}$$

These modifications to Hamilton's formula can account for the preponderance of parental care as opposed to geriatric care in the animal world. It also suggests that older parents may be more altruistically disposed toward offspring than younger parents.

Hamilton's formula initially had been shown to be helpful in interpreting entomological evidence on the establishment and growth of altruistic genes in gene pools once they had "appeared". However, because of the special nature of some of the social Hymenoptera, i.e. reproduction through parthogenesis, and the lack of supportive data from other phyla, the formula had not been fully appreciated. Therefore an examination of

the genetic antecedents of altruistic behaviour in the avian order Passeriformes was undertaken. The hypothesis was that the four classifications of caretaking behaviour would correlate positively with clutch size which was taken to be an index of genetic investment. The significant correlations found in this research support Hamilton's theory.

It was also found that interspecies altruists had the highest clutch averages. As there could be no genetic feedback in such situations unless the behaviour was reciprocal between gene pools, it was suggested that caretaking was developed to such a degree in species with high clutch averages that it would be more susceptible to elicitation with less than optimal stimuli than in species with low clutch averages.

The next investigations involved social behaviours in mammalian groups. A possible critical period was studied in relation to the success rates of ewes in raising twins to weaning. Two groups were studied:

1. Ewes that in their primiparous experience had singles and then the following season had twins, and
2. Ewes that had twins both during the primiparous experience and the subsequent lambing season.

The survival rates of the twins from the second lambing season for both groups were then compared. The non-significant results obtained suggested that, contrary to the initial thinking, it may in fact be maladaptive from the ethological viewpoint for parents to bond to a given number of offspring, especially when that number is dependent upon the apparently low frequency occurrence of multiple births during the primiparous experience.

Social grooming in cows (another abundantly available grazing mammal) was then selected for study, one of the reasons being that the reduced stimulus world of the yard-kept domestic cow would also decrease the number of modalities by which rewards could be returned to the benefactors, and so the formula developed earlier could be applied to differentiate altruists from egoists. It was also here that the nutritional hypothesis could be examined for its relevance in explaining social grooming.

In collating herd parameters of social grooming, it was found that for these cows grooming was related to the milking-grazing cycle. In the heifers studied, a midmorning lull was found, then rather steadily increasing amounts of grooming were given until the evening high at which time observations were broken off due to sunset and decreased visibility. Herd members gave approximately one minute a day social grooming to their respective twins and approximately half that amount of time to the rest of the herd. It is quite clear that the cows were not dispensing grooming randomly. This reinforces the idea that one may use social grooming as an index of social cohesion.

Only age and body weight in Herd 1 correlated significantly with grooming other cows, whereas age, body weight, milk weight and milking order all correlated significantly with the amount of social grooming received. Milking order correlated significantly not only with the amount of grooming received from non-twins, but also with that exchanged between twins. This suggests an evolutionary movement towards increasing the survival margin of those most likely to survive. This in turn could be based upon a conservation of energy principle in order for "Life" to continue most effectively.

Grooming preferences in cows were found to fall into a five point ordinal scale:

- | | | |
|-----------------------------|---|----------|
| 1. Self, |) | egoism |
| 2. Twin, |) | |
| 3. Own age group, |) | |
| 4. Next age group, and |) | altruism |
| 5. Furthest away age group) |) | |

Age was significantly related to cows' increased preference for grooming other cows rather than their twins and in fact proved to be the most pervasive variable correlated with non-twin social grooming. Age was the only variable which correlated significantly with the altruist-egoist dichotomy. These results indicate that a pro-social behaviour - social grooming - may form the basis for the occurrence of altruistic actions within a herd of cows.

The theoretical contributions of this thesis included developing a pair of interacting definitions of altruism which can be used as a basis for unifying and interpreting research findings in the area of pro-social behaviour, and, strengthening the case for altruism to be genetically fixed in populations. It was also considered important to gather a list of relevant studies showing the range of altruism in the animal world as this had been missed by Krebs (1970) in his rather substantial review of the research literature on altruism. Another contribution dealt with the delineation of altruism as a concept from reciprocity and egoism. Research findings were then presented in connection with each of these theoretical aspects of altruism.

As this thesis investigated altruism in animal populations generally, and in domestic animals specifically, the interest in these studies is likely to cover a large range. Some will be

interested in the evolutionary-genetic aspects of "fixing" altruistic behaviours in populations, whereas, philosophers among the social scientists may wish to further develop the discussions surrounding the twelve issues presented in Chapter II.

A question of some interest to Comparative Psychologists deals with the possibility of a critical period as an explanation for the extremely disproportionate amount of time spent grooming by a cow to its identical twin as opposed to any other cow in the herd.

Animal research centres will be interested in the studies on social grooming for many reasons. Where, for example, should anti-bloat solutions be painted on cows to maximize, through social grooming, its ingestion. They may also be interested in the possibility of the control, through social grooming, of diseases carried by ticks and fleas in live-stock, or the development of another possibly more effective index for measuring herd "harmony" or stress for pragmatic use in domestic yarding conditions. Research into the correlations found between grooming and milk production may suggest that a change be made in culling practices which at the present time are based on an individual cow's milk production. These practices may result in a drop in the herd milk production if the cows culled were good groomers which in turn helped to maintain herd "harmony".

One question raised but not resolved in this study of identical twin cows was the ability of cows to differentiate between members of other twin pairs, possibly a rather confounding issue which may effectively reduce subject numbers by half depending on the research hypothesis. In other words, whereas an observer may discriminate 104 different cow ear tags and thus

individuals, any given cow, while theoretically able to "see" 103 other herd members, may in fact only be able to perceive and therefore interact with 52 "individuals".

Density as a variable will, it is thought, be inversely related to the amount of social grooming given as greater numbers will probably lead to greater competition for the advantages conferred by a limited environment.

