MODELLING INDIVIDUAL HETEROGENEITY IN BEHAVIOUR FOR WILDLIFE MANAGEMENT AND CONSERVATION

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GIORGIA VATTIATO

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The Work was supervised by:
PROF. MICHAEL PLANK, DR. RACHELLE BINNY, ASSOC. PROF. ALEX JAMES, ASSOC. PROF. ISABEL CASTRO

Signature

GIORGIA VATTIATO

Per Mamma, che mi ha spinto ad esplorare il mondo
e per Papà, che mi ha insegnato il valore delle piccole cose

Abstract

When modelling the population dynamics of wild animals we traditionally assume individual variation in behaviour is of only minor relevance to population dynamics. However, just like humans, animals exhibit consistent variation in behaviour among individuals ("personality") and most wild populations are behaviourally heterogeneous.

In this thesis, we defend the argument that individual heterogeneity in animal behaviour should not be treated only as a source of "noise" in models. Instead, significant behavioural differences between members of the same species can have important consequences for population-level processes and ecological interactions. We ask to what extent individual heterogeneity affects pest eradication, what modelling strategies can be used and what kind of empirical data allow us to quantify these effects.

Using the example of invasive mammal pest species in New Zealand, we first perform a meta-analysis to summarise some key characteristics of these species' trappability and space use, across a range of population densities, habitats and types of surveillance device. We then used numerical simulations to show that individual heterogeneity and the possible transmission of personalities from parent to offspring can have significant effects on the eradication of these species. Finally,

we analyse empirical data from field trials to explore the different behavioural profiles observable in North Island brown kiwi, a bird species at the core of New Zealand's wildlife conservation efforts.

The significance of this study is that it adds to our theoretical understanding of animal personalities by introducing a focus on their implications on wildlife management, and informs on what factors to consider when designing field experiments aimed at quantifying animal personalities.

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CHAPTER 1

Introduction

1.1 Personal motivation

I was motivated to write this PhD thesis because I found the subject of wild animal personalities fascinating. The study of animal behaviour has always been of great interest to me and I had never before thought that the personalities of individual animals could affect the dynamics of an entire population. In addition, creating mathematical models of such interesting complex systems seemed like a great challenge that I was keen to take on, and one that I hoped would give me a good toolbox to begin my career as a researcher. Finally, I believe that non-human animals should be regarded as sentient individuals, with minds and rights of their own. Describing and analysing the complexity of their behaviours seemed like a great occasion to shine a better light on this issue.

1.2 Scope and aims

Animals have often been observed to display different modes of behaviour, also called "behavioural syndromes" (Sih et al., 2004) or "animal personalities" (Bell, 2007; Wolf and Weissing, 2012). The word "personality" is used to describe individual differences in characteristic patterns of behaviour, emotion and cognition of an individual. Even though the word is commonly associated to humans, "personality" can be used to describe non-human animal behaviour as well. Animal personalities are generally defined as repeatable between-individual differences in behaviour that are consistent across situations (Réale and Dingemanse, 2012; Sih et al., 2004).

The study of animal personalities has been the focus of many behavioural and evolutionary studies for several decades. Much research has been conducted on the *why* and the *how* of animal personalities, with ample explanations of the mechanisms affecting the emergence and transmission of personality traits (Réale et al., 2010a), as well as of the ecological implications of such personalities (Sih et al., 2012). Less is known about the implications that these personalities, or their distribution in wild animal populations, have on management of wildlife populations. Personalities have been observed to play a major role in many mechanisms of population dynamics, ranging from population growth and persistence to species interactions and community dynamics (Wolf and Weissing, 2012). Ecological and evolutionary implications of personalities include, but are not limited to, population density (Hughes et al., 2008), reproduction (Santicchia et al., 2018), dispersal and space use (Wauters et al., 2021; Chapple et al., 2012; Cote et al., 2010), disease transmission dynamics (Vanden Broecke et al., 2019; Barber and Dingemanse, 2010; Lloyd-Smith et al., 2005), evolution (Johnstone and Manica, 2011; Sih et al., 2003), survival and trappability (Vanden Broecke et al., 2021). A more comprehensive review can be found in Table 1 of Wolf and Weissing (2012).

The concept of "animal personality" or "behavioural syndromes" and its novelty or importance was the subject of some controversy in the literature (Beekman and Jordan, 2017; David and Dall, 2016; Réale et al., 2010a). This is mainly due to the complex mechanisms surrounding personality, but also because the terminology

and methodology associated with them are inconsistent (Roche et al., 2016; Réale et al., 2010a). In particular, some of the traits often used to characterise animal personalities (such as "shyness" and "boldness") don't have a universal definition and are often used to refer to different behaviours, it is therefore difficult to make comparison across studies (David and Dall, 2016).

This thesis aims to answer the following questions: (1) what modelling strategies allow us to quantify the effects of animal personalities on pest eradication and threatened-species management? (2) What impact does individual heterogeneity in behaviour have for pest eradication and for the management of the threatened-species at the focus of New Zealand's current conservation efforts? (3) How much and what kind of field data is needed for a robust and accurate prediction of personality distributions in wild animal populations?

This research will add to the growing literature surrounding models of animal personalities. It has the main aim of aiding wildlife managers to make more informed choices to better understand and control animal species. It will be relevant to both theoretical modellers aiming to include animal personalities in their predictions of population dynamics, and to empiricists seeking information on the quantity and quality of field data needed to correctly estimate animal personalities.

A significant portion of this thesis focuses specifically on the detectability and eradication of small mammal pests in New Zealand. In Chapters 2, 3, and 4, we attempt to answer the questions of how and when pest control should be tailored to effectively manage populations where animal personality is a significant contributor to the emergent population behaviour. This work could useful to New Zealand's wildlife conservationists and modellers by providing new insights on the sometimes neglected effects of animal personalities on pest eradication.

1.3 Organisation

This thesis is organised as follows: we begin by providing some background on the biology of animal personalities, the existing models that include them, and the

implications for New Zealand's current conservation efforts and goals (Chapter 1). While this work is mainly theoretical, we apply our models in two contexts that are of particular relevance to New Zealand's wildlife: small mammal pest management, and the behaviour and welfare of a vulnerable endemic bird species.

The second and third chapters are therefore dedicated to the management of invasive small mammals in New Zealand and their behaviour. Following a meta-analysis on their trappability and home-range sizes, under a range of different environmental and surveillance conditions, we present a model where we compare the success and time to eradication for populations exhibiting different levels of trappability.

The fourth chapter explores vertical transmission of personalities. We consider once again the example of invasive mammal pest management, but this time we expand our models to include the transmission of trap-shyness from parent to offspring, as well as density-dependent reproduction and home-range sizes. This chapter also includes a simulation exercise aimed at exploring different ways to model density-dependent encounter probabilities.

The fifth and final chapter focuses on behaviour and personality in North Island brown kiwi (*Apteryx mantelli*), an endemic bird species threatened by invasive predators. We use results from two field experiments aimed at measuring different behavioural responses to external stimuli by a number of males and females, and perform statistical analysis to highlight their different personalities, as well as trying to link these differences to other internal and external factors. We also present a power analysis on the quantity and quality of data needed to correctly detect brown kiwi personalities in different scenarios.

1.3.1 Thesis publications

A paper on the effects of individual heterogeneity on the eradication success, derived from Chapter 3 of this thesis, has been published in 2021 by *Theoretical Ecology* (Vattiato et al., 2021). A literature review on New Zealand's small mammal pest detectability, derived from Chapter 2 of this thesis, is in the final editing

process and will soon be submitted for publication. A paper on North Island brown kiwi's behavioural responses to olfactory stimuli, derived from Chapter 5.1 of this thesis, is currently in the editing process.

1.4 The biology of animal personalities

The multifaceted nature of personalities makes them difficult to measure. Personalities are made up of behavioural traits that are often interlaced with one another (Merrick and Koprowski, 2017) and that can fluctuate depending on the situation. Examples of commonly studied behavioural traits are boldness/shyness, curiosity, aggression, sociability, activity levels. When we consider our own behaviour as humans, we can all agree that it can vary from day to day, depending on our mood, our health, our hormone levels, our life history. That being said, there are recurring trends in our behavioural reactions to certain stimuli. These trends are more or less consistent over time for each individual, but can greatly vary from person to person. The same considerations can be made for non-human animals: any dog or cat owner can attest to their pet's consistent shyness, playfulness, or aggressiveness.

In the next section we review the existing literature surrounding the different factors found to influence animal personalities.

1.4.1 What makes a personality?

Several theories have been proposed regarding which factors may influence an animal's personality. The majority of studies focused on one of four main groupings of factors: vertical transmission (genetic transmission and parental effect), within-generation information transmission (including eavesdropping and behavioural plasticity), and ecological niches.

Vertical transmission When offspring consistently exhibit similar behavioural responses as those of their parents, we say that that's a result of vertical transmission of personality. A considerable body of literature has explored the effects

of vertical transmission (which includes the concepts of genetic heritability and parental effect) on the shaping of personalities. Heritability of personality traits is usually estimated by measuring the similarities between relatives, and is often expressed as the proportion of phenotypic variance that can be attributed to additive genetic variance (*i.e.* the inheritance of a particular allele from parents and this allele's independent effect on a specific phenotype) (Falconer, 1996; Wilson et al., 2010). Evidence was found for the transmission of aggression (Bell, 2005), boldness (Bell, 2005; Réale et al., 2000; Strandberg et al., 2005), exploration (Dingemanse et al., 2002; Drent et al., 2003), risk-taking (White and Wilson, 2019; Van Oers et al., 2004), anti-predator behaviour (Bize et al., 2012), and docility (Martin et al., 2017).

Prior research also suggest that behavioural traits are not inherited independently of each other (van Oers et al., 2005; Dingemanse and Reale, 2005). Several studies highlighted the existence of correlation between traits, *e.g.* aggression and boldness (Bell, 2005; Strandberg et al., 2005), boldness and docility (Réale et al., 2000), assertiveness and sociability (Gosling, 1998).

Additive genetic variance (the deviation from the mean phenotype due to inheritance of a particular allele and this allele's relative effect on phenotype, Falconer (1996)) was found to be a primary contributor to personality (Dochtermann et al., 2015), but not the only contributor (van Oers et al., 2005). Another aspect of vertical transmission is parental effect, *i.e.* the influence that parents have on their offspring's behaviour, beyond genetic transmission (Reddon, 2012). For example, young may learn from the parents to respond to predators with behaviours that we consider reflective of shyness (hiding) or on the contrary of boldness (fleeing).

Interestingly, while some researchers have highlighted how a behavioural trait could only be transmitted by biological parents, but not foster parents (Bize et al., 2012), several studies suggest the opposite: certain behaviours (such as exploration and stress response) are inherited via strictly non-genomic mechanisms (Schuett et al., 2013; Champagne and Meaney, 2001; Francis et al., 1999).

Within-generation information transmission Some authors have also suggested that animal behaviour could be affected by an animal's behavioural plasticity (a behavioural change resulting from exposure to stimuli, such as changing environmental conditions), by epigenetics (the influence of the environment on the genome), and by social interactions with other members of the population different than the parents. Note that while personality is subject to developmental plasticity, the concept of personality implies consistency of behavioural responses to similar stimuli. Consequently, if behaviour remains plastic throughout life it would not be thought of as a personality.

While the shaping of animal personality has a strong genetic component, epigenetic effects have also been proposed as a key mechanism influencing behavioural variation (Verhulst et al., 2016; Groothuis and Trillmich, 2011). This mechanism has been observed in cases where the environment where offspring live differs to the parents'. For example, passerine birds raised with low food availability and high sibling competition were found to develop higher levels of exploration and aggressiveness than their siblings raised with high food availability and low competition (Carere et al., 2005).

Several studies have discussed the influence that external stimuli such as predation and social interactions have on animals' behaviour (Frost et al., 2007; Schuster et al., 2006). The general consensus is that animal behaviour and personality are state-dependent (*i.e.* dependent on strategically relevant features such as age, physical condition, environment type (Wolf and Weissing, 2010)) and that between-individual behavioural variation results from adaptive evolution (the biological mechanism by which organisms adjust to new environments) rather than from stochastic evolutionary processes (Dingemanse et al., 2007). For example, animals may adapt their behaviour after observing that of their peers ("eavesdropping") (Schuster et al., 2006; Katz and Lachlan, 2003). Examples of behavioural traits that can be acquired through social learning include anti-predator behaviour (Vilhunen et al., 2005; Brown and Laland, 2003) and boldness (Frost et al., 2007).

Frost et al. (2007) observed a shift in rainbow trout's boldness level after winning or losing fights. Other life-history elements such as resource competition

(Dingemanse et al., 2004; Cote et al., 2008), foraging patterns (Toscano et al., 2016), predation (Dhellemmes et al., 2021; Bell, 2007; Dingemanse et al., 2007), and parasitism (Barber and Dingemanse, 2010), have also been observed to affect animals' behavioural profiles. For example, (Dhellemmes et al., 2021) identified predation as the main driver for foraging habitat choice and exploration personality in lemon sharks (*Negaprion brevirostris*): when predators were less abundant, the sharks displayed increased exploration and foraged in riskier habitats, and vice versa.

Ecological niche The role that organisms play within their community, their ecological niche, is also a determining factor of personality. Bergmüller et al. (2010) suggested that animal personalities evolve from the drive to reduce niche overlap (individuals using the same resources or other environmental variables) and reduce conflict. On a similar note, Sih et al. (2015) and Wolf and Weissing (2010) review the role of positive feedback loops between state and behaviour in explaining animal personalities, meaning that individual behaviours are shaped by the environment that they find themselves in. An example of this is given by Wauters et al. (2019), who showed that red squirrels' sociability was likely the result of context-related advantages when co-occurring with a competing species.

Groothuis and Carere (2005) also mentioned adaptive plasticity to the environment as a contributing factor to the shaping of animal personalities. However, they highlighted that maternal effects and genetics are just as important. Other studies suggest a so-called "gene-environment" interaction (Stamps and Groothuis, 2010). This interaction can go both ways: environmental pressure can shape an animal personality, or animals with given personalities might either shape ("niche constructing") or choose ("niche picking") the environment that best fits them.

1.4.2 Evolutionary advantage of animal personalities

At first, consistent behavioural responses do not appear to be a very sensible evolutionary strategy: natural selection usually favours more flexible and adaptive traits to make individuals more resilient against a changing environment and dif-

ferent threats. For example, an animal that is only bold when it needs to be (*e.g.* when competing for food), should have a better fitness than one that is always bold, even in risky situations (*e.g.* when confronted with a predator).

Why then do we observe animal personalities, even if they appear maladaptive? Bell (2007) hypothesises that it would be too hard to transform one's personality, as this would require significant amounts of time and energy to rewire neural machinery or to change one's physiology to support a new metabolism. Bell (2007) also state that the environment is often too uncertain for individuals to make correct predictions on what behavioural mode would be most advantageous for a given situation (McElreath and Strimling, 2006). The best strategy for an individual would therefore be to find an "intermediate" personality that enables the animal to cope sufficiently well in most situations.

However, if there exists one intermediate strategy that maximises an animal's fitness, why do we encounter different personalities within the same population? Assuming that personality traits are heritable (van Oers et al., 2005) and related to fitness (Dingemanse and Reale, 2005), then the fitness of a strategy might depend on the frequency of other strategies employed within a population (Dall et al., 2004; Wilson and Yoshimura, 1994). For example, if most individuals in a population exhibit a particular behavioural pattern, a few others might take advantage of the "open niche", void of competitors, by behaving the opposite way (Bell, 2007).

Other hypotheses link individual behaviour to a "life history strategy". For example, Wolf et al. (2007) created a model where individuals could either reproduce early in life, or later, after having acquired higher-value resources. Individuals that followed the former strategy, having less to lose, would then exhibit more risky behaviour (increasing their chance of acquiring high-value resources) in the short time preceding their reproduction. Those following the latter strategy would exhibit a less risk-prone behaviour, as they could more easily die in the long period of time before reproducing. Each individual's degree of risk-taking behaviour would then result from the trade-off in the quality of acquired resources between early versus late reproduction. Similarly, (Réale et al., 2010b) used the hypothesis of "pace of life" syndrome to propose that consistent individual differences in

behaviour covary with life history at the within-population level.

1.5 Existing models incorporating animal personalities

In many contexts, it is important that models account for individual behavioural differences in order to correctly interpret field observations and to make accurate predictions about dynamics of populations. However, modelling animal personalities, whether to explain their emergence under certain conditions, to quantify between-individual behavioural differences, or to assess their effects on the emergent properties of populations, is not a straightforward task. Incorporating animal personalities in models comes with the challenge of having to test the model's assumptions and parameters using empirical data from field experiments. As we will show later in this thesis, these experiments require to be carefully designed in order to extract the necessary information on the population of interest.

In this section we present the existing literature surrounding (1) the quantification of animal personality and (2) the inclusion of animal personalities in models of population dynamics. Some of the methods reviewed here served as a basis for the modelling work presented in later chapters of this thesis.

1.5.1 Quantifying personality

One of the first steps in understanding the relative contribution of animal personalities to population-level behaviour is to quantify behavioural variation within a population. The differences in behaviour observed in a population can be partitioned into two sources: "between-individual" variation and "within-individual". Between-individual variation corresponds to the differences in the average behaviours of different individual animals, for example due to personality or other intrinsic biological traits (*e.g.* age, sex). Within-individual variation, on the other hand, is a measure of an animal's behavioural consistency, *i.e.* how consistent each individual's behaviour is across repetitions of the same situation. Evidence of significantly greater than zero between-individual variation relative to within-

individual variation, for a given behavioural response to an external stimulus, suggest the presence of different personalities within a population.

A useful tool to partition these two sources of variation is mixed effects modelling. These models allow exploration of patterns in hierarchical data structures (such as data including multiple repetitions for each individual) through the introduction of fixed effects (parameters that do not vary) and random effects (parameters that are themselves random variables and can be used to measure within-individual variation). A comprehensive description of this method can be found in Dingemanse and Dochtermann (2013), where the authors present the concept of "repeatability": a standardised measure of individuality, or the phenotypic variation attributable to between-individual differences. In Chapter 4, we apply these concepts to field data measuring the behaviour of kiwi.

In order to measure these behavioural variations, field experiments must be conducted following specific design methods, which we will discuss in Chapter 5. Bell et al. (2009) detailed how repeatability is affected by the experimental conditions (*e.g.* interval between repetitions, field vs. lab), and stated that different behavioural traits can have different levels of repeatability for the same individual. In particular, recent literature highlights the importance of conducting experimental repetitions for each individual to effectively measure behavioural plasticity (Stamps, 2016; Dingemanse and Dochtermann, 2013).

A number of empirical studies have been conducted to quantify animal personalities, with several examples of research aimed at aiding conservation efforts. Examples relating to New Zealand's ecosystem management efforts include studies on the trappability of ship rats (*Rattus rattus*, Nathan (2016)) and stoats (*Mustela erminea*, King et al. (2003)), the effects of stoat trap-shyness on the survival of brown kiwi (*Apteryx mantelli*) chicks (Robertson et al., 2016b), the links between personalities and survival of the *hihi* (*Notiomystis cincta*, an indigenous threatened bird of New Zealand) (Richardson et al., 2019), and the effects of personalities in rodents' foraging patterns (Smith et al.). Some studies conducted overseas have also found evidence of animal personality in some of New Zealand's key pest species, such as the dietary specialisation in brushtail possum (*Trichosurus vulpec-*

ula , Herath et al. (2021)) and individual differences in black rats' (*Rattus rattus*) exploration (Žampachová et al., 2017).

Another approach to quantifying animal personality is through "behavioural reaction norms" (BRN), defined as the set of behavioural phenotypes that a single individual produces in a given set of environments (Dingemanse et al., 2010). In other words, BRN allow to combine between-individual behavioural variation (linked to animal personality) and animals' responses to environmental variation (behavioural plasticity).

1.5.2 Personality in models of population dynamics

As individual personalities have been observed to play a major role in many mechanisms of population dynamics (Wolf and Weissing, 2012), it is important to take them into consideration when building models of such dynamics. This is commonly achieved by using individual-based modelling: a method allowing explicit representation of individuals, each with their own set of attributes.

One of the main difficulties in modelling animal personalities is model calibration. In the previous subsection, we outlined the different techniques used to quantify personality from empirical data. However, most field trials aimed at measuring personality, especially that of wild animals, are conducted in unrealistic and artificial set-ups, which might bias the observed behavioural responses used for model calibration. In addition, some personality traits are extremely difficult to measure in the field because of the very nature of the trait. For example, measuring shyness or trappability of wild animals requires observation of even the shyest individuals in the population, which are by definition very hard to detect without employing highly intensive surveillance techniques.

Individual heterogeneity has been incorporated in a number of existing models. For example, Anderson et al. (2016) included trap-shyness in their models of pest control, Armstrong et al. (2021) included variation in survival, reproduction and detection rates in their model of small population dynamics, García-Díaz et al. (2021) explored different scenarios of individual foraging specialisation in invasive

predators, and Tuck et al. (2015) incorporated individual heterogeneity in susceptibility to fishing in their models of albatross' population dynamics. A number of studies focused specifically on including heterogenous trappability in capture-recapture models for population size estimations. Most of these methods are based on the heterogeneous population models firstly described by Otis et al. (1978), the most common example being the popular SECR (spatially-explicit capture-recapture) model, developed by Efford and Fewster (2013) and used in modern software for population density estimations.

1.6 New Zealand's conservation context

In this thesis we focus on the modelling of individual behavioural differences in two main contexts that are of critical relevance to wildlife conservation in New Zealand: small mammal pest management and the conservation of the native brown kiwi.

Because of New Zealand's geographic isolation from the rest of the world, this country's endemic plant and animal species have evolved in very unique ways. New Zealand's ecosystems have remained completely unperturbed until the arrival of the first human settlers, estimated to have occurred around 1200 and 1300 AD (Wilmshurst et al., 2008). Following the first human settlements, 35 native bird species and several species of native flightless insects and reptiles have been recorded as lost to extinction due to ecosystem perturbations, such as hunting and predation by introduced dogs and Polynesian rats (Anderson, 2002; Clout and Lowe, 2000; Towns and Daugherty, 1994).

New Zealand's ecosystems were further endangered two centuries ago by the arrival of European immigrants, who destroyed large areas of native habitat and introduced numerous invasive species. One of the most destructive groups of introduced species is that of terrestrial mammalian predators, such as possums (*Trichosurus vulpecula*), rats (*Rattus rattus*), mice (*Mus musculus*), stoats (Mustela erminea), ferrets (*Mustela putorius furo*), and cats (*Felis catus*). As the endemic terrestrial mammalian fauna of New Zealand was restricted to only two species of bat (Daniel, 1979), most indigenous species of New Zealand are incredibly vulnerable

to introduced mammalian predators' attacks, having never evolved defence or escape mechanisms against them (Tennyson, 2010; Innes et al., 2009). On top of the increased predation on endemic animal species brought by the invasive mammals, New Zealand's native ecosystems have also suffered from resource competition and over-browsing from invasive species (Clout and Lowe, 2000). For example, invasive herbivorous mammals such as possums, deer and goats continue to perturb the structure of many native plant communities with their selective browsing (Owen and Norton, 1995; Clout and Lowe, 2000). In addition, New Zealand's ecosystems are affected by factors endangering many other countries' ecosystems, such as changes in land and sea use, direct exploitation of species, climate change, and pollution. Overall, introduced alien species have caused the extinction of 78 endemic species (across all taxa), and placed 1037 of the 14255 known native species in the "Threatened" category (Department of Conservation, 2021).

In 2020, the New Zealand Department of Conservation published *Te Mana o Te Taiao* (New Zealand Department of Conservation, 2020), a document outlining strategies aimed at restoring and preserving the declining populations of endemic species. The documents lists New Zealand's goals for 2025, 2030 and 2050 surrounding the protection of its ecosystems through legislation, collaboration with New Zealanders and management of biodiversity threats. One of the main conservation goals outlined in this document is the elimination of key invasive predators (ferrets, weasels, stoats, possums and rats) from New Zealand by 2050. This ambitious goal has inspired several research projects (including the ones presented in this thesis) surrounding the eradication of invasive mammal predators. Another important goal presented in *Te Mana o Te Taiao* is that of reversing the decline of indigenous fauna, such as kiwi, one of New Zealand's endemic bird genus, which has also inspired some of the research presented in this thesis.

In the next three chapters, we focus on one of the greatest threats facing New Zealand's ecosystems: invasive small mammal pests. We first present a systematic review of the trappability of these species, we then explore different eradication outcomes by simulating the population dynamics of behaviourally heterogeneous populations of pests, and we finally study the effects of vertical transmission of

trap-shyness on eradication outcomes.

CHAPTER 2

Analysis and literature review

on the detectability of invasive small mammal predators in New Zealand

As discussed in this thesis' introduction, small mammal pest management is very important in the preservation of New Zealand's ecosystems, and collecting knowledge on the population dynamics and behaviour of these invasive species has been one of the main focus of New Zealand's pest managers.

In this chapter, we provide a comprehensive review of available data on detection parameters for invasive mammal species, highlighting differences in trappability and space use between species and sexes, and across different habitats and seasons. Some of this data will then be used to calibrate our simulation models in the following chapters.

2.1 Introduction

In New Zealand, invasive small mammal predators are driving serious declines in native populations of birds (Innes et al., 2010), invertebrates (**?**), herpetofauna (**?**) and vegetation (**?**). Ship rats (*Rattus rattus*), brushtail possums (*Trichosu-*

rus vulpecula) and stoats (*Mustela erminea*) are generally considered the main threats to native flora and fauna because they are abundant, arboreal and ubiquitous across mainland New Zealand; however, other rodent and mustelid species, European hedgehogs (*Erinaceus europaeus*) and feral cats (*Felis catus*) also contribute to these declines (King and Forsyth, 2021). To conserve threatened species, pest control programmes have been implemented across New Zealand's North and South Islands, and offshore islands. Suppression or eradication of small mammal pests is currently achieved by trapping and/or toxic baiting, where baits are applied across a grid of ground-based stations, usually over relatively small spatial areas, or delivered aerially over larger landscapes (Russell et al., 2015). The success of these programmes relies on having effective control and surveillance methodologies, underpinned by knowledge of the ecology of target species; for example, the dynamics of pest populations, how they disperse, and their interactions with other species in New Zealand's ecosystems.

Surveillance of pests guides conservation and wildlife disease management programmes, both prior to control commencing (e.g. providing baseline data and planning optimal control strategy or eradication monitoring programmes) and during (e.g. (Parkes et al., 2006)). After operations, surveillance also allows managers to assess whether targets for residual levels of pests have been achieved. If the goal is complete eradication, surveillance informs decisions on when eradication can be confidently declared and monitors for future reincursions (Gormley et al., 2021; Russell et al., 2017). Pest surveillance is often undertaken using stationary detection devices, such as live ground traps, trail cameras and tracking tunnels, which provide data (e.g. images of animals or live captures) on the presence or absence of a pest animal at the device's location. Quantitative models play an important role here, by utilising surveillance data to infer information about the current state of a pest population or to predict information ahead of time (e.g. simulation models). Useful parameters include the densities of pest populations over space and time, the sensitivity of pest surveillance systems (i.e. device type, density and layout; and frequency or duration of surveillance operations), the probabilities of local eradication given animals are no longer detected during surveillance operations, or the time required to achieve complete eradication (Gormley et al., 2021; Russell

et al., 2017; Samaniego-Herrera et al., 2013).

Models using surveillance data typically incorporate a parameter of pest 'detectability' for a given surveillance method. Often, the goal is to infer population density while detectability is merely a nuisance parameter. In other contexts, detectability is the main parameter of interest, for example, when assessing the effectiveness or sensitivity of different surveillance systems for detecting target pests. Understanding how varying biological (e.g. sex, age) or environmental conditions (e.g. habitat type, seasonality) affect detectability also provides ecological insight into pest behaviour, fundamental for designing effective approaches to control (Duron et al., 2020). A plethora of simulation models, requiring prior knowledge of detectability or inferring this from data, have been developed. This includes agent-based models which simulate individual animals and track their numbers and/or movements over time. Spatially-explicit capture-recapture (SECR) models (Efford and Fewster, 2013) are commonly applied to infer population density and spatial detectability parameters from live-trapping capture-recapture data (Borchers and Efford, 2008). Proof-of-absence models, a decision-support tool for eradication programmes, estimate the probability of eradication (given no animals are detected during surveillance) and surveillance system sensitivity, and require detectability information as a model input (Anderson et al., 2013; Russell et al., 2017).

The probability of a pest being detected by a stationary detection device, P_{detect}, can be expressed as a product of the probability of a pest encountering the device, and the probability of the pest being detected by that device given it encountered it. For small mammals utilising a home-range area, the likelihood of a pest encountering a device can vary over space so P_{detect} also varies spatially. P_{detect} is often assumed to be highest if the device is located at the animal's home-range centre, and decays for devices located nearer the home-range periphery or beyond. Detection probabilities are therefore commonly defined as decaying spatial detection functions $P_{detect}(d)$ of the distance d between an animal's home-range centre and the device location. A half-normal detection function is commonly assumed, though other functional forms including hazard-rate, negative exponential or uniform, may be more appropriate for certain species or detection methods.

A half-normal detection function comprises two parameters. The first, an intercept g_0, is the probability of an animal being detected by a device that is located at its home-range centre in a single unit of survey effort (often one trap night), i.e. the maximum probability of detection at a distance $d = 0$. The second parameter σ is a spatial-decay parameter that scales the detection function relative to an animal's home-range size. An animal is typically assumed to occupy its home-range, on average, according to a symmetric bivariate normal distribution, such that the area an animal occupies 95% of the time is a circle of radius 2.45σ with area $\pi(2.45\sigma)^2$ (Efford, 2004). A half-normal detection function is therefore given by

$$P_{detect}(d) = g_0 \exp\left(\frac{-d^2}{2\sigma^2}\right) \tag{2.1}$$

These detectability parameters, g_0 and σ, can be inferred alongside population density by fitting SECR models (which assume that home-range centres are Poisson-distributed with density D) to capture-recapture data. Readily available software, such as DENSITY (Efford et al., 2004) and the 'secr' (Efford and Fewster, 2013) package in R statistical software (R Core Team, 2015), has been developed for this purpose. Alternatively, parameters can be inferred using independent methods; for example, σ is related to home-range size, which can be estimated by animal telemetry. Values of g_0 and σ vary depending on the biology of pest species and population density, via differences in average home-range size and behaviour. Environmental factors influencing behaviour and/or density, including habitat (e.g. food supply) and season, therefore also affect both parameters. For example, possum home-range sizes are known to increase during seasonal heavy fruiting of native tree species, as they forage a larger area to utilise this food resource (Ward, 1978). In addition, g_0 (but not σ) depends on the surveillance technique, for example the efficacy of different detection device or lure types Nathan (2016).

For many species, increases in population density are associated with decreases in home-range size due to interactions (e.g. competition) between contiguous neighbours (Adams, 2001). This inverse relationship between density and σ is well documented for possums in New Zealand (Rouco et al., 2013; