Sovereign sojourners: Investigating dispersal of invasive blowflies

A thesis

submitted in partial fulfilment

of the requirements for the degree

of

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at

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by

Max Theobald

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Abstract:

Understanding what drives insect dispersal is essential for predicting species spread, persistence, and the ecological impacts of invasive species, particularly as climate change accelerates range expansions. My thesis investigates the dispersal behaviour of several invasive blowfly species in Aotearoa New Zealand, focusing both on species-specific traits and environmental context. Specifically, I aimed to assess how conspecific density, sex, species identity, and group composition influence movement patterns, and how these patterns differ across contrasting urban and rural environments. My research combined two approaches: controlled laboratory assays and a large-scale field trial. In the lab, I used multi-patch arenas and automated video tracking to assess dispersal rate, exploration, and social spacing in two invasive blowfly species (*Calliphora vicina* and *Calliphora stygia*) under varied social conditions (densities of n = 1, n = 5, and n = 10). In the field, I dusted ~4,000 wild-caught blowflies with fluorescent powder and released them at a central location at the University of Waikato. I then monitored 28 baited traps placed along a radial transect (0.5 km to 3 km) for 10 days to track dispersal across the landscape. In the lab, I found that dispersal increased significantly under group conditions (n = 5), regardless of species or sex, and that *C. vicina*, especially females, exhibited higher exploration and movement metrics than *C. stygia*. Mixed-sex groupings further enhanced exploratory behaviour in *C. vicina*. In contrast, my field experiment yielded no marked fly recaptures. However, unmarked trap catches revealed that *Lucilia spp*. and *Chrysomya* spp. (both globally invasive) were the most frequently captured species across urban and rural sites, while *C. vicina* and *C. stygia* were less common and more restricted to urban areas. Together, these findings provide novel insights into both the behavioural ecology and spatial

dynamics of invasive blowflies. By combining behavioural assays with field-scale observations, my thesis offers a foundation for improving dispersal prediction models and informs future research design in the context of biosecurity and invasive species management.

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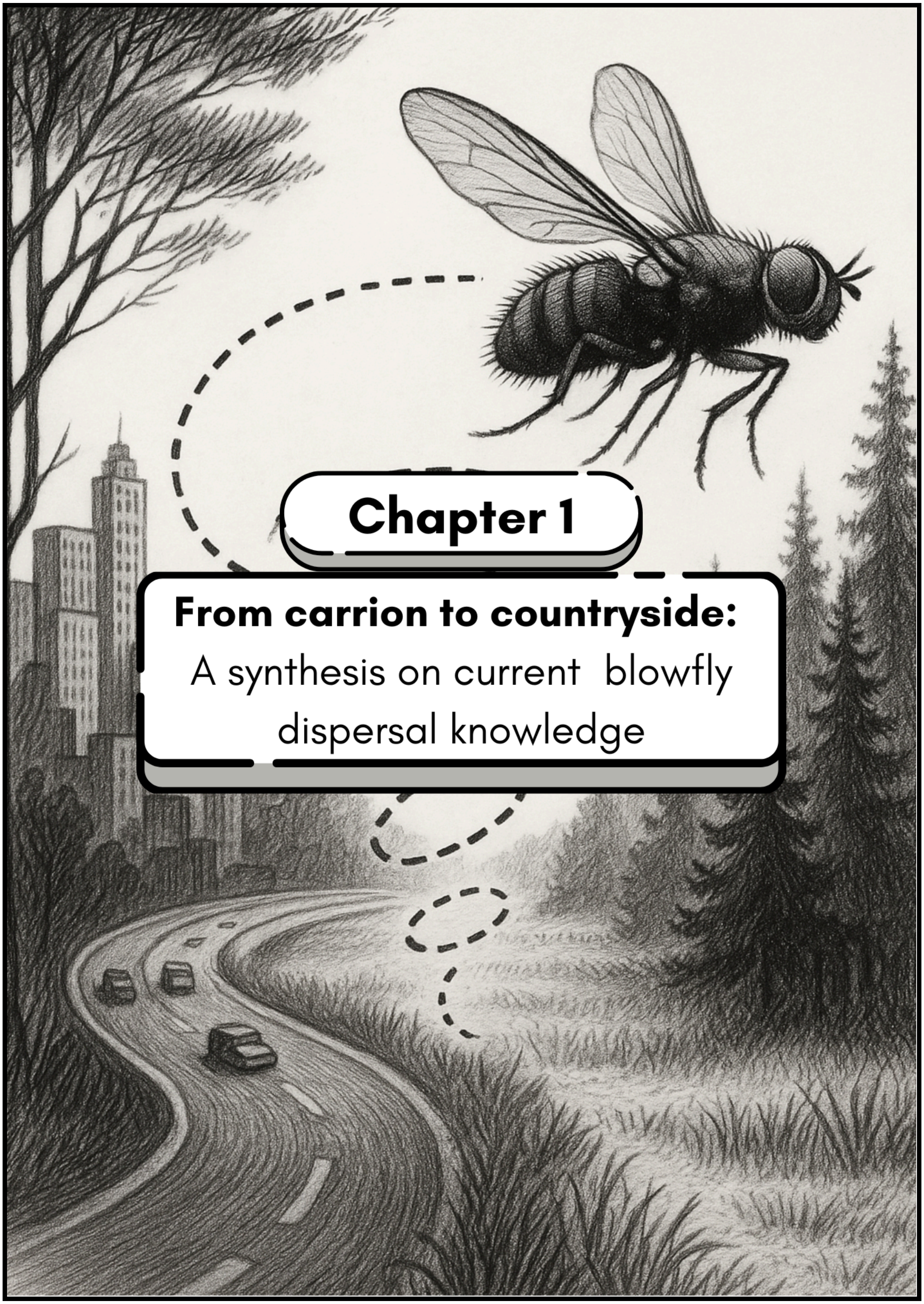


Chapter 1

From carrion to countryside:
A synthesis on current blowfly dispersal knowledge

1. Introduction:

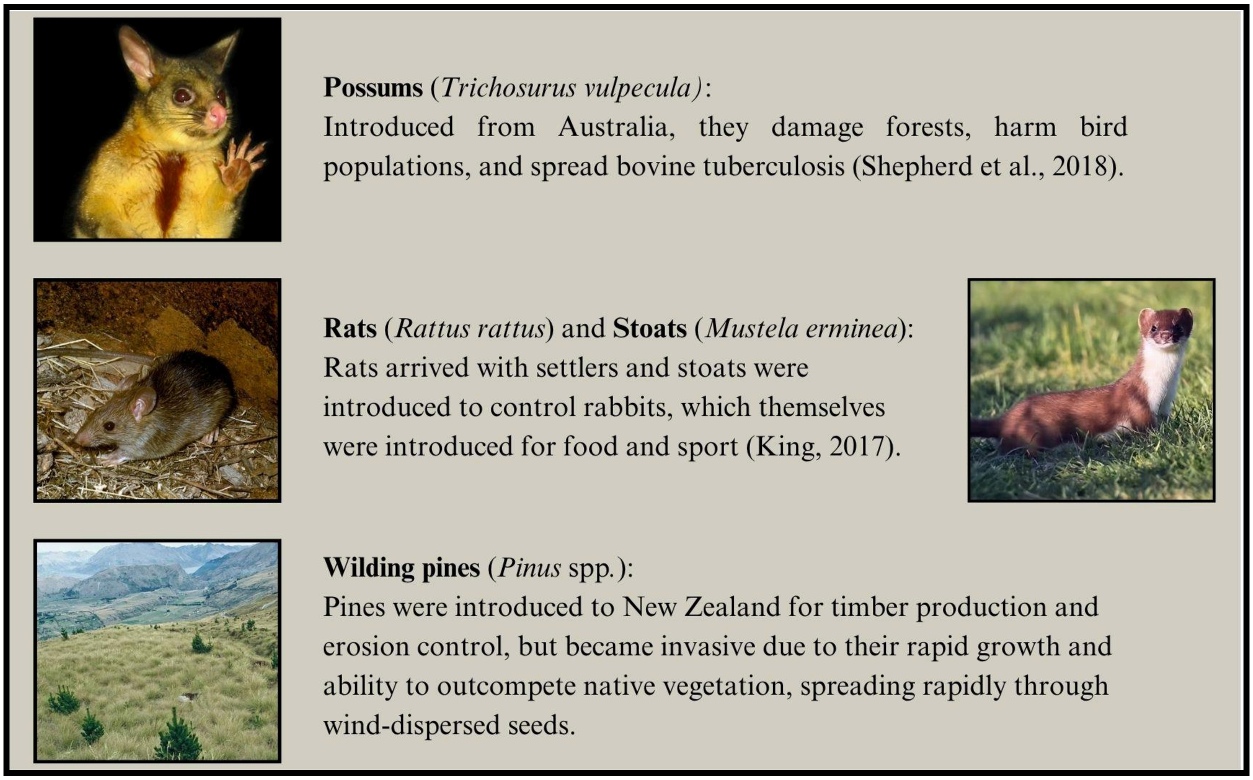
1.1. Invasive species

Throughout Earth's long history, species have moved and spread across different regions – often through natural processes, such as migration or geological events (Jeltsch et al., 2013). However, in more recent times, human activities have significantly accelerated the introduction and spread of species beyond their native ranges (Boivin, 2017). Organisms introduced to new environments are often labeled as "non-native" or "invasive" species. While these terms are sometimes used interchangeably, they have distinct meanings. The term *non-native* refers to organisms that have been transported intentionally or unintentionally into a new environment, often through human activity (Jeschke et al., 2013). These species do not inherently pose a threat to the local ecosystem and may co-exist with native species without causing significant harm. In contrast, *invasive* species are a specific subset of non-native species that spread rapidly due to anthropogenic factors and cause substantial harm to ecosystems, economies, and/or human health (Prakash & Verma, 2022). In fact, the global annual costs to manage and mitigate invasive species' impacts totalled $USD 1.288 trillion between 1970 and 2017 (Diagne et al., 2021), and are set to increase (Roy et al., 2024).

Invasive species often have devastating consequences for local ecosystems and the services they provide (Scholte et al., 2010; Simberloff, 2013). Indeed, they are now recognised as one of the major drivers of biodiversity loss, second only to habitat destruction (Doherty et al., 2016; IPBES, 2019; Roy et al., 2024). In Aotearoa New Zealand (New Zealand, hereafter), long evolutionary isolation has created ecosystems rich in endemic species, many of which lack defences against predators or aggressive competitors. Human settlement and ongoing anthropogenic activities have introduced a range of invasive species, with some of the higher profile invaders including possums, stoats, rats, and plants such as wilding pines and old man's beard (*Clematis vitalba*) (Department of Conservation, 2025). Economically, these species impact our agriculture, forestry, and tourism. For instance, wilding pines (*Pinus* spp.) spread rapidly across farmland and conservation areas, reducing pastoral productivity and requiring costly control efforts (Gous et al., 2014) (Fig. 1.1).

Invasive species can have devastating conservation impacts – outcompeting native species, altering habitats, and disrupting natural ecological processes (Bennett, 2024), often leading to the decline or extinction of native flora and fauna (Pimentel et al., 2005). In New Zealand, they have already caused extinctions of one bat, one fish, three frogs, three lizards, four plants, 51 birds, and countless invertebrates (Holdaway, 2007). Invasive species can also act as vectors for disease - this is the case for malaria, which has high potential for increasing impacts due to climate-driven range expansions of its mosquito hosts (e.g., Liu et al., 2024; Zayed et al., 2023). From an ecological perspective, invasive species can disrupt food webs, challenge native species, destroy habitats, and introduce new pathogens. For example brushtail possums (*Trichosurus vulpecula*; Fig. 1.1), are highly destructive to native forests as they eat leaves, flowers, fruits, and native organisms (Sweetapple et al., 2004), and are also vectors of bovine tuberculosis (Shepherd et al., 2018). Beyond economic and conservation concerns, invasive species can impose cultural costs. In New Zealand for example, they can threaten Māori connections to the land by damaging ecosystems that support traditional food sources (mahinga kai) and materials used in weaving and medicine (rongoā), (Galvan et al., 2024).

Collectively, the ongoing threat posed by invasive species highlights the need for rigorous biosecurity measures, habitat restoration, and control programmes to prevent further biodiversity and economic losses. However, despite extensive research, the mechanistic drivers of invasion success remain poorly understood. In particular, there is a lack of knowledge on how invasion-related traits vary within invasive species, and between species with differing levels of global invasiveness (i.e., geographic extent). My research aims to address these gaps by examining dispersal of blowflies, and its potential role in invasion dynamics.



Possums (*Trichosurus vulpecula*):
Introduced from Australia, they damage forests, harm bird populations, and spread bovine tuberculosis (Shepherd et al., 2018).

Rats (*Rattus rattus*) and **Stoats** (*Mustela erminea*):
Rats arrived with settlers and stoats were introduced to control rabbits, which themselves were introduced for food and sport (King, 2017).

Wilding pines (*Pinus* spp.):
Pines were introduced to New Zealand for timber production and erosion control, but became invasive due to their rapid growth and ability to outcompete native vegetation, spreading rapidly through wind-dispersed seeds.

Figure 1.1. Three key invaders in New Zealand. Brushtail possums (*Trichosurus vulpecula*) were introduced in the 19th century for the fur trade, but have since devastated native forests and bird populations (Image: Peter Firminger). Ship rats (*Rattus rattus*) arrived as stowaways on European ships, preying on native birds, insects, and plants (Image: Ian R McCann). Stoats (*Mustela erminea*) were introduced in the late 19th century to control rabbits, but became major predators of native

wildlife (Image: Linda Lyon). Wilding pines (*Pinus* spp.) were planted for timber and erosion control, but spread uncontrollably, displacing native ecosystems (Image: DOC).

1.2. The invasion process

The invasion process involves four distinct stages that must be surpassed for a species to become 'invasive' (Chapple et al., 2017; Marsico et al., 2010; Williamson, 2006) (Fig. 1.2). The introduction stage occurs when a species is transported, intentionally or accidentally, beyond its native range. If the organism survives this stage, it may move on to the establishment stage, after which it may spread geographically. This last stage of spread can be dramatic, with the species often outcompeting native species and causing significant ecological disruptions, economic burdens, and social consequences (Fig. 1.2). Understanding these stages is crucial for developing effective management and prevention strategies to mitigate the damaging effects of biological invasions.

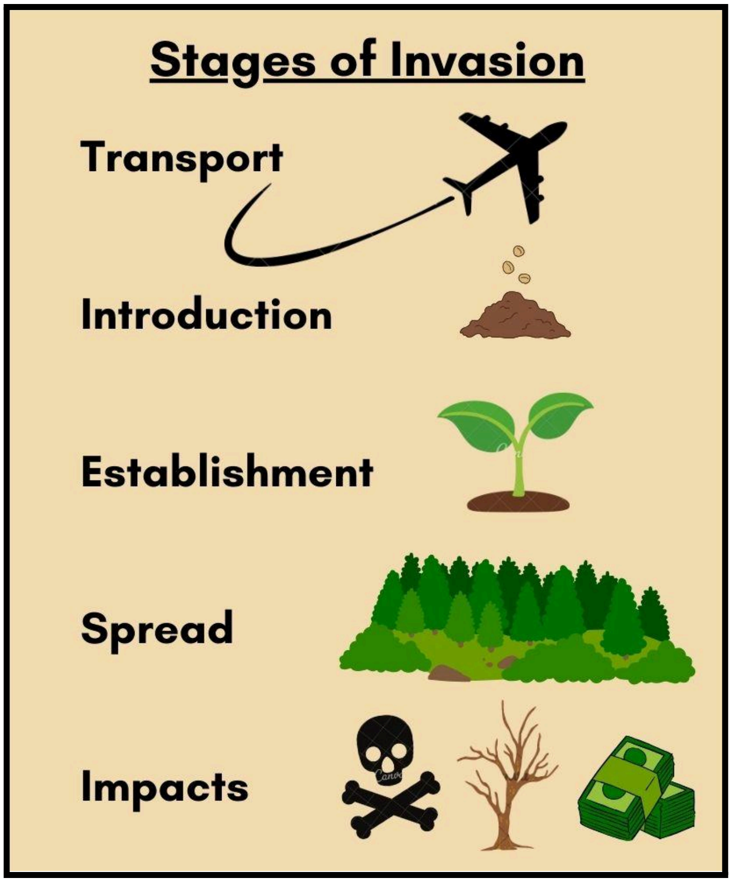


Figure 1.2: The main stages of biological invasion.

Invasive species are introduced to new environments through human-mediated pathways, such as global trade, travel, and the transportation of goods (Banks et al., 2014). While many individuals are likely transported to new regions frequently, few survive the physical toll associated with the transport stage (Briski et al., 2018). Those that do survive transport face a myriad of pressures in the new environment that can then act against establishment, such as less favourable climatic conditions, ecological pressures (e.g., predation, competition), and demographic factors (e.g., genetic bottlenecks; not enough founding individuals to support a viable population; (Sherpa & Depres, 2021). Although only ~10% of individuals survive transport and 10% of those go on to establish populations (Jarić & Cvijanović, 2012; Williamson & Fitter, 1996), increasing globalisation (global movement of trade, technology, culture, etc.) is facilitating greater movement of individuals (i.e., increasing propagule pressure) across the globe (Meyerson & Mooney, 2007). For example increasing temperatures are raising the likelihood of establishment of invasive species in cooler/more temperate regions, with some species moving poleward to track their thermal optimums as the equator heats up (Nagano et al., 2023; Melbourne-Thomas et al., 2021). This shift not only expands the potential range for invasive species but also places new ecological stressors on native populations unadapted to such aggressive competitors, which can result in a biodiversity decline and drastically altered ecosystem dynamics.

1.3. Role of dispersal in invasion

Dispersal – defined as the movement of individuals from one site (emigration) to another (immigration) (Bowler & Benton, 2005; Driscoll et al., 2014; Leibold et al., 2004; Rutherford et al., 2022) – is central to the invasion process. Through dispersal, invasive populations expand beyond their established ranges, allowing them to exploit new resources, outcompete native species, and increase in abundance (Elliott & Cornell, 2012).

1.3.1 Types of dispersal mechanisms

Dispersal mechanisms can vary widely among species and environments. For example, active dispersal involves an individual independently walking, flying, or swimming toward a new area. On the other hand, passive dispersal occurs when organisms rely on wind, water, or other animals to mediate their movement, and allows seeds or small insects to be transported over longer distances without their own propulsion (Merwin, 2019; Van Leeuwen et al., 2012) (Fig. 1.3). Human activities, such as global trade and transportation, greatly accelerate both the active and passive dispersal of invasive species, helping them to bypass natural barriers (e.g., oceans, mountains) or providing suitable habitat for range expansion (Boivin, 2017). In New Zealand, biosecurity risks are heightened as invasive species often arrive through shipping and tourism. Highlighting specific pathways can help to clarify which regions are at higher biosecurity risk.

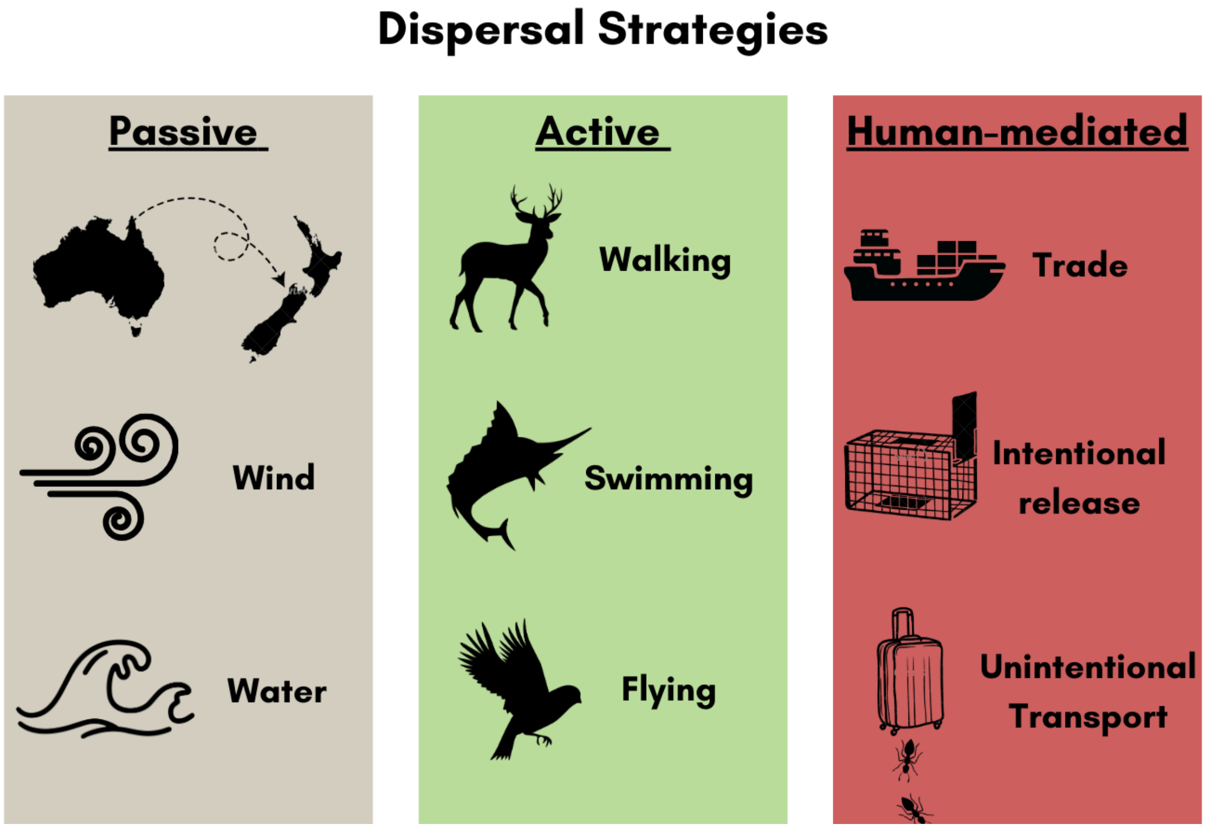


Figure 1.3. The various dispersal strategies of organisms.

1.4 The role of dispersal in invasive insect success

Insects are among the most successful and widespread invaders globally (Fenn-Moltu et al., 2022; Lombaert et al., 2014; Renault et al., 2018). Their typically smaller sizes, rapid reproduction rates, and extreme adaptability can allow them to colonise a vast variety of environments (Szűcs et al., 2017). Insects can disperse passively via the wind, human activity, or animal hosts, or actively through flight, which allows them to surpass geological and/or environmental dispersal barriers (Terblanche et al., 2024; Wright et al., 2023). These traits not only allow for rapid range expansion, but also help to facilitate their establishment in novel environments (Neu & Fischer, 2021). As such, insects are a powerful model for investigating how dispersal mechanisms contribute to the success and continued persistence of invasive species.

1.4.1. General drivers of insect dispersal

Insect dispersal is influenced by a combination of environmental, behavioural, ecological, and physiological factors, and can thus differ across species (Kautz et al., 2016; Marcantonio et al., 2023; Wu & Seebacher, 2022). Environmental factors include wind currents, temperature, rainfall, and humidity, which can together shape patterns of habitat fragmentation or connectivity. For example, migration in the painted lady butterfly (*Vanessa cardui*) is influenced by environmental factors such as wind and temperature (Reich et al., 2025), and movement and population distribution in bumblebees (*Bombus* spp.) are shaped by the loss and fragmentation of flowering habitats (Gómez-Martínez et al., 2020). Dispersal of other species may be driven by behavioural responses to resource limitation or ecological factors, such as potential mating opportunities or competitor/predator avoidance (Hu et al., 2016; Leitch et al., 2021). Finally, physical and physiological factors can also enhance dispersal capabilities. For example, migratory monarch butterflies (*Danaus plexippus*) have larger and more elongated wings for improved flight efficiency (Altizer & Davis, 2010), while locusts (*Schistocerca gregaria*) rely on lipid reserves to sustain long-distance travel (Du et al., 2021).

1.4.2. Dispersal in invasive insects

In the context of invasion success, species with higher dispersal capacities can move beyond their initial introduction sites at alarming rates, accelerating their extent of impact on environments and native species (Ochocki & Miller, 2017). For example, the spotted lanternfly (*Lycorma delicatula)* spreads rapidly through both natural movement and human-mediated transport, posing a significant threat to agriculture and forestry (Elsensohn et al., 2024; Ladin et al., 2023). Similarly, the red fire ant (*Solenopsis invicta*) has expanded its range through a combination of flight, floating on floodwaters, and unintentional human transport – leading to severe ecological and economic impacts (Gotelli & Arnett, 2000; Morrison et al., 2004). The Asian tiger mosquito (*Aedes albopictus*) has also successfully invaded multiple continents, facilitated by its ability to lay drought-resistant eggs in small water containers (Caminade et al., 2012; Piccinno et al., 2025). Dispersal plays a critical role in shaping the invasion dynamics of insects, influencing both the speed and spatial extent of spread (Ochocki & Miller, 2017). While research has identified broad patterns, there remains a growing need to understand how specific landscape features, such as habitat fragmentation, urbanisation gradients, and interspecific interactions, modulate movement behaviour and establishment success, particularly in novel or human-modified environments (Hunter, 2002; Matilda et al., 2024). This limits our ability to predict invasion pathways, local population establishment, and potential ecological impacts.

1.4.3. Measuring dispersal in insects

There are two commonly used approaches for understanding insect dispersal patterns, each with advantages and disadvantages: field-based methods and laboratory based assays (Fig. 1.4), with these encompassing direct and indirect measures of dispersal.

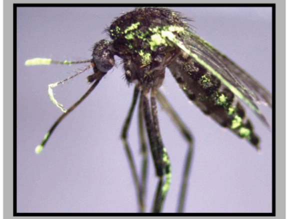
In the field, mark-release-recapture methods involve capturing insects and marking them with easily identifiable materials, such as dyes, powders, paints, or even genetic or chemical tags, before releasing them back into their habitat (Paul et al., 2024). Recaptures are then attempted at set distances and time intervals to estimate dispersal behaviour and movement patterns. This direct dispersal method closely simulates natural conditions, offering valuable ecological insights. However, it is highly labour-intensive, often yields low recapture rates, and typically involves individuals of unknown age unless the population is bred under controlled laboratory conditions prior to release (e.g., Weldon & Meats, 2010). Larger insects are sometimes able to be fitted with micro-transmitting radio frequency identification (RFID) tags that directly track movement in real time (Wikelski et al., 2006). This method allows for fine scale behaviour measurements but has constraints, such as potential short battery times, high economic costs, and potential for behavioural disruption from the tracker itself.

Two indirect field-based methods include stable isotopes and genetic analysis. By analysing the ratios of stable isotopes (e.g., $\delta^{13}C$, $\delta^{15}N$, $\delta^{2}H$) in insect tissues, which reflects the chemical signatures of local food sources, geographic origins and movement history can be inferred (e.g., Hobson et al., 2017). This method is extremely effective for migratory species, but requires a baseline environmental isotope map (isoscapes), which can be very expensive to obtain, and highly specialised expertise to interpret and model the isotopic distribution of a landscape (McCue et al., 2019). Population genetic analysis can provide a relatively more affordable option, depending on the sequenced genetic marker (e.g., microsatellite, mitochondrial, nuclear, and single nucleotide polymorphisms/SNPs). In this case, genetic data can be used to make inferences of population structure and connectivity (gene flow), with reduced gene flow typically indicating limited dispersal and homogeneity among populations implying higher dispersal rates (Bohonak, 1999). Genetic analysis can be incredibly useful, but often requires extensive sampling and then work in the laboratory to extract and sequence DNA (Ballare et al., 2019).

In contrast to field methods, laboratory assays can be used to simulate dispersal, often of small populations or individuals (Arnold et al., 2017). One direct method involves the use of enclosed arenas and mark-recapture, with recaptures recorded at designated points to simulate population dispersal scenarios. This method offers the advantage of semi-natural conditions and facilitates direct behavioural observation. However, its primary limitation lies in the confined space, which may not accurately reflect real-world terrain or environmental stimuli (Hagler & Jackson, 2001). At the individual level, wind tunnels, tethering, or small-scale dispersal arenas can all provide ways of measuring movement. Wind tunnels involve the release of individuals into a tunnel with a controlled airflow for direct observation of flight. These controlled conditions are ideal for studying factors such as orientation and cue response. For example, Baker and Linn (1984) found certain moths fly upwards in response to scent producing females. Tethering typically involves fixing insects to a rotating or stationary arm and then recording flight duration, distance, and speed. This setup allows for the insects' innate flight potential without external cues, making it highly repeatable. However its lack of environmental context may underestimate natural flight conditions (Tran et al., 2022). Finally small-scale arenas can be used to measure dispersal in individuals or small groups. In this case, insects are typically released into observation arenas and closely monitored by cameras or sensors that record walking or flying pathways, pauses, and turning frequencies. This method similarly lacks environmental context, while laboratory methods in general may also be limited in space and thus only able to infer dispersal over short distances (Franzén & Nilsson, 2007).

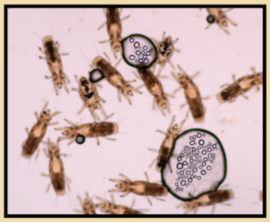
Methods for studying natural dispersal

Mark-recapture



- Mark insects, then recapture to track movement.
- Simple, cost-effective, but low recapture rates.

Genetic



- Uses DNA to infer dispersal patterns.
- Long-term data, but requires widespread sampling.

Radio tracking

- Attaches transmitters to track movement.
- Precise but expensive, better for larger insects.

Stable isotope

- Uses chemical markers to trace migration.
- Non-invasive, but needs baseline isotope data.

Enclosure

- To estimate dispersal distance and patterns.
- Labour intensive; requires large cages.

Wind Tunnels

- Mimics some real flight conditions.
- Limited space; short-range only

Tethering

- Highly controllable and very repeatable
- Doesn’t simulate real-world cues like wind or terrain.

Small scale arena

- Measures dispersal, or exploration.
- Only short-distance movement.

Figure 1.4. Common methods for studying insect dispersal. Mark-recapture (Image: Dr Cameron Webb) involves marking and recapturing individuals to directly assess movement in natural settings. Genetic analysis (Image: Dominik Bleša) uses DNA to infer dispersal patterns over time and across landscapes. Radio-tracking (Image: John P. Rafferty) uses transmitters or RFID tags to directly monitor fine-scale movement. Stable isotope analysis (Image: Bryan Pfeiffer) estimates movement history based on chemical markers obtained from an insect's diet or environment. Laboratory-based approaches include enclosure experiments (Image: Luis Miguel), where insects are marked and tracked within contained environments to estimate movement. Wind tunnels (Image: Amitabh Shrivastava) provide controlled airflow conditions that allow researchers to assess directed flight toward cues. Tethering methods (Image: Katie Hunt) measure how far and how long insects can fly while fixed to a rotating or stationary arm. Finally, small-scale arena tracking (Image: Max Theobald) uses overhead cameras or sensors to monitor walking or short-distance flight in confined spaces.

1.5 Blowflies as a model species for dispersal studies

Blowflies (Calliphoridae) are highly versatile insects that play crucial roles in the ecosystem, acting as scavengers, pollinators, and prey for other species (Gemmellaro et al., 2025). Their ecological ubiquity, rapid life cycle, ease of care in a laboratory setting, and well-documented biology make them valuable for studying a range of biological and ecological processes (Mathew, 2023). For example, in forensic science, blowflies play a critical role in estimation of postmortem intervals (Amendt et al., 2011; Byrd & Castner, 2009), while the blowfly *Lucilia sericata* is sometimes used in the veterinary and medical fields for maggot debridement therapy (the use of sterile maggots to clean dead tissue and bacteria from wounds; Naik & Harding, 2017; Sherman, 2014). Blowflies are also used in agricultural research, as they are capable of pollination in conditions where other insects may fail, due to their ability to tolerate a wider array of environmental conditions (Cook et al., 2020; Saeed et al., 2016). Finally, blowflies can serve as models for studying population dynamics and evolutionary processes due to their responsiveness to environmental changes (Smith & Wall, 1998).

Blowflies are often excellent biological invaders, due to their adaptability, rapid reproduction, and short generation times, which together allow rapid establishment and proliferation in new environments (Croft et al., 2024; Daly et al., 2023). One of the biggest consequences of blowfly invasion is flystrike (a condition where larvae infest living tissue in animals, causing severe health problems in livestock), which affects 2-10% of the national flock in New Zealand and costs farmers an average of $NZD 15 million on sheep dips alone (Heath, 2022). Despite this negative impact, the above characteristics mean invasive blowflies are ideal organisms for investigating movement patterns and habitat connectivity in the context of invasion success.

1.6.1 Blowfly species in New Zealand

New Zealand is home to many blowfly species, including a mixture of both endemics and invasive species. The Invasomics Laboratory (Waikato University, Hamilton) studies eight of these species, including four *Calliphora*, two *Lucilia*, and two *Chrysomya* species (Fig. 1.5), to investigate various aspects of biological invasion.

Calliphora quadrimaculata, a species with striking metallic green to blue coloration, is an endemic blowfly found in New Zealand's alpine environments. It is known for its distinctive black markings on the thorax and abdomen. *Calliphora stygia* and *Calliphora hilli* are species native to Australia that were introduced to New Zealand between 1779-1841 (Dear, 1986). They are found throughout New Zealand and are characterised by their orangey-brown body and black markings. *Calliphora vicina*, metallic blue-green in colour, was introduced to New Zealand from Europe and other parts of the Northern Hemisphere around 1889 (Dear, 1986) and has since become widespread across New Zealand. The common green bottle fly, *Lucilia sericata*, is a highly invasive species originally from Europe and the Middle East. It was first found in 1988 in New Zealand, but evidence suggests that it may have been here from the late 1970s (Stevens & Wall, 1997). Similarly, *L. cuprina* is a highly invasive species that was established in New Zealand in the 1970s. The two *Lucilia* species are extremely difficult to distinguish but are able to be identified based on several morphological traits outlined in Table 2 of Williams & Villet, 2014 (Holloway, 1991). Finally, *Chrysomya rufifacies* spread to New Zealand from tropical and subtropical regions of Asia (CABI, 2022) and is characterised by its green-red coloration, while *Chrysomya megacephala* is a highly invasive blowfly native to Southeast Asia, distinguished by its metallic green body, and large, prominent head. Both *Chrysomya* species are thought to have invaded in the early 1900s.

In my thesis, I leverage this model system to explore the dispersal behaviours of differentially invasive blowfly species to provide insights into the role of dispersal in biological invasion.

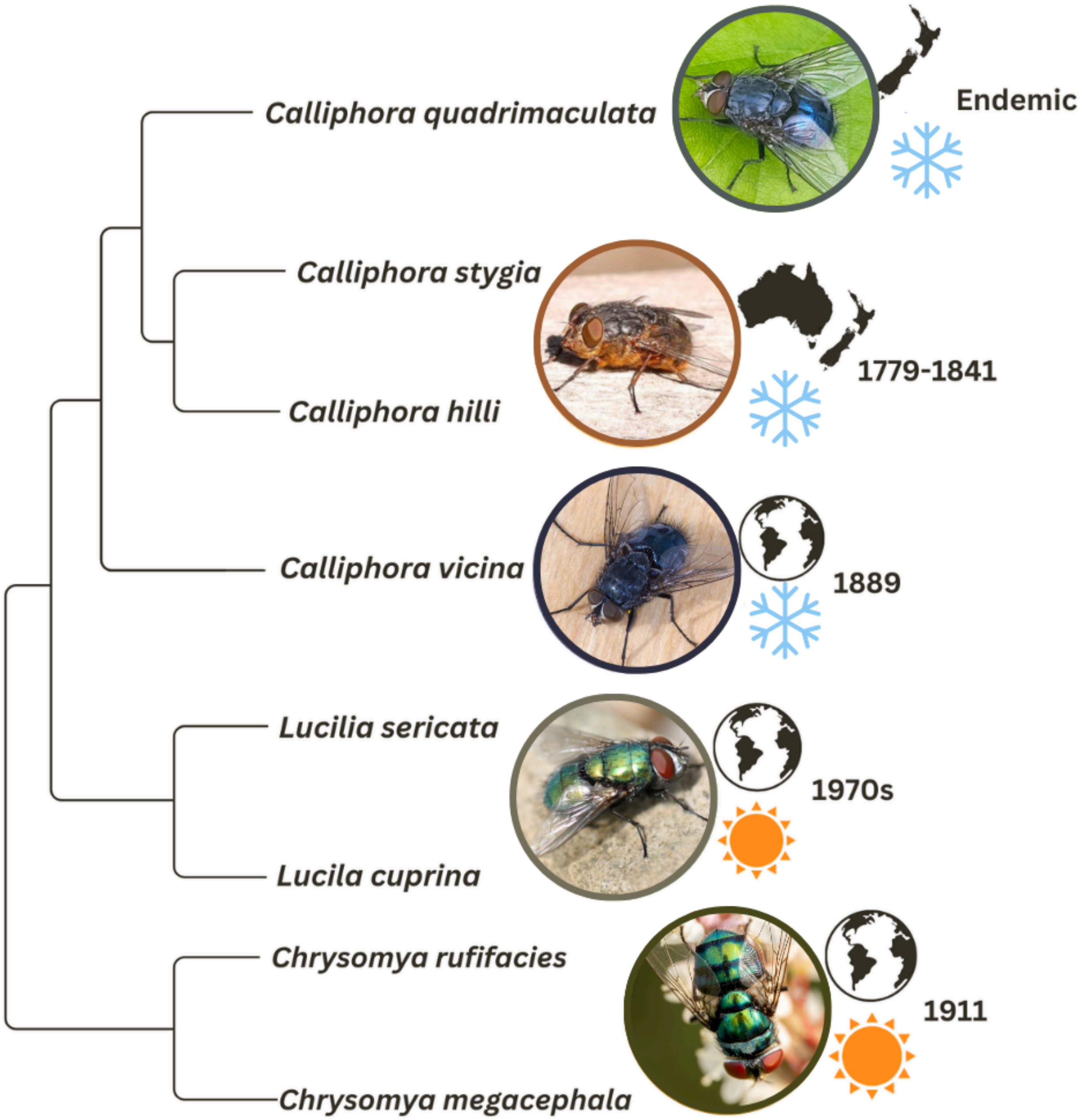


Figure 1.5. Evolutionary relationships of some of the blowflies present in New Zealand, with symbols demonstrating their global distribution and general temperature preference. (Note only one of each sister species is present, those being *C. hilli*, *L. sericata*, and *C. megacephala*). Image obtained from the Invasomics Laboratory (unpublished).

1.7 Thesis Structure

My thesis uses a combination of field experiments and controlled laboratory studies to investigate the dispersal patterns of several invasive blowfly species in New Zealand. Following this introductory chapter, Chapter 2 consists of laboratory-based experiments, focusing on dispersal of two differentially invasive species, *C. vicina* (highly invasive) and *C. stygia* (mildly invasive). Chapter 3 presents a small field experiment aimed at understanding how rapidly and how far wild-caught blowfly species (including many of those described in Section 1.6.1) move following mark and release. Finally, Chapter 4 synthesises the thesis, exploring overarching patterns in the dispersal behaviours of these invasive blowfly species and providing suggestions for future research.

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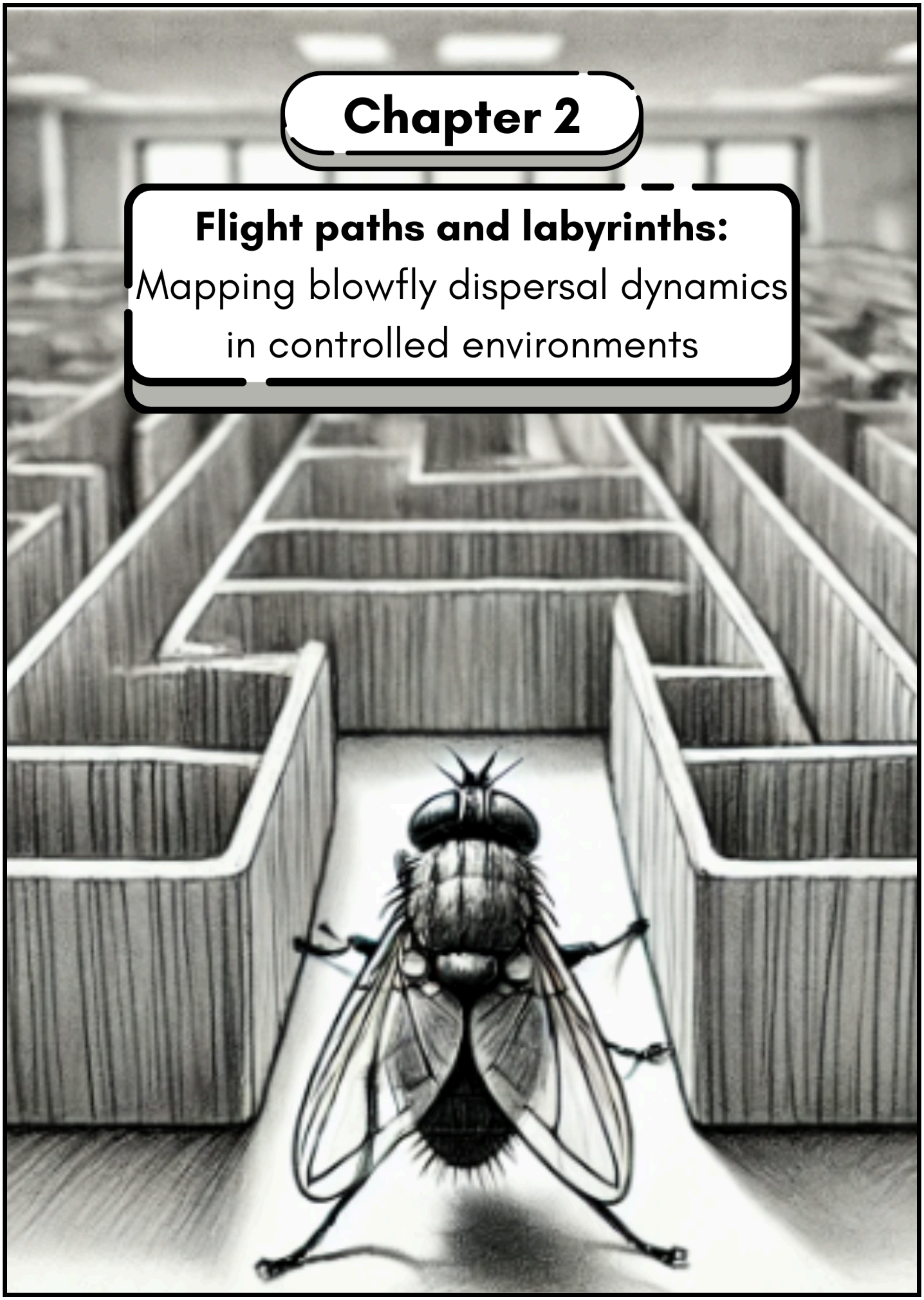
Chapter 2

Flight paths and labyrinths:

Mapping blowfly dispersal dynamics in controlled environments



2.1 Abstract

Understanding the factors that influence insect dispersal is critical for predicting movement dynamics and species persistence across habitats - especially for invasive species, which are expected to continue to increase their ranges in the face of climatic change. We investigated how conspecific density, species, and sex ratios affect dispersal behaviour in two invasive New Zealand blowfly species: *Calliphora stygia* and *Calliphora vicina*. Using custom-built multi-patch arenas, we quantified individual and group dispersal and behavioural metrics (dispersal rate, exploration, and social spacing) under controlled laboratory conditions with automated video tracking. We found that dispersal was significantly higher when flies were in groups (n = 5) compared to when alone (n = 1), regardless of species or sex. *C. vicina*, especially females, consistently exhibited greater movement, exploration, and social spacing than *C. stygia*, which may be reflective of its greater invasive tendencies. Sex ratios further influenced behaviour, with mixed-sex combinations of individuals enhancing exploratory tendencies for *C. vicina*. Our findings highlight how intrinsic and social factors interact to shape blowfly dispersal behaviour, offering new insights into species-specific dispersal strategies and potential responses to environmental change of two key invasive species.

2.2 Introduction

Invasive species can pose major threats to global biodiversity, ecosystem stability, and agricultural productivity, with estimates placing the economic damage they cause at billions of dollars annually (O'Brien et al., 2025; Pimentel et al., 2005). Defined as non-native organisms that establish themselves and spread into new regions, invasive species often have negative impacts on local environments (Simberloff et al., 2013). A contributing reason for this is their dispersal capacity, which enables colonisation of new areas outside the native range (Banks et al., 2014; Ricciardi et al., 2011). While dispersal can occur naturally through movement, flight, or wind, the rapid intensification of globalisation has facilitated invasive species to spread faster and farther than ever before (Banks et al., 2014). Understanding dispersal capacities is therefore crucial for biosecurity efforts and ecological strategies to prevent introductions, contain potential outbreaks, and mitigate ecological damages (Hulme, 2009).

Invasive insects often exhibit dispersal patterns that are both more variable and more expansive than their native or less-invasive counterparts. For example, the fruit fly *Drosophila suzukii* spreads at rates of up to 1,400 km per year in parts of the United States and Europe, with some individuals flying kilometres in a single flight, especially when wind-assisted or during dispersal peaks (Estay et al., 2023). In contrast, native *Drosophila melanogaster* and *Drosophila simulans* typically disperse much shorter distances, with field mark-release-recapture experiments in North Carolina showing that movement of marked flies averaged ~150 m per day (McInnis et al., 1982). Meanwhile, laboratory experiments using reared individuals from field-collected populations from the invasion front and core show that those from the leading edge evolve to fly faster than those from the core (Lombaert et al., 2014). These examples highlight how invasion dynamics can shape dispersal traits between species and within populations, but research that contrasts species with different global ranges (and therefore potentially different dispersal rates) is limited (Driscoll et al., 2014) – particularly in natural field settings. Moreover, the coupling of assays that assess dispersal rates as well as their drivers may help to clarify how far/fast blowflies move, as well as the triggers of dispersal. Such insights will ultimately be crucial for predicting species spread and subsequent management (Baines et al., 2019, Tesson & Edelaar, 2013).

Blowfies (*Calliphoridae*) are globally among the most widespread and ecologically invasive insects, with numerous species successfully establishing populations outside their native ranges (Croft et al., 2024; Whitworth, 2010). In New Zealand, invasive blowflies, such as *Calliphora vicina* and *Lucilia sericata,* have established successfully since 1889 and 1988, respectively, and have the capacity to directly compete with native scavengers (Dear, 1986). Blowflies play an important ecological role – for example, as decomposers they contribute to nutrient cycling by consuming carrion and overturning a substantial portion of the 'brown' food web (Barton & Evans, 2017). Beyond their ecological influence, blowflies can impact agriculture via their role as pollinators (Rader et al., 2011), and/or as parasites of livestock. In the latter case, certain species can cause myiasis (flystrike), leading to significant economic losses (Vallenari et al., 2023). Understanding how invasive blowflies spread is therefore essential for both environmental monitoring and applied science.

Blowflies are widely recognised as capable fliers, with studies suggesting dispersal over distances of up to 65 km (Braack & Retief, 1986). This ability contributes to their ecological success and invasive potential (Amat et al., 2016). However, dispersal capacity varies by species and environment (Baumgartner & Greenberg, 1985). For instance, a field study in southwest England found that *L. sericata* typically dispersed a median distance of 109-150 m within a day, with mean distances ranging from 118-183 m (Smith & Wall, 1998). Meanwhile, a study conducted in tropical Malaysia that used ~3,000 blowflies reported greater dispersal rates in *Chrysomya* species: 79% of individuals travelled up to 1 km, ~21% travelled up to 2-3 km, and one individual dispersed up to 3 km during the 9-day sampling period (Lee et al., 2023).

While traditionally associated with resource-seeking behaviour – especially prevalent in species that use ephemeral resources, such as carrion (Stiegler et al., 2020) – blowfly dispersal can facilitate colonisation, competitive displacement of native detritivores, and potential shifts in decomposition dynamics (Matuszewski & Madra-Bielewicz, 2022; Smith & Wall, 1997). Additional potential drivers for dispersal can include mate finding and avoidance or seeking of environmental conditions (Adetimehin et al., 2024; Laprise et al., 2024), with sex also playing a key role in mitigating dispersal propensity. For example, Baumgartner and Greenberg (1985) found that female blowflies, particularly synanthropic species like *L. sericata* and *C. vicina*, tend to disperse further than males of the same species. This is likely due to the need to locate suitable oviposition sites (and also because females require a protein meal for reproductive development) (Browne et al., 1976). Female-biased dispersal is a common pattern in insects more generally (e.g., butterflies and beetles; Shaw & Kokko, 2014), and contrasts with findings in other species, such as mammals and birds, where males typically disperse farther (Li & Kokko, 2018). This suggests that sex-specific dispersal performance in some species might have an important influence on invasion speed and population spread.

In this study, we focus on the dispersal behaviour of two rampant blowfly species in New Zealand, *C. vicina* (bluebottle fly) and *C. stygia* (brown blowfly). *C. vicina* is native to the Palearctic region, but has spread globally to achieve its now cosmopolitan distribution (Daly et al., 2023; Dear, 1986; Sivell, 2024). *C. stygia* is native to Australia and is widespread throughout New Zealand, but has not spread beyond Australasia (Dear, 1986). These two species differ not only in their region of origin, but also in their ecological associations. *C. vicina*, for example, has a synanthropic index of +83.1, indicating a strong preference for human-influenced environments (Pinilla Beltran et al., 2012). While no formal synanthropic index has been calculated for *C. stygia*, it is predominantly encountered in rural and pastoral environments in New Zealand. For example, in a survey of carrion colonisation in the northern North Island, *C. stygia* was present on 59 % of rural possum carcasses, with far fewer occurrences in urban settings, emphasising its strong association with rural habitats (Dymock & Forgie, 1993). Comparing the dispersal behaviour of *C. vicina* and *C. stygia* under controlled laboratory conditions may therefore allow for a comprehensive understanding of intrinsic movement behaviour among species that have similar life history traits and ecological roles, but differ in their fine-scale habitat preferences and likely overall dispersal dynamics. Thus, we compared dispersal performance of *C. vicina* and *C. stygia* under using custom-built arenas to capture critical behavioural metrics (Table 2.1). We hypothesised that *C. vicina*, as the more widely distributed invasive and synanthropic species, would show higher performance in a range of dispersal metrics compared to *C. stygia*.

2.3 Methods

2.3.1 Field capture

Blowflies were collected with permission from an urban dumpster (37° 47 '42.2"S, 175° 16' 56.0"E, Hamilton, New Zealand) on 6th July 2025 using manual netting. Immediately after capture, flies were identified following Dear (1986) and transferred into a ventilated insect 47.5 × 47.5 × 47.5 cm, nylon mesh rearing cage (BugDorm-4H4545; MadHornet, New Zealand) to minimise stress and ensure survival. To prevent dehydration, a plastic water container fitted with a cotton wick was provided, which allowed flies to access moisture without the risk of drowning. Additionally, a 38 × 10 × 2 cm weighboat filled with granulated sugar was placed inside the cage to provide an immediate energy source. After collection, the flies were transported to the University of Waikato invertebrate facility for colony establishment.

2.3.2 Laboratory maintenance

Two separate *C. stygia* and *C. vicina* laboratory colonies were established using 12 wild-caught individuals of each (6 males and 6 females for *C. vicina;* 5 males and 7 females for *C. stygia*). Colonies were housed in insect rearing cages in a temperature controlled room (22°C ± 1°C) with a 12-hour day-night photoperiod. The flies were provided with a constant supply of sugar, water, and fresh beef mince through multiple breeding generations. Flies from F1 and subsequent generations (up to F6) were used in dispersal assays to ensure prior acclimation to laboratory conditions, with breeding stock kept separate from assay populations.

2.3.3 Trait assays

To quantify dispersal metrics for each species, we used a 2-patch linear dispersal arena (75 × 17 × 7.9 cm) consisting of two plastic 2L containers (Sistema; www.sistemaplastics.com), each with two 3.6 cm diameter holes bored into the sides (Fig. 2.1). Containers were connected to each other by three joined 50 ml plastic tubes (Falcon, Tarsons), with a total length of 25 cm, using transparent duct tape. A clear lid was placed on one container to allow easy relocation of flies into the assay and a clear gate was installed in the release patch to hold flies until the acclimation period had ended.

Finally, white paper was placed at the bottom of both containers to allow the flies to be easily identified.

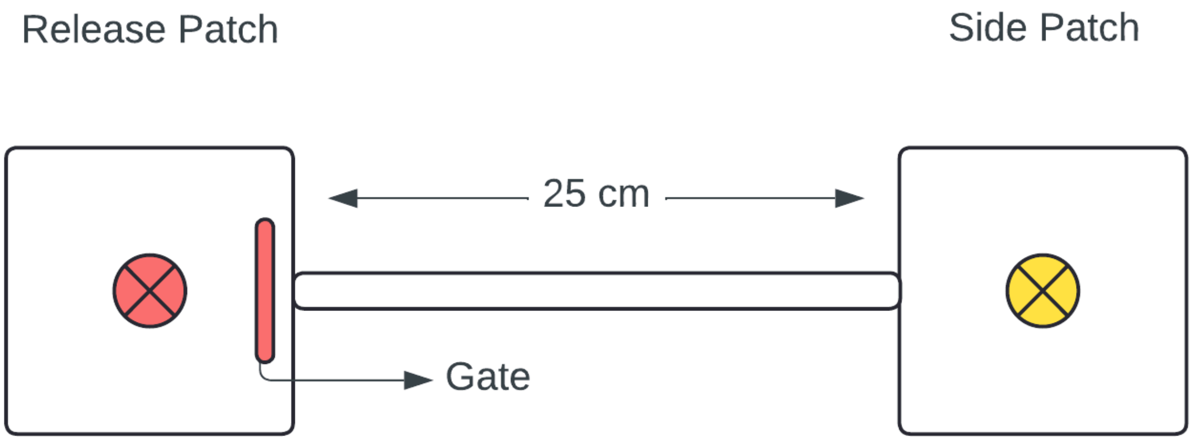


Figure 2.1. Diagram of the 2-patch system for blowfly dispersal assay, showing the dispersal distance and gate.

Each fly was initially placed into the empty release patch and allowed a 10-min acclimation period. The time taken for the individual to move into the empty second patch following the lifting of the gate was then recorded, with flies that did not disperse within the assay time recorded as non-dispersing. This experiment was conducted for individuals and groups. In individual assays, a single blowfly was tested per trial and allowed up to 2 hr to disperse to evaluate inherent movement behaviour without social influence (n = 80 replicates; 40 per species). In group assays, five individuals of the same sex were introduced to the arena simultaneously to assess collective dispersal dynamics under social conditions. The group assay was run for 1 hr (n = 24 replicates; 12 per species).

To explore group dynamics when blowflies had access to more physical space, a 9-patch system consisting of eight empty side patches and one empty central release patch was constructed using 1.15 L Sistema containers (Fig. 2.2), with 3.7 cm diameter holes bored into the side for connective tubing (18 cm). A clear, plastic lid was placed on the central release patch to allow for observation of flies during the assay and four clear gates were installed on the central patch to prevent flies from dispersing until the acclimation period had ended. To enhance visibility for the recording software, white paper was placed at the bottom of all nine containers as per the 2-patch system.

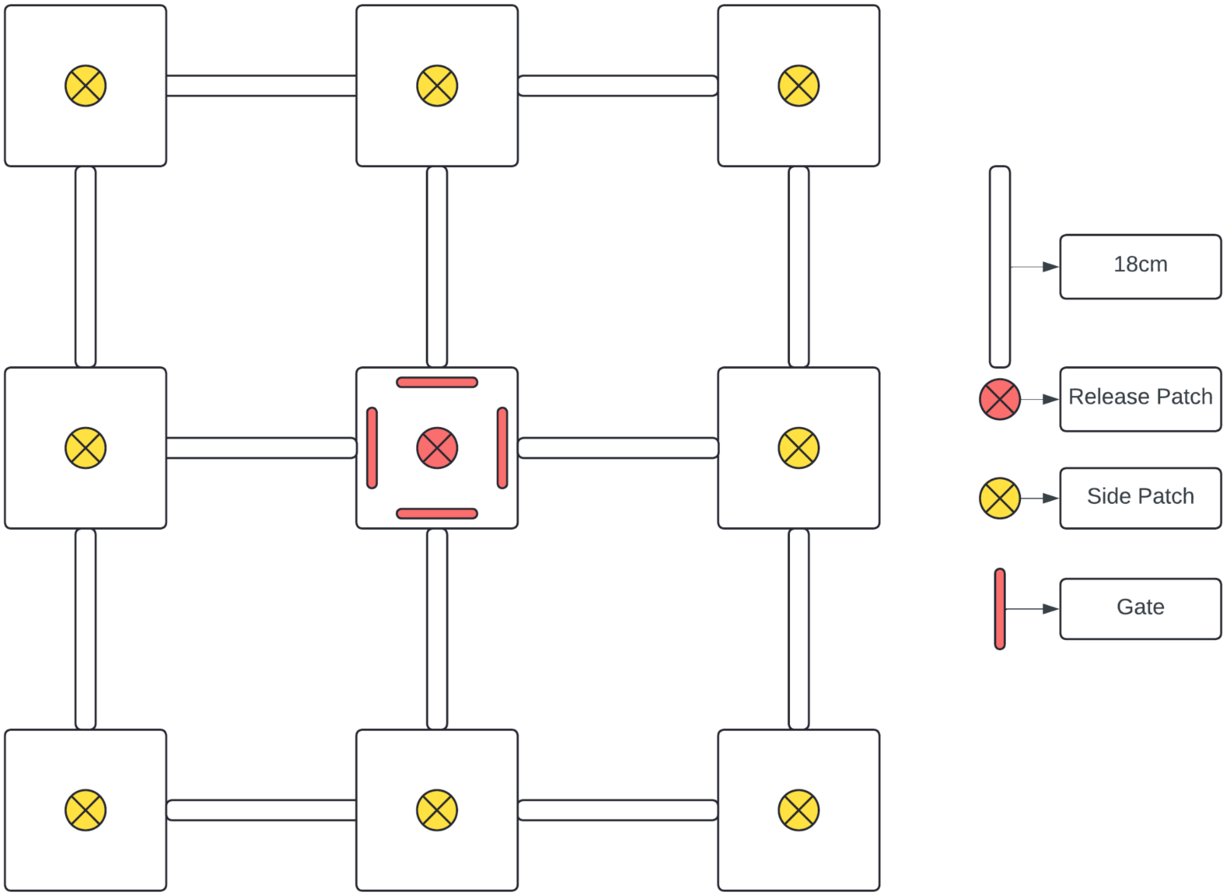


Figure 2.2. Diagram of the 9-patch system for blowfly dispersal assay.

Ten individuals were placed in the central patch of the 9-patch arena and their movements were tracked for up to 1 hr following the lifting of the release gates after a 10-min acclimation period in the central patch. Ten blowflies were tested in three sex ratio combinations: all males, all females, and a 50:50 mix of both sexes. A total of 72 trials were conducted (n = 24 replicates per sex ratio combination; 12 per species).

All assays in this study were performed at constant temperature (22°C ± 1°C) and all individuals were only used for a single assay before removal from the experiment. To minimise potential variation in dispersal metrics across generations, equal numbers of same-generation flies were used for both species in all assays. All assayed flies were exposed to minced beef meat immediately after emerging from pupation (for 2-3 days) to enable sexual maturation. Assays were conducted on 6-day-old flies to ensure consistency in developmental stage, sexual maturity, and feeding status. The movement and behaviour of individuals during the assay period were recorded from a fixed point using a 4K HD Camcorder (FDR-AX53; Sony, Tokyo, Japan).

2.3.4 Metrics measured

All behavioural metrics were quantified using AnimalTA version v3.2.2, an open-source video tracking software developed for automated analysis of movement and spatial behaviour in small organisms (Chiara & Kim, 2023). The software detects individuals by analysing changes in pixel intensity and applying motion thresholds to distinguish movement. It computes location-based metrics on a frame-by-frame basis, using only frames where the animal was successfully detected. To ensure consistency across videos, a ratio-based calibration system was applied to account for any slight variations in camera height or angle. By setting a known reference length within each arena (e.g., the diameter or width of the container), the software converts pixel-based distances into real-world units, allowing accurate comparison of behavioural metrics across all trials. A movement threshold was also applied to distinguish active motion from resting or background noise. Although multiple metrics were extracted (Table 2.1), only one representative per behavioural category was analysed to avoid redundancy (e.g., distance travelled rather than proportion time moving; mean shortest interindividual distance rather than mean sum interindividual distances).

Table 2.1. Summary of behavioural metrics extracted from dispersal assays using tracking software. All values were calculated based on automated tracking data recorded in millimetres (mm) or as proportions relative to trial duration or arena size.

Metric	Description	Biological meaning	Unit
Propensity	Whether individual dispersed	Dispersal decision	Yes/No
Dispersal rate	Time to disperse (reach other patch)	Speed of initiating dispersal	Minutes
Average speed	Mean speed across the entire trial (including stationary time)	General mobility	mm s^{-1}
Proportion time moving	Proportion of time the individual was in motion	Overall activity level	Proportion (0–1)
Traveled distance	Total distance traveled over the trial	Locomotor output	mm
Exploration relative value	Proportion of the arena explored during trial	Distance Explored / spatial coverage	Proportion (0–1)
Mean shortest interindividual distance	Mean distance to nearest neighbor across all frames	Social spacing / proximity	mm
Mean sum interindividual distances	Mean summed distance to all other individuals per frame	Group cohesion / social dispersion	mm

2.3.5 Data analysis

All analyses were conducted in R version 4.4.2 (R Core Team, 2024). For the 2-patch assays, dispersal probability (dispersed = 1, not dispersed = 0) was first compared between patch densities ($n = 1$ vs $n = 5$) using a binomial generalised linear mixed model (GLMM), fitted with the glmmTMB version 1.1.9 package; (Brooks et al., 2017). Species, sex, and patch density were modelled as fixed effects, and their interactions were also included. Within the group 2-patch assays ($n = 5$), dispersal and continuous behavioural metrics (i.e., travelled distance, exploration relative value, and mean shortest interindividual distance) were analysed using GLMMs with a gaussian error distribution, with species, sex, and their interaction as fixed effects. For the 9-patch assays ($n = 10$), dispersal probability was modelled with a binomial generalised linear model (GLM), with the species × sex ratio combination (female, male, mixed) as fixed effects, and group (because 5 or 10 flies were run together) as a random effect. Travelled distance was scaled from millimetres to metres for interpretability.

For all models, residual diagnostics were conducted using the DHARMa version 0.4.7 package (Hartig, 2024) in R, to check for deviations from model assumptions, including overdispersion and zero-inflation for binomial models. Estimated marginal means for pairwise comparisons among groups were calculated using the emmeans version 1.11.2 package (Lenth, 2025) in R. Model significance and effect sizes were reported using Type III Wald chi-square tests, with $p < 0.05$ considered statistically significant and trends with $p < 0.1$ noted. All visualisations were generated in ggplot2 version 3.5.2 (Wickham, 2016).

2.4 Results

2.4.1 Dispersal variation in 2-patch assays between densities

A binomial generalised linear model revealed a significant effect of density on dispersal probability ($\chi^2_1 = 12.650$, $p < 0.001$), with individuals dispersing less frequently at higher densities ($n = 5$) than at lower densities ($n = 1$) (Fig. 2.3; Table 2.2). There was also a significant interaction effect between species and density ($\chi^2_1 = 6.070$, $p = 0.014$), indicating that the effect of density differed between *C. stygia* and *C. vicina*. No other main effects or interactions were significant (all $p > 0.110$). Post-hoc comparisons averaged across species and sex showed dispersal probabilities of 44.4% ± 5.8% at $n = 1$ and 11.8% ± 2.2% at $n = 5$ (95% CI: 33.6–55.8% and 8.1-16.8%, respectively) (Fig. 2.3; Table 2.2).

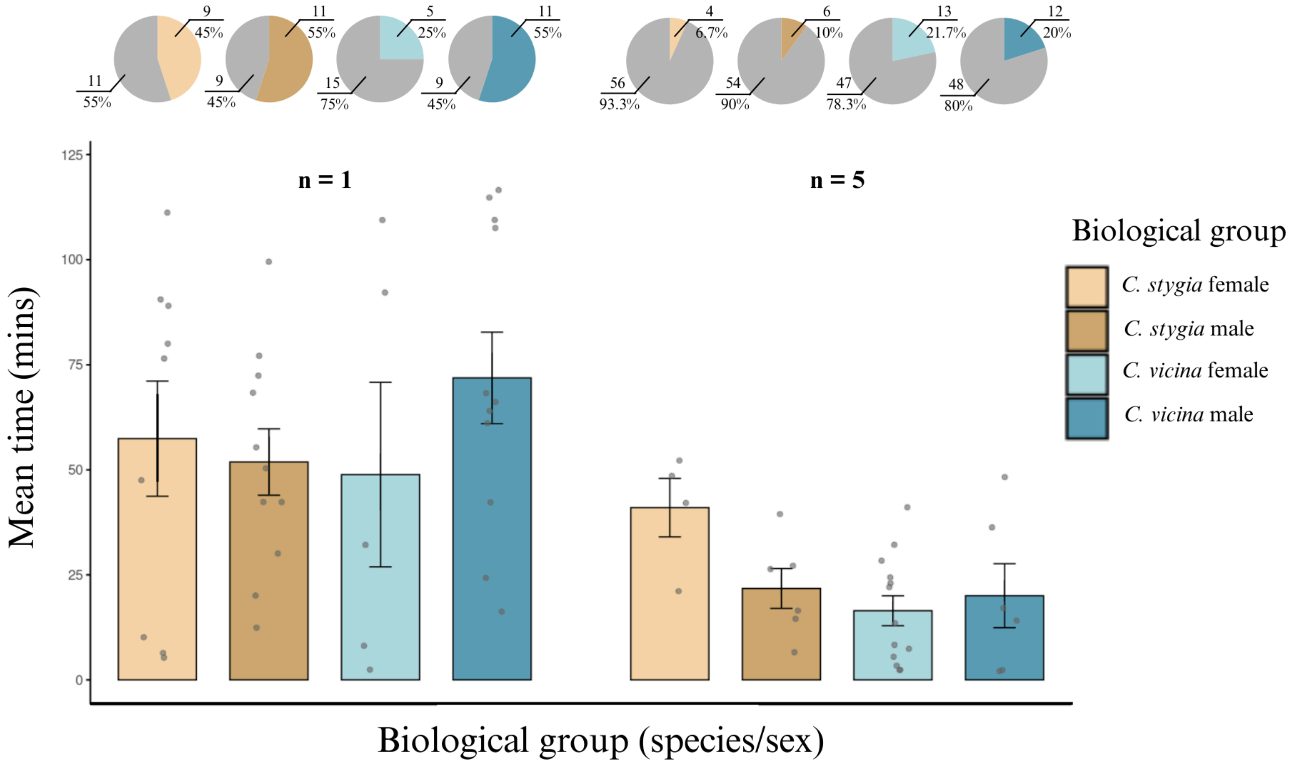


Figure 2.3. Mean time (min) ±1 standard error for an individual blowfly of a given species and sex to cross into a new patch in the 2-patch arena for individual (n = 1; left-hand side) and group (n = 5; right hand side) assays. Above each bar, pie charts display the percentage of flies that dispersed (colour) versus those that did not (grey).

Table 2.2. Results of Type III likelihood ratio tests from a generalised linear mixed model (family = binomial), examining the effects of species (*C. vicina*, *C. stygia*), sex (all male or all female), and patch density (n = 1 and n = 5) on dispersal probability (dispersed = 1, did not = 0) in the 2-patch arena, with assay included as a random effect to account for replicate-level variation. The table reports chi-square statistics (χ^2), degrees of freedom (df), and p-values for each main effect and interaction. Significant values highlighted in bold.

Effect	χ^2	**df**	***p*-value**
Species	1.724	1	0.190
Sex	0.400	1	0.528
Density	12.652	1	**<0.001**
Species × Sex	0.923	1	0.336
Species × Density	6.067	1	**0.014**
Sex × Density	0.002	1	0.965
Species × Sex × Density	2.465	1	0.116

Analysis of dispersal rate (i.e., time to dispersal) revealed a significant main effect of density (χ^2_1 = 14.140, p < 0.001), with individuals dispersing faster at higher densities (Fig. 2.3; Table. 2.2). There was a trend for species effects (χ^2_1= 2.990, p = 0.084), though this did not reach statistical significance. Estimated marginal means indicated that, across species and sexes, mean dispersal times were generally shorter at higher densities (n = 5), with mean time ranging from ~16.5-41.0 minutes compared to ~48.9-71.9 minutes at lower densities (n = 1) (Fig 2.3; Table 2.3).

Table. 2.3. Results of Type III likelihood ratio tests from a generalised linear mixed model (family = Gaussian) examining the effect of species (*C. vicina, C. stygia*), sex (all male or all female), and patch density (n = 1 and n = 5) on time to dispersal in the 2-patch arena,with assay included as a random effect to account for replicate level variation. The table reports chi-square statistics (χ^2), degrees of freedom (df), and p-values for each main effect and interaction. Significant values highlighted in bold.

Effect	**χ^2**	**df**	***p*-value**
Species	2.989	1	0.084
Sex	2.468	1	0.116
Density	14.139	1	**< 0.001**
Species × Sex	2.245	1	0.134
Species × Density	1.245	1	0.265
Sex × Density	0.957	1	0.328
Species × Sex × Density	0.039	1	0.843

2.4.2. Behavioural variation in 2-patch assays

The generalised linear mixed model revealed a trend for species effects, though it did not reach significance ($\chi^2_1 = 3.697$, $p = 0.055$) (Fig. 2.4A; Table 2.4), and no significant effect of sex ($\chi^2_1 = 0.055$, $p = 0.815$), or the species and sex interaction ($\chi^2_1 = 1.637$, $p = 0.201$) on dispersal propensity (i.e., the tendency of an individual to move from its current location). *C. vicina* dispersed 2.5 times more often than *C. stygia,* though estimated marginal means indicated uniformly low dispersal probability across all sex ratios (female *C. stygia*: $1.99\times10^{-6} \pm 6.23\times10^{-6}$; male *C. stygia*: $3.16\times10^{-6} \pm 8.40\times10^{-6}$; female *C. vicina*: $8.36\times10^{-6} \pm 1.72\times10^{-5}$; male *C. vicina*: $4.21\times10^{-6} \pm 1.06\times10^{-5}$).

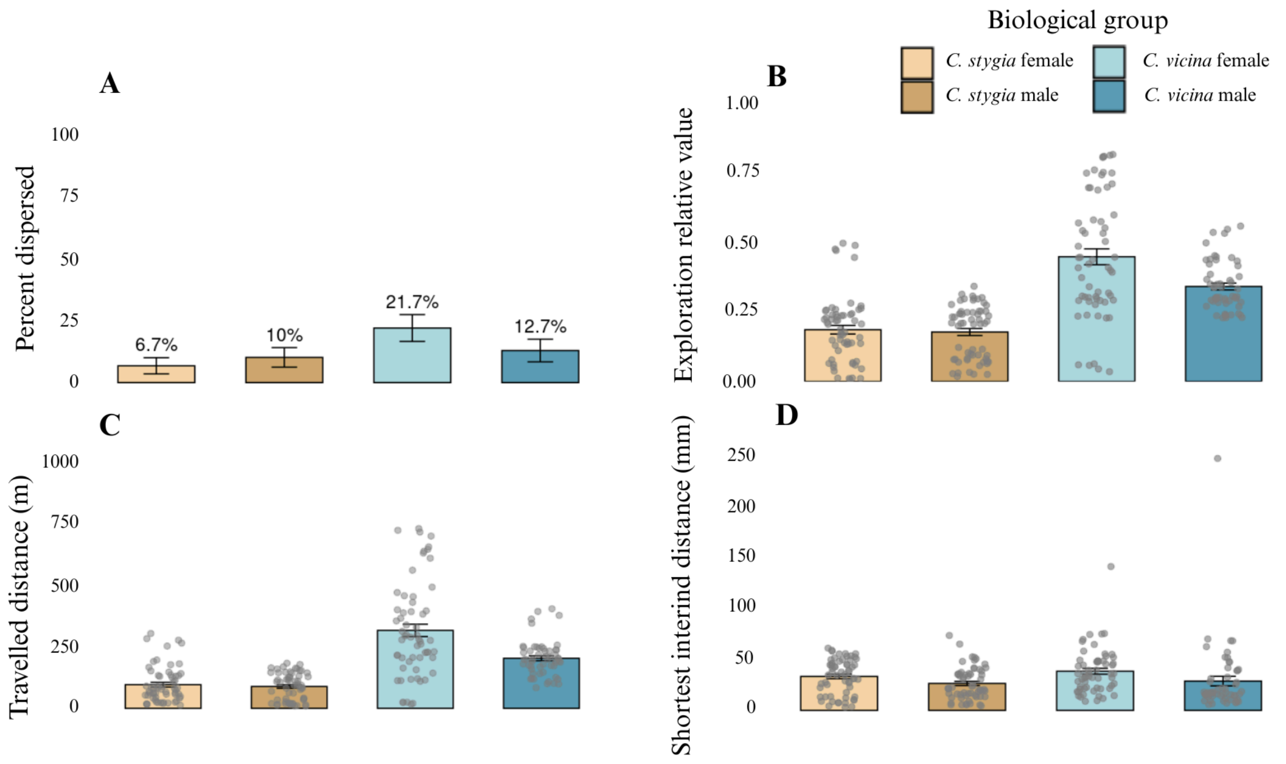


Figure 2.4. Behavioural trait comparisons between *Calliphora vicina* and *Calliphora stygia* across sexes in the group 2-patch assays: **A.** The percentage of individuals that dispersed during the assay;. **B.** The exploration relative value, indicating how much of the arena each individual explored;. **C.**

The total distance travelled (m); **D.** The shortest interindividual distance (mm), which reflects how close individuals remained to their nearest conspecific. In all panels, vertical error bars indicate ±1 standard error and individual-level data points are shown in grey. The legend indicates the corresponding biological groups across all figures.

Table 2.4. Type III likelihood ratio tests from generalised linear mixed models examining the effects of species, sex, and their interaction on dispersal tendency (family = binomial), travelled distance, exploration relative value, and mean shortest interindividual distance (family = Gaussian) in the 2-patch arena. All models included a random intercept for assay to account for replicate-level variation. Significant values indicated in bold.

Response variable	**Variable**	**χ^2**	**df**	***p*-value**
Dispersal probability	Species	3.697	1	0.055
	Sex	0.055	1	0.815
	Species * Sex	1.637	1	0.201
Travel distance	Species	119.338	1	**< 0.001**
	Sex	22.290	1	**< 0.001**
	Species * Sex	17.714	1	**< 0.001**
Exploration relative value	Species	132.718	1	**< 0.001**
	Sex	9.717	1	**0.002**
	Species * Sex	7.110	1	**0.008**
Mean shortest interindividual distance	Species	1.494	1	0.222
	Sex	7.444	1	**0.006**
	Species * Sex	0.212	1	0.645

Exploration relative value differed strongly among groups (species: $\chi^2_1 = 132.72$, $p < 0.001$; sex: $\chi^2_1 = 9.72$, $p = 0.002$; species×sex: $\chi^2_1 = 7.11$, $p = 0.008$) (Fig. 2.4B; Table 2.4). *C. vicina* females had the highest exploration (0.450 ± 0.018), followed by *C. vicina* males (0.343 ± 0.019), whereas *C. stygia* females and males exhibited lower values (0.187 ± 0.018 and 0.178 ± 0.018, respectively).

Similarly, the total distance travelled (m) during the assay differed significantly among groups (species: $\chi^2_1 = 119.34$, $p < 0.0001$; sex: $\chi^2_1 = 22.29$, $p < 0.001$; species×sex: $\chi^2_1 = 17.71$, $p <0 .001$) (Fig. 2.4C; Table 2.4), with female *C. vicina* moving the farthest (315.4 m ± 14.3 m), followed by male *C. vicina* (185.7 m ± 15 m), and*C. stygia* females and males travelling shorter distances (95.7 m ± 14.3 m and 88.3 m ± 14.3 m, respectively).

Finally, mean shortest interindividual (mm) distance varied with sex ($\chi^2_1 = 7.44$, $p = 0.006$), but not species ($\chi^2_1 = 1.49$, $p = 0.222$) or their interaction ($\chi^2_1 = 0.212$, $p = 0.645$) (Fig. 2.4D; Table 2.4). Females maintained greater minimum distances (*C. stygia*: 33.9 mm ± 3.05; *C. vicina*: 39.1 mm ± 3.05) than males (*C. stygia*: 26.9 mm ± 3.05; *C. vicina*: 29.3 mm ± 3.18).

2.4.2 Behavioural variation in 9-patch assays

Dispersal probability (dispersed = 1, not dispersed = 0) in the 9-patch assays did not vary significantly with species (*C. vicina* vs. *C. stygia*: $\chi^2_1 = 0.476$, $p = 0.490$), sex ($\chi^2_2 = 1.586$, $p = 0.453$), or their interaction ($\chi^2_2 = 2.301$, $p = 0.317$) in the GLMM (Fig. 2.5A; Table 2.5). Estimated marginal means indicated broadly similar probabilities across groups (*C. stygia* female = 0.777, male = 0.750, mixed = 0.767; *C. vicina* female = 0.733, male = 0.783, mixed = 0.833), with overlapping 95% confidence intervals.

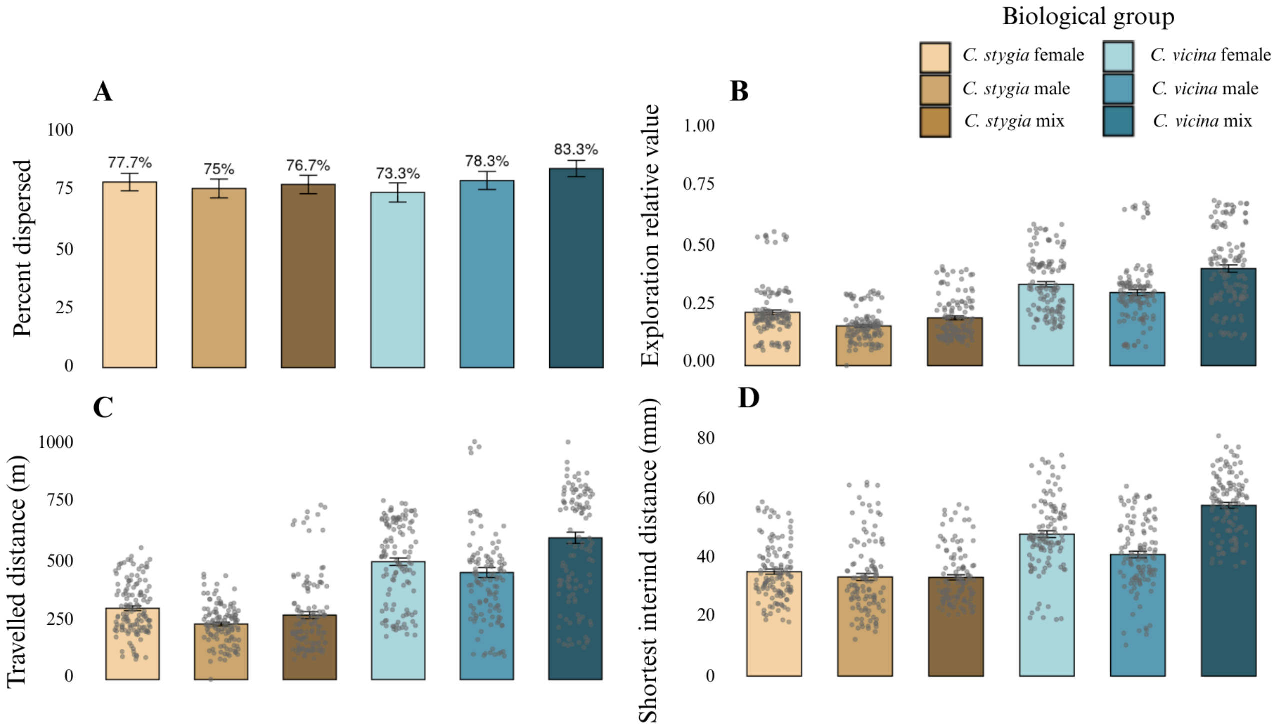


Figure 2.5. Behavioural trait comparisons between *Calliphora vicina* and *Calliphora stygia* across sexes ratios in the 9-patch assays: **A.** The percentage of individuals that dispersed during the assay; **B.** The exploration relative value, reflecting the proportion of the arena explored by each individual; **C.** The total distance travelled (m); and **D.** The shortest interindividual distance (mm), indicating proximity to the nearest conspecific. In all panels, vertical error bars indicate ±1 standard error and individual data points are overlaid in grey. The legend indicates the corresponding biological groups across all figures.

Table 2.5. Type III likelihood ratio tests from generalised linear models examining the effects of species, sex, and their interaction on dispersal probability (binomial), traveled distance (m), exploration relative value, and mean shortest interindividual distance (mm) (Gaussian) in the 9-patch arena. Significant values indicated in bold.

Response variable	**Variable**	**χ^2**	**df**	***p*-value**
Dispersal probability	Species	0.476	1	0.490
	Sex	1.586	2	0.452
	Species * Sex	2.301	2	0.316
Travel distance	Species	345.737	1	**< 0.001**
	Sex	3503.064	2	**< 0.001**
	Species * Sex	18.247	2	**< 0.001**
Exploration relative value	Species	309.641	1	**< 0.001**
	Sex	40.233	1	**< 0.001**
	Species * Sex	18.484	2	**< 0.001**
Mean shortest interindividual distance	Species	1.494	1	**< 0.001**
	Sex	18.736	2	**< 0.001**
	Species * Sex	29.076	2	**< 0.001**

Exploration relative value differed significantly by species (χ^2_1 = 309.641, p < 0.001), sex (χ^2_1 = 40.233, p < 0.001), and their interaction (χ^2_2 = 18.484, p < 0.001) (Fig. 2.5B; Table 2.5), with *C. vicina* exhibiting higher exploration than *C. stygia*, females exploring more than males, and mixed groups generally showing intermediate values. The highest exploration was observed in the *C. vicina* mixed assay (*C. stygia* female = 0.217, male = 0.162, mixed = 0.194; *C. vicina* female = 0.331, male = 0.298, mixed = 0.395).

Likewise, the total distance travelled differed strongly among species (χ^2_1 = 345.737, p < 0.001), sex (χ^2_2 = 3503.064, p < 0.001), and their interaction (χ^2_2 = 18.247, p < 0.001) (Fig. 2.5C; Table 2.5), with *C. vicina* moving farther than *C. stygia*, and females generally travelling farther than males for both species. Mixed groups were intermediate or exceeded males, with the highest distances recorded in the *C. vicina* mixed group (*C. stygia* female = 344.0 m, male = 377.9 m, mixed = 383.4 m; *C. vicina* female = 416.0 m, male = 409.4 m, mixed = 430.5 m).

Finally, mean shortest interindividual distances varied significantly with species ($\chi^2_1 = 1.494$, $p < 0.001$), sex ($\chi^2_2 = 18.736$, $p < 0.001$), and their interaction ($\chi^2_2 = 29.076$, $p < 0.001$) (Fig. 2.5D; Table 2.5). *C. vicina* maintained greater distances than *C. stygia*, females had longer distances than males for both species, and mixed groups were intermediate or exceeded males, with the *C. vicina* mixed assay showing the highest distances overall (*C. stygia* female = 0.039 m, male = 0.037 m, mixed = 0.036 m; *C. vicina* female = 0.050 m, male = 0.043 m, mixed = 0.059 m).

2.5 Discussion

We assessed a variety of dispersal behaviours in two invasive blowflies and found that the more invasive species (*C. vicina*) consistently demonstrated greater mobility and exploratory behaviour under controlled conditions. This is consistent with its higher invasive potential and widespread presence in urban environments. In contrast, the less invasive *C. stygia* showed lower mobility and exploration in our assays, consistent with its more frequent occurrence in rural or semi-natural habitats and potentially reflecting differences in resource use, habitat preference, or tolerance of human disturbance rather than dispersal capacity alone.

In our 2-patch assays, we found that group density significantly affected dispersal likelihood; with individuals in groups (n = 5) substantially more likely to disperse compared to solo individuals, irrespective of their sex. This is consistent with theories of density-dependent dispersal, which predict that individuals are more likely to disperse as conspecific density increases, due to social pressures and the potential for reduced resource availability (Bowler & Benton, 2005; Jreidini & Green, 2024). Such density-dependent dispersal may not only reflect avoidance of competition, but also information-mediated dispersal, where individuals use conspecific presence as a cue to the suitability of the local environment (Clobert et al., 2009). In our study, the lack of sex-based differences in group (and individual) dispersal rates may reflect a behavioural response to spatial uncertainty or crowding. Future research could further investigate how intrinsic traits, such as sex, influence dispersal behaviour, especially in situations where social density is constant, but the ability for individuals to move around or interact with each other differs. We also found a significant species × density interaction on dispersal probability ($\chi^2_1 = 6.07$, $p = 0.014$), with *C. stygia* showing greater sensitivity to density exhibiting higher social grouping at n = 5 than at n = 1 – whereas *C. vicina* maintained a more consistent dispersal probability across density treatments.

Sex-specific dispersal patterns are common in many animal systems and can have important implications for invasion dynamics with empirical studies in a range of taxa showing that differences in movement between sexes can influence the speed and success of range expansion. For example, when one sex is markedly less mobile, invasion fronts may be constrained by the dispersal of that sex – particularly if both sexes are required for successful reproduction at the leading edge (Miller & Inouye, 2012). Our findings suggest that female-biased mobility in *C. vicina* may facilitate rapid colonisation of new patches in the wild, while the more uniform behaviour of *C. stygia* males and females may contribute to slower or more limited expansion.

Alongside sex and density effects on dispersal likelihood in the 2-patch arena, we found that associated metrics of dispersal performance were correlated within species. For example, movement (distance travelled), exploration (exploration relative value) and social (interindividual distances) measures were consistently high in *C. vicina* – particularly in females. This aligns with the concept of correlated behavioural traits influencing dispersal strategies (Bonte et al., 2011; Clobert et al., 2017; Cote et al., 2010) and suggests that dispersal probability (i.e., did or did not disperse) may reflect a threshold-based decision. While many flies are motivated to move, only some cross into the adjacent patch, depending on internal thresholds or stochastic factors (Travis et al., 2012) – reinforcing the idea that dispersal is a multi-component process involving both motivation and capacity (Bonte et al., 2011).

Although species effects did not reach conventional significance in the dispersal propensity model ($\chi^2_1 = 3.70$, $p = 0.055$), they nevertheless provide an intriguing hint that species effects were important in driving dispersal outcomes in our assays. Indeed, *C. vicina* travelled up to 3.3x and 1.2x more than *C. stygia* during the 2-patch and 9-patch assays, respectively. Higher dispersal propensity and rate are often hypothesised to correlate with greater invasiveness (Jessop et al., 2024); although confirming this relationship requires broader comparative studies across multiple taxa (Renault, 2020; Steyn et al., 2016), empirical work in insects has shown that dispersal capacity can facilitate range expansion and invasion success in some systems. For example, rapid evolution of dispersal ability has been demonstrated in the bean beetle (*Callosobruchus maculatus*), where spatial sorting promotes increased spread and variability in invasion dynamics (Ochocki & Miller, 2017).

As the more widespread invasive species, the fact that *C. vicina* individuals (especially females) also maintained greater distances from conspecifics compared to *C. stygia*, suggests that greater social spacing or avoidance tendencies may play a role in invasive species spread in the wild. Consistent with this, *C. vicina* showed higher dispersal behaviours in mixed-sex social environments in our assays, exhibiting enhanced exploration, locomotion, and social spacing – all traits that may be advantageous at invasion fronts, where populations are typically at low densities and individuals can face extreme selective pressures to locate mates and resources efficiently (Berec et al., 2017). In contrast, *C. stygia* displayed more conservative and uniform behaviour across the tested sex ratio compositions, potentially indicating a less flexible strategy that may limit its success in novel environments.

Alternative (or complementary) explanations for our findings include differences in intrinsic activity rates for the two species. For example, *C. vicina* consistently showed higher exploration rates and travelled greater total distances than *C. stygia* in the 9-patch assay. However, these metrics were both highest in the mixed-sex assays, suggesting at least some role for social facilitation, where the presence of the opposite sex stimulates activity (Uzsák et al., 2014). Notably, the *C. stygia* mixed-sex group did not follow the same pattern, showing a lower behavioural responsiveness in the group setting. Increased movement in *C. vicina*, particularly in mixed-sex groups, may also have been driven by non-dispersal motivations, including heightened mate-searching behaviour or hunger-induced foraging, which can both be expected to contribute to an individual's spatial footprint and likelihood of encountering new habitats (Malek & Long, 2019; Muniz et al., 2018). However, hunger-driven movement is an unlikely explanation for our findings, as all blowflies were provided food and water ad libitum until the assay period, thus any hunger effects should have been consistent across individuals and assays. Meanwhile, if mate-searching behaviour was an important trigger for movement, we would have expected to see higher dispersal metrics for males versus females (Miller & Inouye, 2012). Finally, although dispersal traits likely facilitate the use of human-associated habitats (Gippet et al., 2019), it is important to note that synanthropy is more directly linked to dietary breadth, ecological plasticity, and tolerance of human disturbances (Sévêque et al., 2020) – thus, differences among species in our assays are likely representative of a complex suite of factors that interact to ultimately determine species distributions.

Dispersal can contribute to invasion in multiple ways, including through the facilitation of rapid colonisation of new habitats and increased gene flow, and via the avoidance of competition (Kaňuch et al., 2020; Tesson & Edelaar, 2013). Its role is highly important during the early stages of invasion, with factors such as phenotypic plasticity, environmental tolerance, and niche exploitation likely becoming more critical in determining invasive success following population establishment (Davidson et al., 2011). Our study provides valuable insights into species- density-, and sex-specific behavioural strategies that may influence the invasion potential of blowflies. Future research could seek to disentangle the environmental and genetic bases of these behavioural differences. For example, rearing both species under common garden conditions across multiple generations could help clarify whether observed traits are heritable or shaped by early life experiences. Additionally, manipulating resource levels, mating opportunities, or predation cues could reveal how extrinsic ecological factors interact with species identity and social environment to drive movement decisions.

Finally, examining these behaviours across natural gradients of invasion (e.g., urban to rural transitions, or core versus edge populations) would provide real-world context to laboratory-based findings and help refine predictions about the spread and impact of invasive blowfly populations.

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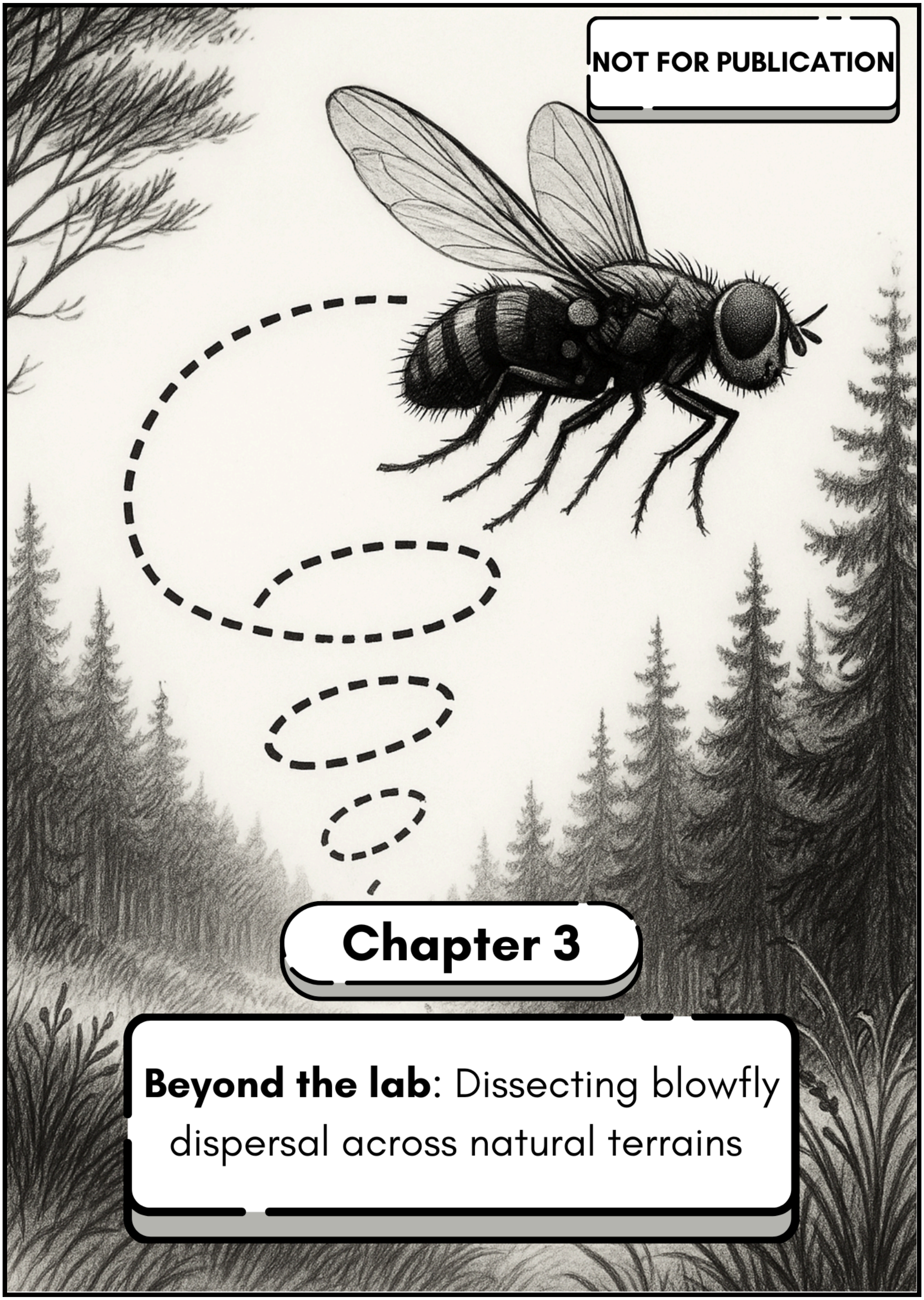


Chapter 3

Beyond the lab: Dissecting blowfly dispersal across natural terrains

3.1 Abstract

The spread of an invasive species depends in part on how successful the organism is at dispersing to new habitats and establishing populations beyond its area of introduction. However, the dispersal behaviour of many invasive species, including New Zealand's invasive blowflies, is not well understood despite their significant ecological roles and economic impacts. In this study, we investigated how invasive blowflies move across two contrasting environments. We captured approximately 4,000 flies, dusted them with fluorescent orange powder, and then released them from a central location at the University of Waikato, Hamilton. A total of 28 baited traps were placed at set intervals along a circular transect (0.5 km, 1 km, 2 km, and 3 km) from the release point. Traps were monitored daily over a 10-day period to assess the movement patterns of released individuals and establish how these differed among species with potentially differing invasive potential. Unfortunately, no marked flies were recaptured in our experiments, suggesting environmental influences, unexpected dispersal behaviours, or possible issues with the experimental design. Nevertheless, we assessed the daily trap catches and found that *Lucilia* spp. had the highest capture rate (50% of all species) and was found in both urban and rural areas. Next abundant was *Chrysomya* spp., which we also captured in both urban and rural traps. In contrast, *Calliphora vicina* was predominately captured in urban-placed traps and had lower recapture rates alongside *Calliphora stygia* and *Calliphora hilli*. These trapping patterns corresponded well with the global invasiveness of the blowflies, with *Lucilia* spp. and *Chrysomya* spp. among the most invasive of the studied species group. Thus, our study provides new data on invasive insect species captured at different sites, and a foundation for future studies by highlighting key areas for refinement in blowfly dispersal research.

3.2 Introduction

Dispersal plays a vital role in range expansion, as organisms with greater dispersal ability have the potential to reach sites faster and further than less dispersive individuals/species, thus aiding their expansion and establishment in new habitats (Perkins et al., 2013; Suarez et al., 2001). Dispersal can be enhanced by natural factors, such as wind and water, or through human-mediated activities, which can rapidly accelerate the introduction of species to novel habitats (Gippet et al., 2019). However, innate dispersal ability differs among species, and has been shown to play an important role in biological invasion (Keenan & Cornell, 2021; Ochocki & Miller, 2017). Understanding how dispersal varies among species is crucial for developing strategies to predict invasion potential and implement effective biodiversity management strategies. Yet, the dispersal behaviour of many invasive species is not well understood.

Insects play a significant role in biological invasions due to their high mobility and adaptability (Meurisse et al., 2018). As per their definition, invasive species have negative impacts on native ecosystems. For example, locusts (e.g., *Schistocerca gregaria*) can form massive swarms and devastate crops, mosquitoes (e.g., *Aedes aegypti* and *Anopheles* spp.) can spread diseases like dengue and malaria (Carlson et al., 2023; Mamo & Bedane, 2021; Maeno et al., 2020), and beetles like the emerald ash borer (*Agrilus planipennis*) can cause widespread ecological and economic damage by attacking native tree populations (Flower et al., 2012).

While dispersal has been well-studied in the model organism *Drosophila melanogaster* (the common fruit fly) the movement patterns of many other fly species with distinct ecological roles and behaviours remain poorly understood. Moreover, dispersal studies of wild populations, particularly multispecies studies, are rare because they are logistically challenging and demand extensive fieldwork and/or genetic analysis to capture accurate data (Clobert et al., 2012). This has left significant gaps in our understanding of insect invasion dynamics and how dispersal differences among species potentially contribute to biological invasions.

Blowflies (*Calliphoridae*) play essential ecological roles in decomposition and disease transmission (Andere et al., 2016; Klong-Klaew et al., 2018). As primary decomposers, they contribute extensively to the nutrient cycling system by consuming organic matter and accelerating the breakdown of animal carcasses and organic waste (Pechal et al., 2014). They also have practical applications in forensic entomology and maggot debridement therapy (Owings et al. 2022; Tombulturk & Kanigur-Sultuybek, 2021). Beyond these roles, blowflies are known for their propensity to invade non-native ecosystems (Daly et al., 2023). Their rapid reproduction cycles, ability to feed off a large variety of food, and strong flight capabilities enable them to rapidly spread. For example, *Chrysomya rufifacies* and *Chrysomya megacephala*, originally native to Africa and Asia respectively, have expanded their ranges to Australia, New Zealand, the Americas, and various Pacific Islands, where they often outcompete native species and disrupt local ecosystems (Chong et al., 2014; Shiao & Yeh, 2008). Meanwhile, *Lucilia sericata* and *Lucilia cuprina* are pervasive causes of flystrike, with both species found across temperate and tropical habitats globally (Baumgartner & Greenberg, 1984; Cruickshank & Wall, 2002). In invaded habitats, blowflies can alter carrion decomposition rates, impact native scavenger species, and even influence forensic investigations by shifting local insect succession patterns (Cruickshank & Wall, 2002; Kerslake & Perkins, 2006).

In this study, we investigated how invasive blowflies in New Zealand disperse across a natural landscape that encompasses both urban and rural habitats. We hypothesised that species with wider global geographic distributions (i.e., putatively 'more invasive') would have greater abundance in our traps overall, as well as in urban habitats due to their higher potential invasiveness and the role of urbanisation in biological invasion, respectively (Owings & Picard, 2018; Potgieter et al., 2024).

3.3 Methods

3.3.1 Collection sites, captured species, and dusting methodology

To maximise species diversity, six blowfly species were collected over a total 6-hr period on 25/03/2024 at two distinct central North Island locations: between 09:00 and 12:00 at the University of Waikato, Hamilton (an urban environment with significant human activity, manicured green spaces, and built infrastructure), and between 12:00 and 15:00 at Ed Hillary Hope Reserve, Waitetuna (a privately owned bush reserve located 40 minutes northwest of the university that features native vegetation and minimal human disturbance). Captured species included: *Calliphora quadrimaculata* (endemic to New Zealand), *Calliphora stygia* and *Calliphora hilli* (found in New Zealand and Australia; 'mildly invasive'), *Calliphora vicina* (spread globally; 'moderately to highly invasive'), *Lucilla* spp (located globally; 'highly invasive'), and *Chrysomya* spp (located globally; 'highly invasive').

Blowflies were actively captured at each location using baited mince traps and manual netting in warm, sunny conditions between 0900 h and 1300 h to coincide with their peak daily activity. Captured flies (~4,000 in total) were immediately transferred into a large, ventilated insect cage 47.5 × 47.5 × 47.5 cm, nylon mesh rearing cage (BugDorm-4H4545; MadHornet, New Zealand) with water and sugar to minimise stress, before being transported to the invertebrate facility at the University of Waikato, Hamilton and thoroughly dusted with an orange fluorescent powder marker (DayGlo, Barnes Products Pty Ltd, Auckland, New Zealand) that allowed for identification under ultraviolet light (Fig. 3.1A). The powder was applied evenly using hand-held fans to create a dust storm inside each blowfly cage, ensuring optimal adherence while minimising any potential impact on fly behaviour (Clymans et al., 2020).

3.3.2 Experimental set-up, including trap construction

A circular study area with a 7 km diameter centered on the University of Waikato was selected to provide a representative mix of environmental and ecological conditions (Lee et al., 2023), encompassing both urban and rural habitats. A network of 28 traps were distributed along four distance transects radiating from the central release site: four sites 0.5 km from the release point and eight sites each at distances of 1 km, 2 km, and 3 km.

Baited bottle traps were constructed using clean 1.5 L soda bottles (Fig. 3.1B). Each trap consisted of a base bottle and an additional top bottle that was cut in half and affixed to the top of the base bottle using black duct tape, forming an enclosed design. The lower portion of the base bottle was painted black and wrapped with black tape to minimise light penetration. Slits (10 mm) were cut into the lower section to serve as entry points for blowflies. A plastic 20 mm tube was inserted into the neck opening of the base bottle and affixed with zip ties, providing an easy surface for flies to ascend towards the upper light part of the trap, while making escape from the base bottle more difficult. The bait, which consisted of decomposing minced beef, was placed inside small breathable plastic bags to allow odour dispersion while restricting access to the meat by eggs and maggots. Traps were deployed in sunny concealed locations, where they were hung from trees in an attempt to avoid predators.

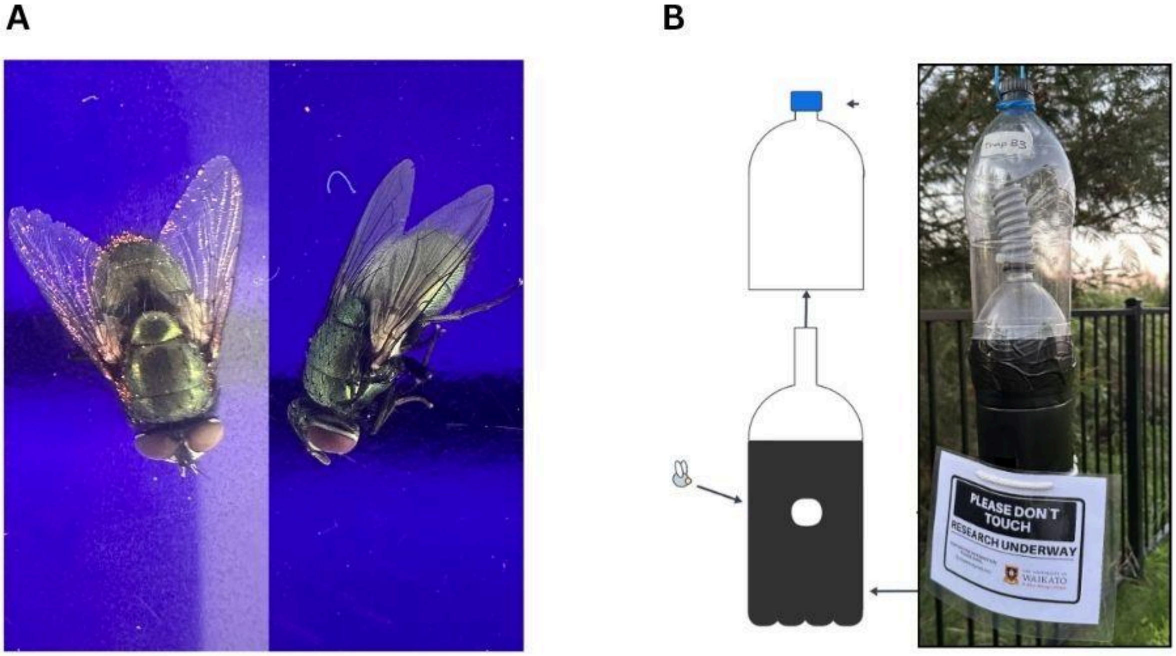


Figure 3.1. Dusting and trap methods: **A.** *Lucilia sericata* under UV light. Left: dusted individual; right: undusted individual. Photo: M. Theobald; and **B.** Blowfly traps. Left: schematic diagram of the trap design. Right: a deployed trap at location B3. Photo: M. Theobald.

3.3.3 Mark and recapture experiment

On the day of release (25/04/2025), all 28 baited traps were first deployed at their designated locations before midday. At 1500 h, marked ~4,000 blowflies were released in a field at the University of Waikato campus by opening the cages and allowing the flies to disperse naturally. For the next ten days, all traps were inspected daily between 0900 h and 1100 h, with bait replaced on Day 5 to counteract natural degradation and loss of potency. Traps were emptied daily and all captured insects were transported to the laboratory and examined under UV light to detect the presence of the fluorescent dust, then sorted and identified to species level using the taxonomic keys of Dear (1986). Daily weather conditions, including temperature, humidity, wind speed, and precipitation were recorded using data collected by Earth Sciences New Zealand to assess potential environmental influences on fly movement and capture rates.

3.3.4 Data analysis

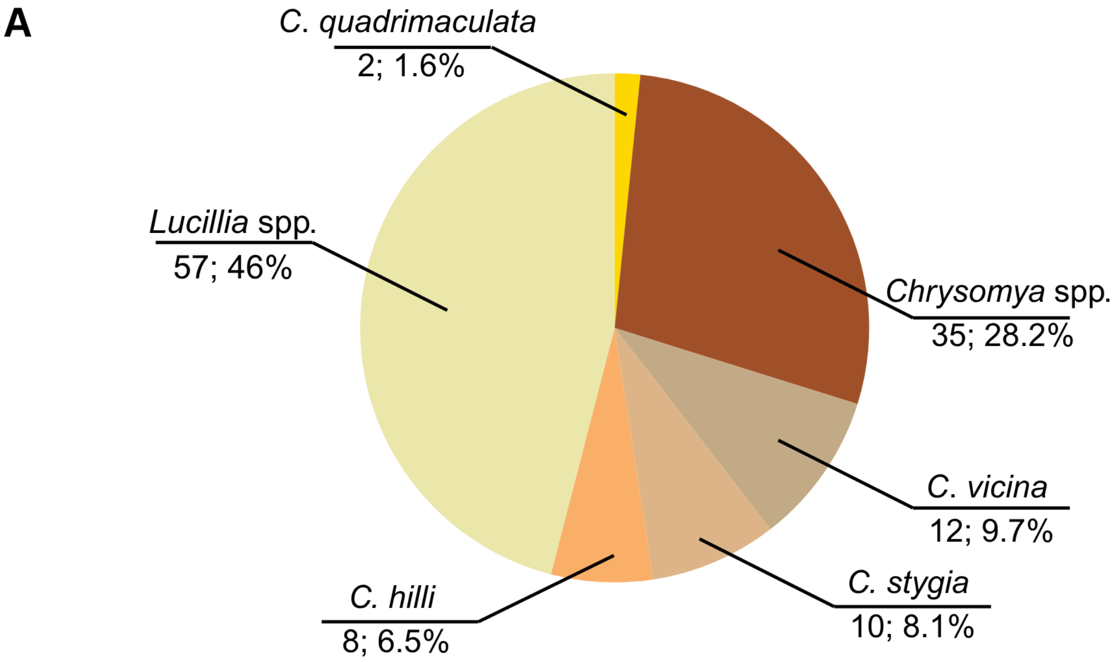
Data was analysed in R version 4.4.2 (R Core Team, 2024). ANOVA was used to assess differences in blowfly species capture across the experiments' temporal and spatial span. Bar plots depicting daily species counts were overlaid with line plots of mean temperature and wind speed, scaled appropriately to allow visual assessment of temporal trends and potential covariation between fly activity and climatic conditions.

3.4 Results

A total of 124 blowflies were captured over the 10-day study period, with a significant majority ($F_{5,48}$ = 5.070; p = 0.001) identified as *Lucilia* spp. (n = 57, ~46%) and *Chrysomya* spp. (n = 35, ~28.2%) – the two more invasive groups in the study (Fig. 3.2A). In contrast, the comparatively less invasive species were more rarely captured (e.g., *C. vicina, n* = 12, ~9.7%; *C. stygia*, n = 10, ~8.1%, and *C. hilli*, n = 8, ~6.5%), while the endemic *C. quadrimaculata* was only found on two days (n = 2, ~1.6%). None of these blowflies were identified as mark-recaptures. In addition to blowflies, the traps also captured 356 flesh flies (*Sarcophagidae*), 2 bumblebees (*Bombus* spp.), 3 beetles (*Coleoptera* spp.), and 6 cockroaches (*Blattodea* spp.).

Blowfly species collections varied temporally across the study period, but these differences were not significant ($F_{8,4 0}$= 1.270, p = 0.290). From Day 4 onward, there was an increase in capture of the more invasive species *Chrysomya* spp. and *Lucilia* spp., which peaked on Day 7 (n = 17 and 12 individuals, respectively; Fig. 3.2B). These two genera maintained counts above n = 5 through Days 8 and 9. In contrast, less invasive species, such as *C. vicina*, *C. stygia*, and *C. hilli* were recorded at low and irregular abundances throughout the study, never exceeding n = 3 per day. The endemic *C. quadrimaculata* was only detected on Days 6 and 9, with a single individual recorded on each occasion. Weather observations indicated that the lowest collection rates occurred when wind speeds were high, and then increased once the wind died down (Fig. 3.2B).

Differences in the abundance and diversity of trapped blowflies were also observed across trap sites, however these were also not significant ($F_{27,252}$ = 2.060, p = 0.130). Specifically, five traps contained only a single blowfly species (*Lucilia* spp., *C. vicina*, or *C. quadrimaculata*), two contained two species, and six traps contained three or more species (Fig. 3.2C). Notably, 15 traps did not capture any flying insects. While there was a trend toward a greater total number of blowflies collected from rural sites (n = 95, 78.5%) compared to urban sites (n = 26, 21.5%), this difference was not statistically significant ($T_{26} = 1.280$, $p = 0.210$). Howerver, rural sites were dominated by the more invasive species, particularly *Lucilia* spp. (n = 52, 55.9%), and showed a higher relative abundance of species such as *Chrysomya* spp. (n = 31, 33.3%), and *C. stygia* (n = 3, 3.2%). Urban sites were dominated by *C. vicina* (n = 7, 30.4%) and *C. stygia* (n = 7, 30.4%), with smaller contributions from *Chrysomya* spp. (n = 4, 17.4%) and *Lucilia* spp. (n = 2, 8.7%).



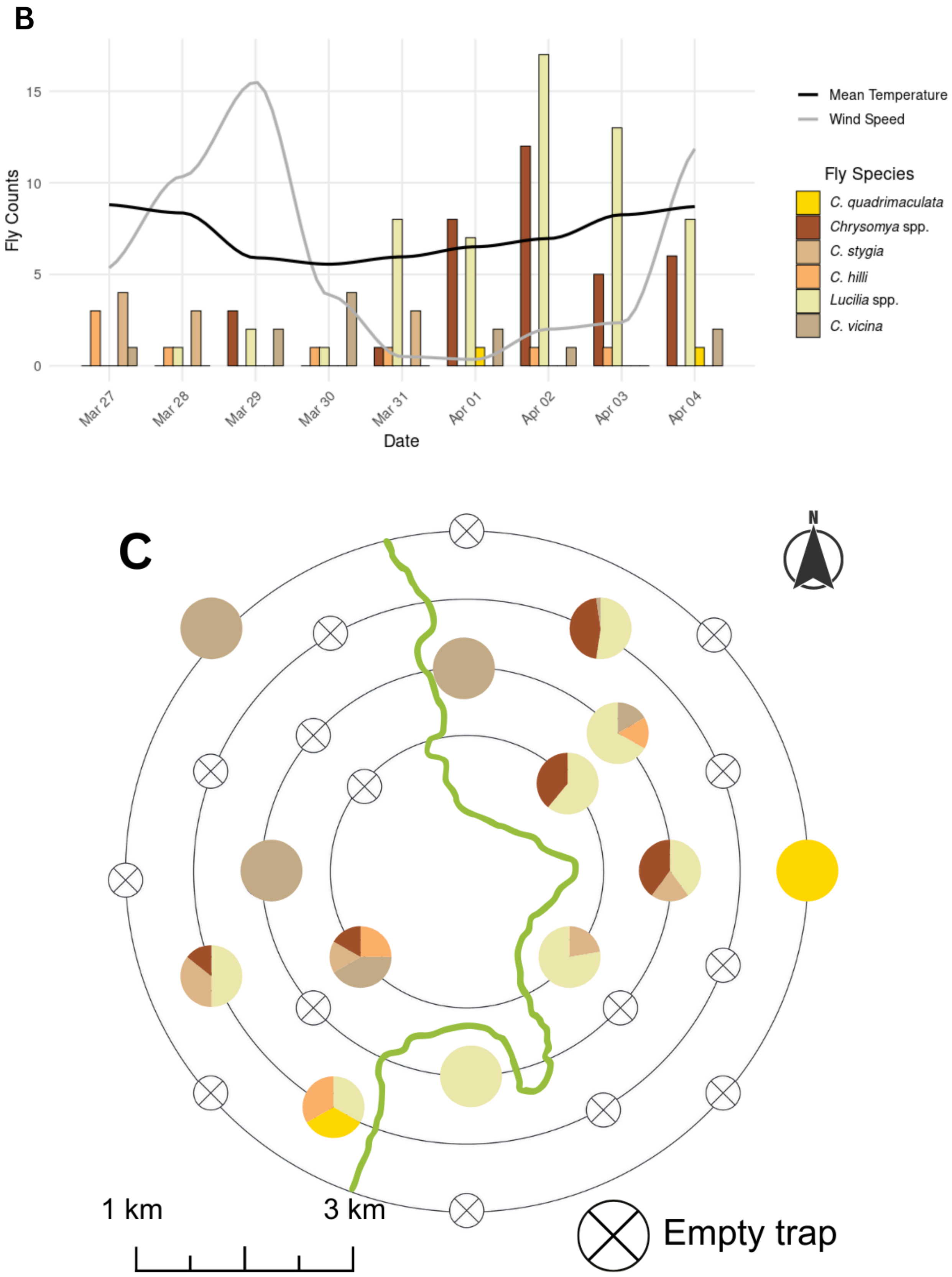

B
Fly Counts
0
5
10
15
Mar 27
Mar 28
Mar 29
Mar 30
Mar 31
Apr 01
Apr 02
Apr 03
Apr 04
Date
Mean Temperature
Wind Speed
Fly Species
C. quadrimaculata
Chrysomya spp.
C. stygia
C. hilli
Lucilia spp.
C. vicina
C
N
1 km
3 km
Empty trap

Figure 3.2. A. The proportion of each blowfly species collected over the 10-day period. **B.** The number of blowfly individuals captured per day for each species, alongside mean temperature and wind speed. **C.** Spatial differences in blowfly capture, with pie charts showing the proportion of each fly species caught at each trap site over the 10-day period. The green line down the centre of the trapping area indicates the habitat divide: the left side is dominated by urban habitats, while the right side is dominated by rural farming sites.

3.5 Discussion

We assessed the natural dispersal behaviour of blowfly species across a 50.27 km^2 field setting using a mark-release-recapture approach. Although no marked blowflies were recaptured, the blowfly species we did trap varied by day and surrounding environment type. Despite being non-significant statistically, they may suggest potential temporal and habitat-specific biological differences in blowfly activity and abundance that could be explored in future research.

While multiple species can co-inhabitat the same environment, their abundances often vary considerably, reflecting the influence of competitive exclusion and other ecological mechanisms that enable them to co-exist in sympatry (Chesson, 2003). Here, we found that some blowfly species were trapped more regularly than others throughout the summer sampling period. Notably, *Lucilia* spp. accounted for over half of all captured blowflies, while *Chrysomya* spp. accounted for 30 percent of all captures. Though these differences were not significant, they aligned with our hypothesis that more geographically widespread invasive taxa would be more frequently trapped, and with literature indicating that these species are highly competitive, often displacing native blowfly species in disturbed or open environments (Cruickshank & Wall, 2002; Rusch et al., 2025). Their high capture rates in this study may therefore reflect their competitive dominance over less invasive blowflies. Experimental studies have shown that *Lucilia sericata* exhibits strong competitive interactions with other blowfly species, such as *Phormia regina* and *C. vicina*, leading to reduced survival and development of the competing species (Hans & Vanlaerhoven, 2021). Similarly, *Lucilia cuprina* has demonstrated significant competitive advantages in various contexts, including intraguild predation and resource monopolisation, which can suppress the presence of other blowfly species (Ivorra et al., 2022).

As well as interspecific competition within genera, blowfly access to necrobiome resources in our study was likely influenced by competitive interactions with more distantly related taxa. Indeed, non-blowfly taxa were captured in our study, with flesh flies in particular showing a high capture rate in urban areas. In fact, a total of 204 flesh flies (out of 356 total) were recorded in urban traps across the study period (compared to 121 total blowflies), likely reflecting their synanthropic tendencies and ability to exploit human-modified environments (Battán‐Horenstein et al., 2020). Though not studied here, the successional order of arrival of individuals and species per trap likely plays a role in influencing competitive outcomes. For example, Eberhardt and Elliot (2008) conducted an experiment in Auckland, New Zealand, using pig carcases to model human decomposition. They found that the primary colonisers at all sites included *C. stygia*, *Chrysomya rufifacies*, and *Hydrotaea rostrata*. Among these, *C. stygia* typically persisted until day 27; *C. rufifacies* larvae appeared from days ~13 to 47; and later stages of decay attracted *H. rostrata*, *Lucilia sericata* larvae, *Psychoda* spp., and *Sylvicola* spp (Eberhardt & Elliot, 2008).

Alongside ecological interactions, microclimate conditions such as temperature, wind, and humidity are known to affect blowfly activity patterns and therefore play a role in shaping their abundance and distribution (Amat et al., 2016; Matilda et al., 2024). We found that blowfly captures varied across the 10-day sampling period in a manner that was consistent with wind speed variability. We also found that species capture varied between traps located at open rural areas versus populated urban regions, with rural areas yielding higher overall blowfly numbers, especially for *Chrysomya* spp. and *Lucilia* spp. Collectively, these patterns are consistent with the work of Goulson et al. (1999), who demonstrated that blowfly abundance and diversity were strongly influenced by microclimatic factors and habitat openness. These findings partially supported our hypothesis. As predicted, the more invasive species (*Lucilia* spp. and *Chrysomya* spp.) were more abundant overall. However, contrary to expectations, these species were captured more frequently in rural sites rather than urban ones. Thus, while global invasiveness may contribute to overall abundance, local habitat features or ecological interactions may mediate their distribution across urban and rural environments (Charabidze et al., 2017; Oh et al., 2024). Variation in the presence of carrion or livestock at rural areas in particular may have contributed to the differences in capture rates we observed, while the cumulative scent from baits may have varied their attractiveness (e.g., Payne, 1965) over both time and space in the different traps. Despite their overall non-significance, the temporal and spatial dynamics in trapping rates we observed highlight the importance of accounting for such variation in sampling efforts when designing similar ecological studies (see also Magni et al. 2019).

We invested considerable effort in designing and executing the mark and recapture trial, though no marked blowflies were ultimately recaptured. Several factors may have contributed to this outcome, ranging from biological and environmental influences to methodological limitations. One possibility is that the dispersal distance of the marked blowflies exceeded the trapping range, particularly if these insects were more mobile than anticipated. Conversely, it is possible that the marked blowflies did not disperse far enough from the release point, remaining within an unmonitored zone within the transect. However, these scenarios collectively seem unlikely when evaluated against previous research. For example, Lee et al. (2023) conducted a mark-recapture study in a Malaysian zoo and oil palm plantation using ~3,000 marked wild blowflies and successfully recaptured 43 (1.5%) individuals at distances ranging from 1 km to 5 km, thus confirming that blowflies are capable of dispersing across our study’s temporal and spatial span. Another important factor could have been the attractiveness of our traps. If the bait we used was less appealing than alternative food sources, such as nearby livestock carcasses or decomposing organic matter, released flies may not have been drawn to our traps. Another plausible explanation lies in the experimental design. The number of flies we released may have been too low relative to the local population, significantly reducing the statistical likelihood of recapture, which was very low in the cited studies (Lee et al., 2023). In addition, the spacing between traps may have allowed for fly movement corridors that bypassed our trap network. Finally, the marking method, although tested under laboratory conditions, may have failed under field conditions due to environmental degradation or abrasion of the fluorescent dust, while UV dusting could have increased predation rates, as some predators, including other insects, can detect UV-reflective surfaces (Lyytinen et al., 2004).

Despite the limitations of the mark-recapture component, this study yielded new insights into blowfly trapping frequency, which may be reflective of local abundance, habitat preference, and temporal variation in blowfly activity. In particular, it highlighted the predominance of invasive species like *Chrysomya* and *Lucilia* across urban habitats and demonstrated that blowfly presence can vary between environments and across time. These preliminary findings should be explored further in hopes that higher trapping rates may reveal significant patterns that hold biological relevance. To improve the likelihood of successful recapture in future trials, we suggest increasing the number of traps deployed and reducing the distance between them, while also exploring the use of different and potentially more attractive bait types. Alternative marking methods should also be compared and stress-tested under field conditions, and the number of released individuals increased to ensure a greater likelihood of recapture. Such modifications would help build a more robust understanding of blowfly dispersal ecology in natural settings.

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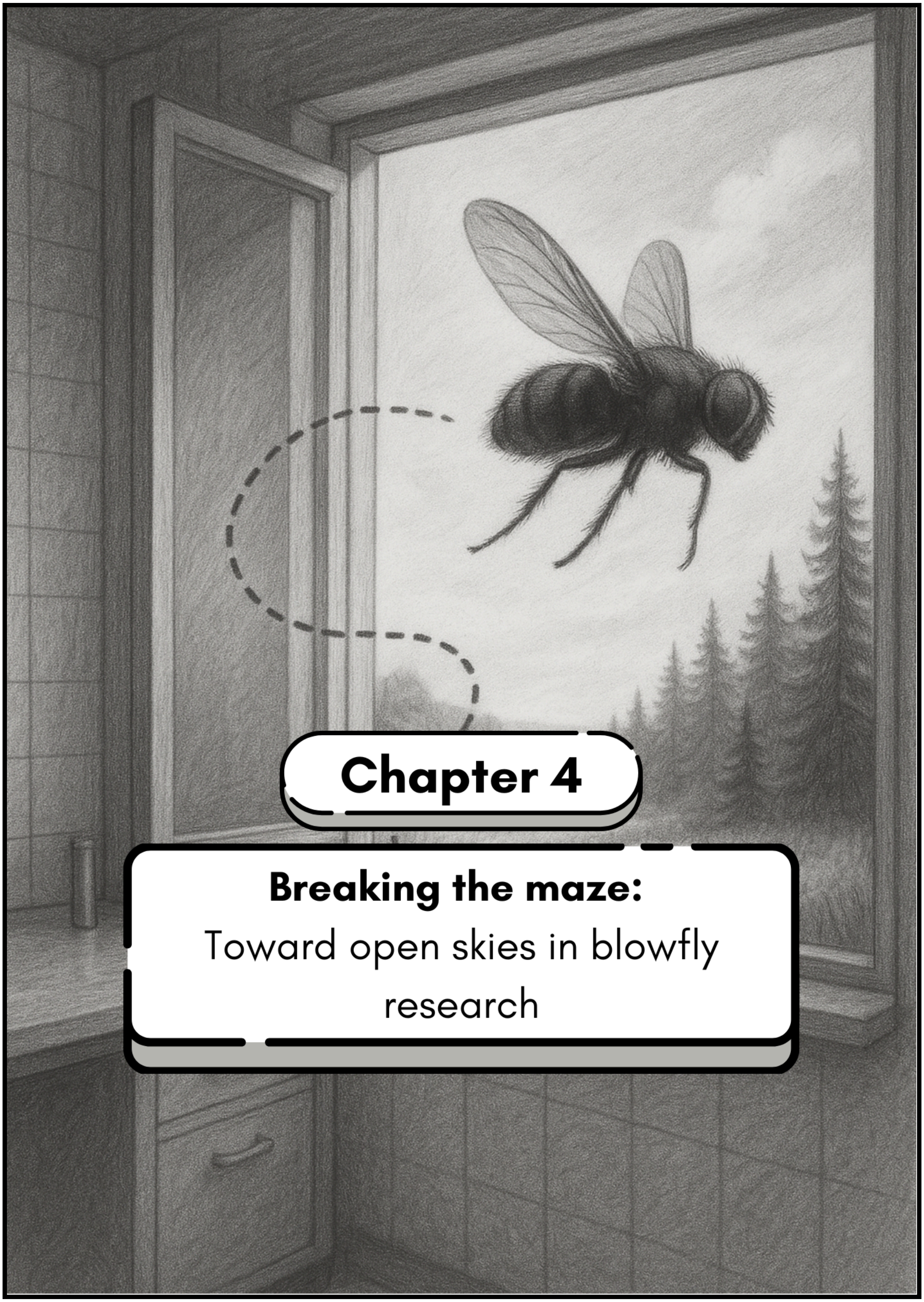

Chapter 4

Breaking the maze:
Toward open skies in blowfly research

4.1 General Overview

The overarching goal of this research was to better understand the dispersal behaviour of invasive blowflies in New Zealand. Understanding behavioural traits, such as dispersal, is critical for predicting and managing the spread of invasive species. Despite the ecological and economic impacts of blowflies, their dispersal behaviour in New Zealand's unique environments remains poorly characterised, limiting our ability to design targeted management strategies.

From the outset, my aim was to investigate how these species disperse across different environments and what factors might drive variation in their movement patterns. This research project began with a field-based mark-recapture trial (Chapter 3) designed to track blowfly dispersal across urban and rural landscapes. Although the lack of marked fly recaptures meant the primary objective of this trial could not be achieved, the study still yielded valuable ecological insights, particularly regarding species composition, relative abundance, and spatial-temporal patterns of blowflies across sites. To further investigate species level dispersal, I shifted my focus to laboratory-based behavioural assays (Chapter 2). This provided more controlled conditions to explore dispersal behaviours in detail. These trials produced statistically robust findings that highlighted the importance of social context, sex, and species identity in shaping dispersal behaviours. Despite early challenges, the combined field and laboratory approach ultimately offered a comprehensive and insightful perspective on the ways in which dispersal behaviour may underlie invasive potential in blowfly species.

4.2 Broader implications / Caveats

One of the more intriguing insights to emerge from this research concerns the potential role of density-dependent dispersal in shaping invasive behaviour. While classical models of invasion often emphasise the role of individual-level traits like mobility or reproductive rate, the behavioural ecology of blowflies in this study was influenced by social dynamics (Elliott & Cornell, 2012). For example, in Chapter 2, we observed a tendency for *C. stygia* to engage in social clumping, a behaviour that may suppress dispersal under high-density conditions. In contrast, *C. vicina* individuals were more spatially dispersed, often found alone or in small groups of one to three. This contrast may reflect fundamental differences in social dynamics between species. Travis et al. (2012) developed an eco-evolutionary framework for dispersal that explicitly models emigration, movement, and settlement as distinct, condition-dependent processes – each with its own set of potential costs (e.g., increased mortality risk, energetic expenditure, reduced fecundity). Their approach allows density to directly influence dispersal decisions, making it particularly relevant to our findings. In this context, the suppressed dispersal we observed in *C. stygia* at high densities aligns with the kind of density-dependent emigration the framework predicts, whereas the more solitary distribution of *C. vicina* may reflect a lower sensitivity to density in the emigration phase.

The differing social dynamics in Chapter 2 raises the possibility that not all invasive species succeed by being hyper-mobile; some may thrive simply because they don’t exhibit the social cohesion that limits movement in other taxa. Indeed, other studies have found that the direction and strength of density-dependent dispersal vary widely across species, with methodological choices strongly influencing observed patterns (Jreidini & Green, 2024). This has important implications for how we conceptualise and model invasions. If dispersal is, in part, inhibited by sociality, then species that are less inclined to aggregate, or whose dispersal increases with density rather than decreases, may hold a competitive advantage in colonising new areas. In other words, the key trait may not be how far individuals can go, but how willing they are to leave when the party gets crowded.

Of course, several caveats should be acknowledged. The behavioural assays were conducted in laboratory settings, which, while controlled, may not fully capture the complexity of natural environments. Moreover, while sociality was clearly a major factor for *C. stygia* dispersal, it is not clear how much of a role it may play in determining dispersal in other species that differ in their general invasiveness. Field validation of these behavioural tendencies will be an important next step. A further consideration is the potential for behavioural plasticity in driving dispersal behaviour in the studied species. It is possible that dispersal and social behaviours shift depending on environmental context. For example, winter moth (*Operophtera brumata*) larvae disperse more when feeding on foliage that has been previously damaged by conspecifics, indicating that host plant condition can trigger dispersal independently of crowding (Pepi et al., 2016). Thus, what appears to be a species-level trait in controlled trials could, in fact, reflect a dynamic response to recent experience, environmental cues, or resource availability. Exploring this further by controlling the recent experiences of the tested blowflies would be beneficial.

The results from Chapter 3 highlighted a potential dominance of the more invasive *Lucilia* spp. and *Chrysomya* spp. in both temporal and spatial dimensions of the trapping array. Despite the absence of any marked recaptures, the dominance of these taxa, particularly in rural habitats, suggests that their true abundance in the wild may be maintained through high local recruitment or ongoing immigration from surrounding areas. The increase in *Chrysomya* spp. and *Lucilia* spp. captures from Day 4 onwards, peaking around Day 7, could reflect alignment between dispersal and meteorological conditions with drops in wind speed coinciding with elevated catch rates. Thus, dispersal in blowflies may not be constant over time but instead modulated by short-term environmental variability, potentially influencing both detection probability and real-world invasion dynamics.

Species-specific differences in spatial distribution were also found in Chapter 3, with rural traps capturing a greater proportion of the invasive taxa and urban traps containing a higher relative abundance of *C. vicina* and *C. stygia*. If reflective of abundances in the wild, these trends may be indicative of habitat preferences shaped by resource availability, microclimate, or competitive interactions. For example, the prevalence of *Lucilia* spp. in rural sites may be linked to the greater availability of livestock-associated resources, whereas the persistence of *C. vicina* in urban habitats may align with its synanthropic nature, exploiting both the cooler microclimates (e.g., air-conditioned buildings) and the abundant anthropogenic resources (e.g., human waste) such environments provide. Though unfortunately non-significant in nature, our findings lay a preliminary foundation for future work and reinforce previous work showing similar habitat-linked patterns in blowfly distribution. For example, in Switzerland, *C. vicina* was most frequently recovered from cooler, shaded, and often urban or indoor environments, reflecting its tolerance for lower temperatures and reduced light (Hodecek & Jakubec, 2022). Likewise, Cruickshank and Wall (2002) *Lucilia* blowflies have been shown to aggregate along pasture edges in warmer, more humid microhabitats associated with livestock, suggesting that resource availability and microclimate jointly shape their distribution.

The absence of recaptures in Chapter 3 prevented direct measurement of movement distances; however, the temporal turnover and habitat bias in species composition in our trapping data suggested the potential for dynamic dispersal processes in the wild that are influenced by both abiotic and biotic factors. When considered alongside the social dynamics described in Chapter 2, these results reinforce the idea that invasion success in blowflies is not solely a function of high mobility; rather, it emerges from an interplay of species-specific habitat affinities, environmental windows for movement, and potentially density- or socially mediated dispersal thresholds.

4.3 Recommendations

During the course of my research, I identified a few key areas where my approach could have been strengthened. In hindsight, some of these were avoidable. For instance, in my mark-recapture experiments, I now believe that I used too few traps and released too few blowflies to adequately capture movement dynamics. If I were to repeat this work, I would add at least two additional interior trap rings (16 more traps, which would undoubtedly have increased general capture rates) and substantially increase the number of released blowflies to improve recapture rates and spatial resolution. Furthermore, though the main focus of my research was blowflies, I regret not extending the scope of my laboratory assays to include additional species (e.g., *C. quadrimaculata* and *Lucilia* spp.) as well as to conduct comparative studies of interspecific dispersal patterns within my study area. Expanding both the taxonomic and methodological breadth of the research would have provided a more comprehensive understanding of movement behaviour and its ecological drivers. Meanwhile, in the laboratory experiments, I could have expanded the scope by incorporating a broader range of environmental variables, such as temperature fluctuations, humidity levels, and light cycles, to better mimic natural habitat conditions influencing dispersal behaviour. Including multi-species interactions would also have allowed examination of how social cues and interspecific competition shape movement and settlement decisions.

Building on the insights discussed above, several key recommendations emerge for future research on blowfly behaviour and invasive ecology more broadly. One particularly relevant application of this work lies in understanding dispersal behaviour within fragmented populations. Invasive species often persist in patchy or human-modified habitats, where the ability (or willingness) to disperse between fragments is critical for persistence and spread (O'Reilly-Nugent et al., 2016). Behavioural mechanisms, such as density-dependent dispersal, social aggregation, or species-specific movement tendencies could strongly influence invasion dynamics in these settings (Galib et al., 2022; Mahdjoub et al., 2023). For instance, highly social species like *C. stygia* may experience self-imposed dispersal bottlenecks in isolated patches, while more asocial species like *C. vicina* may be better equipped to exploit fragmented environments.

If I were to continue this research, I would focus on experimentally manipulating population density and spatial configuration in semi-natural field enclosures to test how habitat fragmentation influences dispersal decisions in *C. stygia* and *C. vicina*. These experiments could be paired with mark-recapture or molecular tracking methods to quantify real-time movement across fragmented landscapes. Additionally, I would aim to explore behavioural plasticity in response to changes in social environment, resource availability, and habitat structure. A promising avenue for future work would be to explicitly compare species under shared experimental conditions, ideally across a gradient of densities and resource distributions. This would help isolate which traits are species-specific versus other kinds of context-dependent. Such comparative frameworks could also be expanded to include native blowfly species (e.g., *Calliphora quadrimaculata*) to investigate whether behavioural traits linked to invasiveness show clear divergence from native counterparts.

Parallel genomic research currently being conducted by the Invasomics Lab at the University of Waikato, New Zealand is providing critical insights into dispersal mechanisms from the perspective of population structure, gene flow, and evolutionary dynamics in invasive blowflies (e.g., Croft et al. 2024). Combining behavioural data with these genomic datasets could help reveal whether certain dispersal or social behaviours are genetically conserved, recently evolved, or potentially under selection in the introduced range. This integrative approach could deepen our understanding of how behaviour and genetics jointly shape invasion potential.

4.4 Conclusions

This research set out to uncover the behavioural mechanisms underpinning dispersal in invasive blowflies, with the broader aim of understanding how these traits might contribute to their ecological success in New Zealand. While initial field-based attempts to track dispersal via mark-recapture were limited by a lack of recaptures and low numbers of general blowfly captures, these early challenges provided valuable lessons and prompted a shift toward behavioural assays under controlled conditions. This pivot yielded robust and insightful results, revealing that dispersal is not simply a matter of movement capacity, but is shaped by social context, sex, and species identity. In particular, the tendency of *C. stygia* to engage in social clumping suggests that conspecific density may actively suppress dispersal, a pattern that contrasts with the more solitary and spatially dispersed behaviour of *C. vicina*. These findings challenge the assumption that invasive species always disperse further or faster and instead highlight that invasion potential may be just as much about when individuals choose not to move. Together, my research underscores the importance of integrating behavioural ecology into the study of biological invasions. Dispersal is not a fixed trait, but a dynamic, context-sensitive behaviour influenced by both internal states and external environments. As such, understanding how these behaviours operate and vary across species, densities, and landscapes is essential for predicting invasion patterns and managing their impacts.

Flies don’t just invade landscapes, they invade living rooms, kitchens, and every annoying corner in between. Like them or not, their persistence is a lesson in relentless movement shaped by subtle behaviour and circumstance. Understanding these sovereign sojourners means peeling back the layers of what drives them, because to outsmart an invader, you first have to understand why it won’t leave. This research is a step in that direction.

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