Other suggestions for additional research relate to the examination of "warning calls" in other dimorphic avian species, particularly where females rather than males are more likely to be the objects of greater predation. With increased ornithological information a more precise study of the relation between caretaking and clutch sizes may be obtained using species as the unit of measure rather than using the coarser unit of families. Then moving from Avian orders to Mammalian, a list may be developed of altruistic behaviours against which various breeding patterns can be checked and theoretically related to the genetic coefficients of relationship existing within the plausible reproductive gene pool (e.g. per thirty individuals).

The five point grooming hierarchy found in Chapter VII whereby a cow grooms self most, then twin and the furthest away age group least, would suggest a genetic explanation similar to the one discussed at the end of Chapter V. However, due to the nature of domestic herds it is difficult if not impossible to tease out the environmental production of age "classes" from the genetic feelings for such "classes". Research with feral herds as well as other wild social groups may bear out the reasoning developed in this connection.

APPENDIX A

The Original French of Comte's Statement on the Biological Roots of Altruism

"Cette coordination partielle prépare graduellement la noble terminaison de la série affective par l'ensemble des penchants sociaux ou altruistes. L'accroissement de dignité et le décroissement d'énergie, qui dirigent toute ma classification morale, s'y manifestent autant que possible. Mais leur infériorité de puissance trouve une certaine compensation dans leur aptitude naturelle à un essor plus complet, puisque tous les êtres peuvent y participer à la fois sans aucun conflit, et même en retirant de ce concours un surcroît de satisfaction. Quoique cette propriété caractéristique ne doive se réaliser pleinement que chez notre espèce, comme je l'ai expliqué, son ébauche appartient réellement à la biologie, qui peut seule en préparer convenablement l'étude sociologique. Il est certain, en effet, que ces nobles penchants sont communs à beaucoup de races animales. Outre qu'ils y offrent quelquefois plus d'intensité que dans l'homme, ils s'y trouvent mieux dégagés des résultats sociaux et des influences mentales. C'est là surtout que leur nature devient nettement irrécusable, de manière à dissiper toute incertitude. Notre faible raison dut d'abord recourir à l'observation des animaux pour repousser systématiquement les funestes sophismes de la théologie et de l'ontologie contre l'existence propre des instincts sympathiques, encore méconnus par les esprits qui rejettent une telle autorité.

La principale tendance de ces penchants supérieurs consiste à changer la constitution fondamentale de l'unité vitale. Dans chaque existence complexe, l'harmonie générale ne peut résulter que d'une suffisante subordination de toute les impulsions spontanées à un seul moteur prépondérant. Or, ce penchant dominateur est égoïste ou altruiste: d'où dérive ma distinction antérieure entre les deux modes que comporte le consensus vital. Non-seulement le second régime surpasse le premier comme seul compatible avec l'état social. Mais, en outre, il constitue, même chez l'individu, une unité plus complète, plus facile, et plus durable. Les instincts inférieurs dirigent la conduite d'après des motifs purement internes, dont la multiplicité et la variation ne lui permettent aucune marche fixe, ni même aucun caractère habituel, sauf pendant les exigences périodiques des principaux appétits. Il faut que l'être se subordonne à une existence extérieure afin d'y trouver la source de sa propre stabilité. Or, cette condition ne peut se réaliser assez que sous l'empire des penchants qui disposent chacun à vivre surtout pour autrui. Tout individu, homme ou animal, qui, n'aimant rien au dehors, ne vit réellement que pour lui-même, se trouve, par cela seul, habituellement condamné à une malheureuse alternative d'ignoble torpeur et d'agitation déréglée. Le principal progrès

de chaque être vivant doit, sans doute, consister à perfectionner ce consensus universel où réside l'attribut essentiel de la vitalité. C'est pourquoi le bonheur et le mérite, même personnels, dépendent partout d'un juste ascendant des instincts sympathiques. Vivre pour autrui, devient ainsi le résumé naturel de toute la morale positive, dont la biologie doit déjà ébaucher le principe universel, mieux dégagé alors des diverses influences perturbatrices."

(Comte, 1851, p.699)

APPENDIX B

The Good Samaritan

And, behold, a certain lawyer stood up, and tempted him, saying, "Master, what shall I do to inherit eternal life?" He said unto him, "What is written in the law? how readest thou?" And he answering said, "Thou shalt love the Lord thy God with all thy heart, and with all thy soul, and with all thy strength, and with all thy mind; and thy neighbour as thyself". And he said unto him, "Thou hast answered right: this do, and thou shalt live". But he, willing to justify himself, said unto Jesus, "And who is my neighbour?" And Jesus answering said, "A certain man went down from Jerusalem to Jericho, and fell among thieves, which stripped him of his raiment, and wounded him, and departed leaving him half dead. And by chance there came down a certain priest that way: and when he saw him, he passed by on the other side. And likewise a Levite, when he was at the place, came and looked on him, and passed by on the other side. But a certain Samaritan, as he journeyed, came where he was: and when he saw him, he had compassion on him, and went to him and bound up his wounds, pouring in oil and wine, and set him on his own beast, and brought him to an inn, and took care of him. And on the morrow when he departed, he took out two pence, and gave them to the host, and said unto him, 'Take care of him; and whatsoever thou spendest more, when I come again, I will repay thee'. Which now of these three, thinkest thou, was neighbour unto him that fell among the thieves?" And he said, "He that shewed mercy on him". Then said Jesus unto him, "Go, and do thou likewise".

The Gospel According to Luke 10 : 25-37
The Reader's Bible (1951 p.99)

APPENDIX C

Summary Statements Used in the Decision- Making for Compiling Table IV

1. Icteridae - Euphagus cyanocephalus

"... in some species the male may assist in the feeding and in one, Brewer's Blackbird, has been observed systematically feeding the young in two adjacent nests" (Bent, 1958, p.374).

2. Acanthisittidae - Acanthisitta chloris

"According to M.F. Soper the young of the first brood sometimes assist in feeding second, and Soper's observations show that this species is frequently polygamous." (Falla, Sibson and Turbott, 1966, p.192)

3. Sylviidae - Mohoua albicilla

"Quartets combining to incubate and feed young were noted by Guthrie-Smith in his investigation of the breeding habits of this species on Little Barrier Island and in Hawke's Bay; he was doubtful whether these comprised two pairs, or a male and three females, but according to Soper's recent observations the male Yellowhead (see below) is commonly polygamous. It seems likely that the latter explanation is the correct one. Guthrie-Smith found four adults present at a majority of the nests examined, but at some there was only a single pair." (Falla, Sibson and Turbott, 1966, p. 209)

4. Sylviidae - Mohoua ochrocephala

"Soper has shown that polygamy is of regular occurrence in this species. He was able to observe the breeding cycle closely at five nests and found that three birds (a male and two females) were associated at two of the nests, the females being of different ages and thus distinguishable by the degree of shading on the nape. The number of eggs in these nests was three or four, the same as in nests with one female; both females shared the work of incubation." (Falla, Sibson and Turbott, 1966, p.210)

5. Neosittidae - Neositta pileata

"Several individuals (as many as eight have been seen) may assist in nest building and in feeding the young, but normally only one female lays in a nest. In one case noted two females used the same nest, laying a total of seven eggs in it, and both birds sat together, side by side." (Hindwood, 1966, p.84)

6. Neosittidae - Neositta chrysoptera

"They are always in groups of six to eight birds and more than two birds have been seen to feed young in the nest." (Firth, 1969, p.378)

7. Campephagidae - Pteropodocys maxima

"It may be seen singly or in pairs, but more often in small parties of up to six or so birds, sometimes more, at most seasons. Even when breeding, several birds may associate. In one instance three adults were seen to bring food to the same nestlings. In another case, two nests, both containing young birds, were seen on the same branch within 3 feet of each other, and five adults were tending the chicks.

The Ground Cuckoo-Shrike is an aberrant member of its group, with specialized feeding habits and some unusual nesting and social practices. Frequently three or four of the birds will perch close together on a limb, with feathers fluffed out, meanwhile indulging in mutual preening." (Hindwood, 1966, p.58)

8. Malurinae - Malurus melanotis

"A male and two females were seen feeding the same nestlings, while an immature male of the party kept the nest clean." (Hindwood, 1966, p.82)

9. Grallinidae - Struthidea cinerea

"...; it is almost certain that several birds help to build the nest, while from the number of eggs found there, more than one hen seems to use it to lay her eggs in." (Gould and Rutgers, 1967, p.294)

10. Artamidae - Artamus insignis

"They hunt in flocks, nest in colonies and assist each other in rearing the young." (Gould and Rutgers, 1970, p.245)

APPENDIX D

SERENDIPITOUS FINDINGS

While working over the data in Chapter VI an unexpected sex distribution came to light. The evolutionist's problem in handling sex ratios has several times been connected to discussions in the literature on the possibilities for altruism to be genetically fixed in populations (Kalmus, 1969). The sex ratio is derived by dividing the total number of males by the total number of both sexes found within any given population. The case for sexual reproduction being an overall advantage is made by Williams and Mitton (1973). Uneven sex ratios can be the result of several factors, in either or both parents. For example, in humans blood group 'B' mothers tend to have high sex ratios (more males than females) among their 'B' offspring, whereas blood group 'A' mothers have low sex ratios among their 'A' offspring. One explanation postulates selective elimination of fetuses based on known immunological phenomena regarding the passage of antibodies through the placenta. It has also been postulated that differential viability and motility of sperm may account for different sex ratios. The selective agents suggested have to do with various pH concentrations in the venous blood, arterial blood and along the entrance to the cervix. Lower pH levels increase the likelihood of the more mobile Y cell sperm to survive and impregnate (Osler, 1971; Weir, 1966). In farm livestock, significant deviations in sex ratios may occur within the same species when different breeds, strains, or families are considered: "Jersey cattle averaged 52% males at birth, Guernseys 44%; most breeds of sheep show an excess of females." (Weir, 1966, p.421).

However, a study by Napier and Mullaney (1974) found no evidence that breed or strain of sheep affects sex ratio (see Table XXXIV). Possibly their study was too limited in scope (only two breeds compared).

Table XXXIV Sex ratio and Lamb numbers in Merino and Corriedale sheep. (After Napier and Mullaney 1974)

	At Birth		
	Merino	Corriedale	Both Breeds
Total number of lambs	7840	4122	11962
Sex ratio of all lambs	.513	.500	.508

EXPERIMENT

The hypothesis here stated that a difference in sex ratios exists between Romney and hybrid Border Leicester x Romney lines of sheep and their backcrosses.

Subjects and Procedure

The flocks from which the imprinting study drew its sample, i.e. 7,670 male and female lambs, formed the experimental group. Sex was established from birth rather than weaning records. As the various crosses were raised more or less at the same time during 1959-1967, they form their own controls against such random variables as weather, change of personnel and food supply. Each of the six genetic groups was compared with the group immediately following using a chi square test and Yates correction for continuity. The first two control groups were then combined, the straight crosses of the F_1 and F_2 generations were combined and the so-called F_3 and F_4 generations, both of which used backcrossed

rams from the F_1 group, were combined. These three groups were also chi square tested using Yates correction for continuity.

Discussion

"Frequently hybrids show anomalous sex ratios; an excess of females is commonly encountered when parents belong to different species" (Weir, 1966, p.421). The significant results (see Table XXXV) obtained suggest that for some reason as yet unknown backcrossing may counteract the swing in sex ratio favouring females over males. This finding, while somewhat at a tangent to the main line of investigation, was considered worth recording for future reference.

Table XXXV. χ^2 Analyses of Sex Ratios in Consecutive Genetic Crossings of Sheep

Parents			Offspring				
			Male	Sex ratio	Female		
Romney experimental flock			590	.506	577	$\chi^2 = .9089$ df=1, n.s.	} $\chi^2 = 2.8908$ df=1, n.s. (p < .10)
Romney control flock			693	.486	733	$\chi^2 = .5953$ df=1, n.s.	
F_1							
Border Leicester		x Romney	604	.470	680	$\chi^2 = .0009$ df=1, n.s.	} $\chi^2 = 10.3962$ df=1 p < .01
Ewe(F_1)	F_2	Ram(F_1)					
(BLxR)		x (BLxR)	808	.470	910	$\chi^2 = 9.5703$ df=1, p < .01	
Ewe(F_2)	F_3	Ram(F_1)					} $\chi^2 = .6685$ df=1, n.s.
[(BLxR)x(BLxR)]		x (BLxR)	746	.526	671		
Ewe(F_3)	F_4	Ram(F_1)					
[(BLxR)x(BLxR)]		x (BLxR)	333	.506	325		
Total Flock			3774	.492	3896		

Appendix E Herd 1 Number of Grooming Interactions

Time of day	12 Feb.	13 Feb.	14 Feb.	15 Feb.	16 Feb.	Total
0700-0759	3	5	0	0	3	11
0800-0859	0	29	0	0	10	34
0900-0959	7	0	16	10	17	50
1000-1059	4	9	5	4	6	28
1100-1159	3	3	3	3	4	16
1200-1259	4	3	7	1	1	16
1300-1359	4	1	8	1	12	26
1400-1459	0	1	1	14	7	23
1500-1629*	0	0	0	0	0	0
1630-1729	0	0	0	1	0	1
1730-1829	7	23	8	8	11	57
1830-1929	4	9	2	14	28	57
Total	36	78	50	56	99	320

* Milking time

Appendix F Herd 2 Number of Grooming Interactions

Time of day	12 Feb.	13 Feb.	14 Feb.	15 Feb.	16 Feb.	Total
0700-0759	0	2	1	4	10	17
0800-0859	0	0	1	0	3	4
0900-0959	0	0	1	0	1	2
1000-1059	2	0	2	0	1	5
1100-1159	4	1	4	3	7	19
1200-1259	1	4	1	6	0	12
1300-1359	1	3	0	10	1	15
1400-1459	4	1	4	1	0	10
1500-1629*	1	3	3	6	14	27
1630-1729	3	0	6	5	6	20
1730-1829	10	0	5	1	7	23
1830-1929	5	6	8	16	7	42
Total	31	20	36	52	57	196

* This time division was used to conform with the period occupied by milking in Appendix E

Appendix G Herd 1 Grooming Seconds

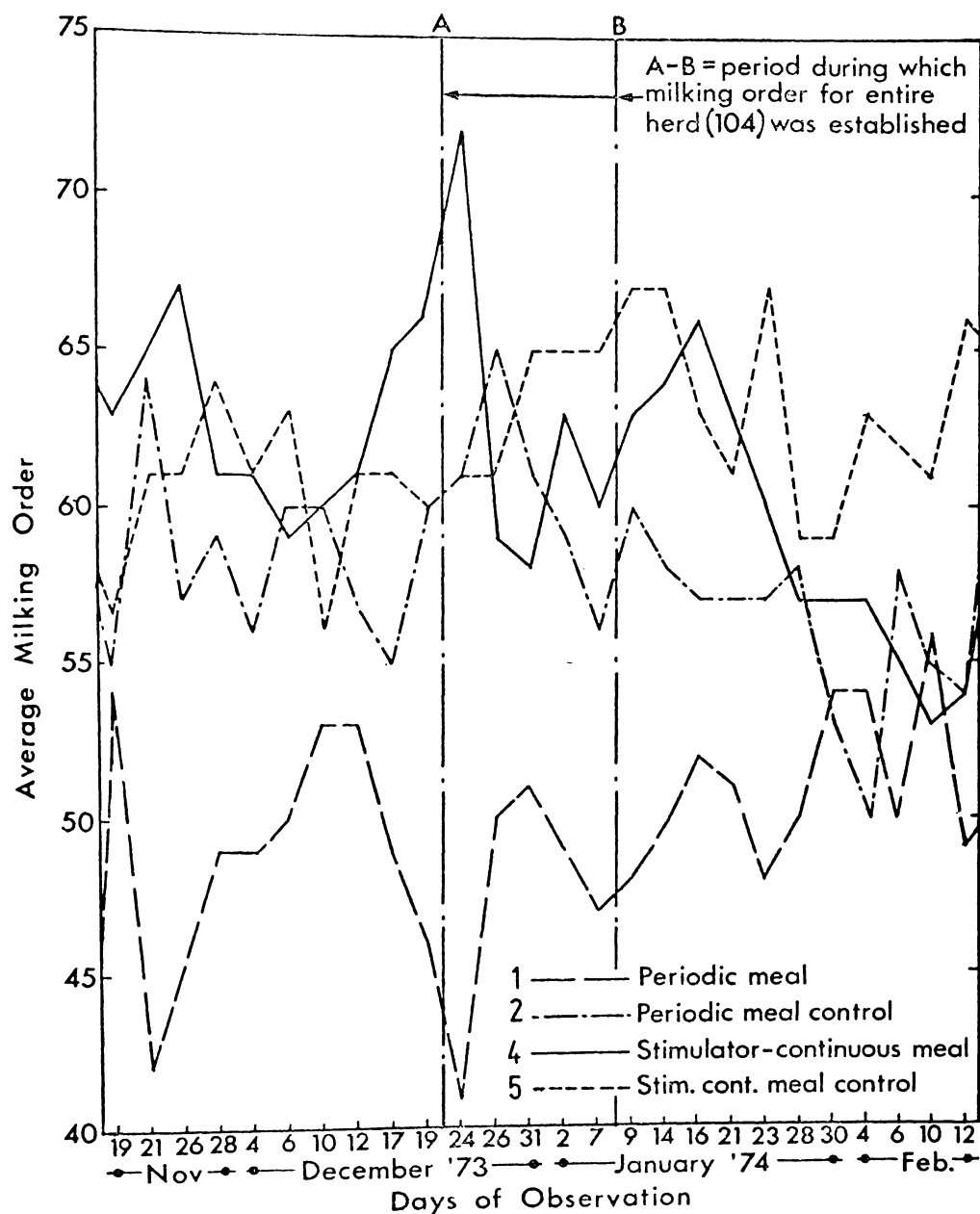
Time of day	12 Feb.	13 Feb.	14 Feb.	15 Feb.	16 Feb.	Total
0700-0759	65	675	0	0	105	845
0800-0859	0	2,930	0	0	2,400	5,330
0900-0959	1,460	0	2,725	1,400	1,820	7,405
1000-1059	225	1,030	685	715	795	3,450
1100-1159	100	145	170	415	905	1,735
1200-1259	145	290	875	240	330	1,880
1300-1359	1,495	495	810	50	2,800	5,650
1400-1459	0	40	110	2,175	2,120	4,445
1500-1629*	0	0	5	0	0	5
1630-1729	0	0	0	10	0	10
1730-1829	1,035	2,510	440	485	1,445	5,915
1830-1929	585	945	190	1,375	3,120	6,215
Total	5,110	9,060	6,010	6,865	15,840	42,885

* Milking time

Appendix H Herd 2 Grooming Seconds

Time of day	12 Feb.	13 Feb.	14 Feb.	15 Feb.	16 Feb.	Total
0700-0759	0	10	50	935	1,270	2,265
0800-0859	0	0	40	0	40	80
0900-0959	0	0	15	0	85	100
1000-1059	55	0	70	0	10	135
1100-1159	65	5	210	495	445	1,220
1200-1259	35	290	170	405	0	900
1300-1359	155	105	0	1,295	45	1,600
1400-1459	305	345	150	10	0	810
1500-1629*	475	655	345	570	2,205	4,250
1630-1729	390	0	545	345	425	1,705
1730-1829	860	0	605	40	625	2,130
1830-1929	105	690	810	1,400	555	3,560
Total	2,445	2,100	3,010	5,495	5,705	18,755

*This time division was used to conform with the period occupied by milking in Appendix G



Appendix I Graph showing results of reinforcement schedules on milking order.

APPENDIX J

Herd 1 Distribution of Choices Over the
Various Age Groups for 4+ Age Group (excluding
interactions occurring within twin pairs)

Ear Tag No.	No. of Cows			Seconds		
	Same Age Group	Younger Group	Youngest Group	Same Age Group	Younger Group	Youngest Group
4117	5	2	1	780	270	125
4118	2	0	0	135	0	0
861	6	3	3	905	785	190
862	8	4	3	2,180	475	65
921	3	0	0	160	0	0
922	2	2	0	200	30	0
937	0	0	0	0	0	0
938	1	0	0	10	0	0
989	7	2	0	920	520	0
990	4	2	0	430	315	0
017	6	0	0	360	0	0
018	5	1	2	235	70	60
021	0	2	0	0	115	0
022	2	0	0	35	0	0
029	0	0	0	0	0	0
030	0	0	0	0	0	0
031	6	2	0	330	310	0
032	4	1	1	455	340	10
103	0	0	0	0	0	0
104	0	0	0	0	0	0
105	2	0	0	20	0	0
106	0	0	0	0	0	0
107	3	1	1	280	15	65
108	4	2	0	575	185	0
109	2	0	0	10	0	0
110	3	1	0	270	60	0
111	2	0	0	150	0	0
112	1	0	0	15	0	0
115	6	6	3	500	410	535
116	4	1	4	335	80	625
117	1	0	0	150	0	0
118	1	0	0	60	0	0
123	0	0	0	0	0	0
124	0	0	0	0	0	0
127	3	4	2	110	1,040	35
128	4	3	1	485	830	20
133*	11	1	1	1,955	5	105
Total	108	40	22	12,050	5,855	1,835

* Single

APPENDIX J (contd)

Herd 1 Distribution of Choices Over
the Various Age Groups for 3 Year Olds

Ear Tag No.	No. of Cows			Seconds		
	Same Age Group	Older Group	Younger Group	Same Age Group	Older Group	300's
201	5	4	1	440	530	20
202	4	10	2	330	580	180
203	2	0	3	30	0	175
204	0	0	0	0	0	0
205	0	0	0	0	0	0
206	0	0	0	0	0	0
207*/	0	1	0	0	15	0
211/	0	2	0	0	105	0
212/	0	0	0	0	0	0
213	1	1	1	70	95	10
214	1	0	0	20	0	0
215	0	0	0	0	0	0
216	0	0	0	0	0	0
221/	0	0	0	0	0	0
222/	1	1	3	90	30	120
223	0	1	0	0	5	0
224	0	0	1	0	0	30
225	1	1	0	20	165	0
226	0	0	0	0	0	0
227	3	6	2	590	750	310
228	3	2	1	115	210	15
229	0	0	0	0	0	0
230	0	1	0	0	40	0
231	0	0	0	0	0	0
232	0	1	0	0	70	0
233/	3	5	2	190	210	60
234/	6	4	3	155	295	225
235	1	1	0	15	85	0
236	1	0	0	180	0	0
237	3	0	0	195	0	0
238	1	2	0	155	155	0
239/	0	0	0	0	0	0
240/	0	2	0	0	15	0
259	2	1	1	85	30	65
260	0	1	0	0	65	0
Total	38	47	20	2,680	3,450	1,180

* Single
/ Nose rings

APPENDIX J (contd.)

Herd 1 Distribution of Choices Over
the Various Age Groups for 2 Year Olds

Ear Tag No.	No. of Cows			Seconds		
	Same Age Group	Older Age Group	Oldest Age Group	Same Age Group	Older Age Group	Oldest Age Group
301/	1	2	0	55	100	0
302/	1	0	1	35	0	25
303	0	0	0	0	0	0
304	0	1	0	0	30	0
305	6	1	3	135	15	145
306	1	3	2	25	90	155
307	11	4	2	2,065	945	240
308	8	3	3	1,330	185	160
309	0	0	0	0	0	0
310	0	0	0	0	0	0
311	1	1	0	20	55	0
312	0	0	0	0	0	0
313*	0	0	0	0	0	0
315	0	0	0	0	0	0
316	0	0	0	0	0	0
317	0	1	1	0	30	60
318	0	0	0	0	0	0
319/	0	0	0	0	0	0
320/	0	0	0	0	0	0
321	0	0	0	0	0	0
322	0	0	0	0	0	0
323/	0	0	0	0	0	0
324/	2	0	0	285	0	0
325	0	0	0	0	0	0
326	0	0	0	0	0	0
328*	0	0	0	0	0	0
329	1	1	0	15	240	0
330	0	0	0	0	0	0
331	0	0	2	0	0	20
332	2	0	0	115	0	0
391/	1	1	0	230	105	0
392/	1	0	0	160	0	0
Total	36	18	14	4,470	1,795	805

* Singles
/ Nose rings

APPENDIX K

Herd 1 Proportions and Amounts
of Grooming to Receiving (excluding
interactions occurring within twin pairs)

Cow Ear Tag No.	Age (1973)	Groomed/Received	
		No. Cows	Seconds
4117	11	8/10	1175/2240
4118	11	2/ 5	135/ 340
!! 861	7	12/ 2	1880/ 270
!! 862	7	15/ 7	2720/ 990
921	6	3/ 4	160/ 440
922	6	4/ 3	230/ 335
937	6	0/ 1	0/ 60
938	6	1/ 0	10/ 0
!! 989	6	9/ 4	1440/ 245
!! 990	6	6/ 2	745/ 45
! 017	5	6/ 3	360/ 125
! 018	5	8/ 3	365/ 100
II 021	5	2/ 9	115/1000
II 022	5	2/ 6	35/ 430
II 029	5	0/ 4	0/ 415
030	5	0/ 3	0/ 105
031	5	8/ 8	640/ 550
032	5	6/ 8	805/ 750
II 103	4	0/ 4	0/ 700
104	4	0/ 1	0/ 180
105	4	2/ 5	20/ 240
106	4	0/ 5	0/ 265
107	4	5/ 2	360/ 565
! 108	4	6/ 2	760/ 275
II 109	4	2/ 7	10/1020
110	4	4/ 7	335/ 755
111	4	2/ 3	150/ 145
112	4	1/ 6	15/ 230
115	4	15/ 8	1445/ 190
116	4	9/ 7	1040/ 420
117	4	1/ 5	230/ 450
118	4	1/ 2	60/ 300
II 123	4	0/ 7	0/ 535
II 124	4	0/ 8	0/ 445
! 127	4	9/ 4	1185/ 225
!! 128	4	8/ 1	1335/ 145
!! 133*	4	13/ 3	2065/ 790

cont. next page

Appendix K cont.

Cow Ear Tag No.	Age (1973)	Groomed/Received	
		No. Cows	Seconds
!! !! 201	3	10/ 2	990/ 100
!! 202	3	16/ 1	1090/ 55
203	3	5/ 4	205/1000
204	3	0/ 1	0/ 130
205	3	0/ 0	0/ 0
206	3	0/ 0	0/ 0
± 207*	3	1/ 5	15/ 530
± 211	3	2/ 4	105/ 460
± 212	3	0/ 4	0/ 405
213	3	3/ 2	175/ 240
214	3	1/ 2	20/ 75
215	3	0/ 2	0/ 180
216	3	0/ 0	0/ 0
± 221	3	0/ 4	0/ 380
222	3	5/ 0	240/ 0
223	3	1/ 0	5/ 0
224	3	1/ 3	30/ 230
± 225	3	2/ 4	185/ 500
226	3	0/ 2	0/ 80
227	3	11/ 8	1650/ 580
228	3	6/ 11	340/ 835
229	3	0/ 2	0/ 30
230	3	1/ 2	40/ 40
231	3	0/ 3	0/ 625
232	3	1/ 5	70/ 215
233	3	10/ 3	460/ 275
! 234	3	13/ 3	675/ 90
235	3	2/ 1	100/ 40
236	3	1/ 0	180/ 0
237	3	3/ 3	195/ 250
238	3	3/ 0	310/ 0
± 239	3	0/ 4	0/ 785
240	3	2/ 3	15/ 710
259	3	4/ 5	180/ 545
260	3	1/ 3	65/ 940
301	2	3/ 3	135/ 295
± 302	2	2/ 5	60/ 415
303	2	0/ 1	0/ 150
304	2	1/ 2	30/ 40
305	2	10/ 0	205/ 0
306	2	6/ 2	270/ 165

cont. next page

Appendix K cont.

Cow Ear Tag No.	Age (1973)	Groomed/Received	
		No. Cows	Seconds
!! 307	2	17/ 0	3250/ 0
!! 308	2	14/ 1	1675/ 125
309	2	0/ 2	0/ 165
310	2	0/ 3	0/ 195
± 311	2	2/ 4	75/ 495
312	2	0/ 1	0/ 0
313*	2	0/ 2	0/ 310
315	2	0/ 3	0/ 750
316	2	0/ 2	0/ 345
317	2	2/ 2	90/ 130
318	2	0/ 5	0/ 100
± 319	2	0/ 4	0/ 460
320	2	0/ 1	0/ 15
321	2	0/ 1	0/ 50
322	2	0/ 0	0/ 0
323	2	0/ 4	0/ 125
324	2	2/ 1	285/ 100
325	2	0/ 2	0/ 115
326	2	0/ 3	0/ 70
328*	2	0/ 5	0/ 140
± 329	2	2/ 5	255/ 1215
±± 330	2	0/ 5	0/ 535
±± 331	2	2/ 5	20/ 555
± 332	2	2/ 4	115/ 370
391	2	2/ 2	335/ 170
392	2	1/ 0	160/ 0

! Altruists - gave at least 330 seconds in interactions with at least four cows and received back less than $\frac{1}{2}$ from less than $\frac{1}{2}$ of the cows

!! These cows gave at least 900 seconds to at least seven cows and were therefore one or more standard deviations from the mean

± Egoists - received at least 330 seconds in interactions with at least four cows and gave back less than $\frac{1}{2}$ to less than $\frac{1}{2}$ of the cows

±± These cows received at least 675 seconds from at least six cows and were therefore one or more standard deviations from the mean

* Singles

APPENDIX L

Herd 2 Proportions and Amounts
of Grooming to Receiving

Ear Tag No.	Groomed/Received	
	No. Cows	Seconds
401	0/4	0/220
402	3/3	85/ 35
403	1/4	65/115
404	6/4	315/215
405	4/1	260/ 65
406	2/2	90/140
407	7/1	315/ 95
408	6/1	590/ 40
409	2/3	20/ 90
410	5/5	135/230
411	1/5	5/310
412	0/2	0/ 45
413	5/1	540/ 0
414	9/5	625/265
415	2/3	15/360
416	2/5	125/890
417	2/5	30/365
418	1/5	35/250
419	6/9	755/560
420	3/5	70/395
421	1/5	175/285
422	0/1	0/ 80
423	3/2	275/ 75
424	1/1	50/ 70
425	3/3	230/ 95
426	1/1	60/125
427	5/0	395/ 0
428	4/3	230/ 50
429	1/1	15/ 10
430	0/1	0/ 50
431	3/2	160/410
432	4/3	215/270
433	3/4	240/165
434	5/1	275/ 60
437	2/1	130/ 10
438	8/3	1035/ 65
441	0/3	0/210
442	1/5	10/895
497	2/1	70/ 10
498	1/1	15/ 40

APPENDIX M

Dairy I Culling Criteria
for the 1974 season

No.	Age (1974)	Breed	Reason for Disposal
(4117	12	J	(Large difference in milk production.
(4118	12	J	
(861	8	J	(Large difference in due calving date.
(862	8	J	
(017	6	J	Empty (not pregnant). Twin empty.
(018	6	J	
(021	6	F	Empty.
(022	6	F	Twin empty.
(029	6	J	(Large difference in milk production.
(030	6	J	
(031	6	JxF	(Large difference in milk production.
(032	6	JxF	
(105	5	J	(Large difference in due calving date. Also poor producers.
(106	5	J	
(109	5	J	(Large difference in milk production possibly due to mastitis.
(110	5	J	
(123	5	J	Twin empty.
(124	5	J	Empty.
(201	4	3/4F	Twin empty.
(202	4	3/4F	Empty.
(203	4	JxA	Empty.
(204	4	JxA	Twin empty.
(213	4	J	Twin empty.
(214	4	J	Empty (Acute Metritis*).
(227	4	J	Empty.
(228	4	J	Twin empty.
(237	4	J	(Large difference in due calving date.
(238	4	J	
(303	3	AxJ	(Large difference in milk production and calving date.
(304	3	AxJ	
(313	3	J	Empty.
(314	3	J	Empty (never been pregnant).
(331	3	J	Empty.
(332	3	J	Twin empty.
(401	2	JxF	Twin empty.
(402	2	JxF	Empty.
(323	3	J	(Low milk production.
(324	3	J	

* Inflammation of uterus

APPENDIX N

Sample Page From Collation Notebooks

No. 989
6 years

Jersey
Medium coat colour

Red Collar
328 kilos

Initiated Grooming				Received Grooming			
Date	No.	Min.	Sec.	Date	No.	Min.	Sec.
29.1.74	123		55	10.2.74	990		05
10.2.74	990		10	11.2.74	201		50

13.2.74	017		30	13.2.74	228	1	00
13.2.74	032	4	00	15.2.74	921		15
13.2.74	228	3	25	15.2.74	862	2	00
14.2.74	922		45				
15.2.74	203	5	15				
15.2.74	921	3	50				
15.2.74	031		30				
15.2.74	862	4	50				

----- Intensive observation period
(12-16 February) begins

APPENDIX O

Summary Statistics of Dairy Herds

Variable	Herd 1 (104 cows)			Standard Deviation
	Low	High	Average	
Age (years)	2	11	3.43	1.64
Milking order	1.4	103.2	53.08	27.10
Average milk weight (kilos)*	28.71	101.97	59.53	13.81
Average body weight (kilos)	253.79	482.29	349.46	47
Gave to No. of non-twin others	0	17	3.30	4.33
Received from No. of non-twin others	0	11	3.31	2.43
Seconds given to non-twin others	0	3250	329	596
Seconds received from non-twin others	0	2240	329	342
Seconds given to twin	0	4090	439	599
Seconds received from twin	0	4090	439	599
Variable	Herd 2 (40 heifers)			Standard Deviation
	Low	High	Average	
Average body weight (kilos)	214.40	382.10	290.28	39.74
Gave to No. of non-twin others	0	9	2.88	2.32
Received from No. of non-twin others	0	9	2.85	1.93
Seconds given to non-twin others	0	1035	190	235
Seconds received from non-twin others	0	895	192	211
Seconds given to twin	0	1390	281	345
Seconds received from twin	0	1390	281	345

* Average per week over the observational period

APPENDIX PHerd Breed Composition According
to Dairy I Records

Breed No.	Breed Composition	Herd 1 (cows)	Herd 2 (heifers)
-	Ayrshire x Jerseys	2	0
-	(AxJ) x J	2	0
0	Jerseys	58	8
2	(JxF) x J	0	2
4	Jersey x Friesians	32	18
6	(JxF) x F	6	4
7	(JxF) x F x F	1	0
8	Friesians	3	8
Total		104	40

Appendix Q Herd 1 (104 cows) Intercorrelations between Giving
and Receiving, the Dependent Variables

	Gave No. of Cows	Gave Seconds	Gave Twin*	Received Twin*	Received No. Cows	Received Seconds
Gave No. Cows	X	.967	.289	.154	.183	.182
Gave Seconds	.967	X	.315	.175	.152	.161
Gave Twin*	.289	.315	X	.659	-.120	-.138
Received Twin*	.154	.175	.659	X	-.092	-.198
Received No. Cows	.183	.152	-.120	-.092	X	.777
Received Seconds	.182	.161	-.138	-.198	.777	X

* 100 cows four singles removed.

Appendix Q (contd) Herd 2 (40 heifers) Intercorrelations between Giving
and Receiving, the Dependent Variables

	Gave No. Cows	Gave Seconds	Gave Twin	Received Twin	Received No. Cows	Received Seconds
Gave No. Cows	X	.884	.293	.111	.044	.036
Gave Seconds	.884	X	.309	.079	-.060	-.145
Gave Twin	.293	.309	X	.446	-.087	-.134
Received Twin	.111	.079	.446	X	-.156	-.170
Received No. Cows	.044	-.060	-.087	-.156	X	.809
Received Seconds	.036	-.145	-.134	-.170	.809	X

APPENDIX R

GENERAL CONSIDERATIONS INVOLVED IN DATA COLLECTION AND ANALYSIS

The methods and techniques used for collecting and analyzing the data presented in the various chapters of this thesis were felt to be standard procedures for such research. For a while it was imagined in Chapter V that in order to analyze the data obtained about passeriformes regarding the number of primary caretakers the Fisher test (Siegel, 1956) might be the most suitable test, as the data at first glance seemed nonparametric in character, i.e. one recorded instance of helping versus more than one recorded instance times small versus large clutch sizes. It was thought that an unusual case of altruism or helping behaviour in a species would be recorded whereas usual or relatively common observations in another species would receive an attenuated scoring. However, upon further consideration it was reasoned that the point biserial correlation (r_{pbi}) (Ferguson, 1971) would more closely fit the demands of the research design, insomuch as clutch size could reasonably be considered a continuous normally distributed variable whereas one instance or more than one instance of altruism was clearly best described as a dichotomous variable.

Also, r_{pbi} is readily convertible to the more generally used t by the formula $t = r_{pbi} \sqrt{\frac{N - 2}{1 - r_{pbi}^2}}$. However, it may be considered that the dichotomous variables are in fact continuous and normal in distribution, and that the biserial correlation rather than point biserial would more clearly illustrate the relationship between the independent and dependent variables. As biserial correlations tend to be larger than point biserial correlations,

it was felt wiser to err on the conservative side and slightly increase chances of a Type II error.

An examination into the suitability of the Fisher test found that an apparently rather normal procedure asks the researcher to indulge in a game of chance through the use of Tocher's modification. After going through the various computations, the researcher is supposed "... to go to a table of random numbers and at random draw a number between 0 and 1. If this random number is smaller than our ratio (derived from the Fisher test) above, we reject H_0 . If it is larger, we cannot reject H_0 ." (Siegel, 1956, p. 103).

Surely it would be advisable in the above case to state the likelihood of drawing a random number smaller than the above ratios rather than in fact carrying out the "dart game" suggested.

Systematic observations of behaviour were used for the data collection in Chapters III and VI. The pheasant population at the Hilldale game farm and the cows studied at the Ruakura Animal Research Centre both have the disadvantage of being captive populations with all that that entails with regard to the ontogeny of behaviour patterns when generalized to greater populations of organisms living in their natural state. The advantages, however, outweighed the disadvantages for this thesis. This is due to:

1. Accessibility.
2. Records which have been kept regarding birth, genetic strains, feeding, etc.
3. The cows studied were identical twins which allowed several refinements of hypotheses about

the relationship to "others".

4. The altruism studied discussed the usefulness of the definitions of altruism and the possibilities for altruism to exist or not exist.

A re-analysis of existing information was used in Chapters V and VI. This re-analysis was considered particularly apt in Chapter VI as it was felt that it increased the objectivity and reliability of the initial observations as distinct from the hypotheses growing out of the literature subsequent to the data collection. In both Chapters V and VI if this method had not been used it would have taken several years just to set up the experiment and to collect first hand data. This made it possible in Chapter VI to draw upon nearly twenty years of careful data collection, which is one of the main reasons for such careful work at Ruakura. And in Chapter V it was possible to draw on more than fifty years of ornithological record keeping.

Non-parametric tests were applied to the data in Chapters III, V, VI and VII. Additional parametric tests used were the Pearson product moment correlation in Chapter V and the point biserial correlation in Chapters V and VII.

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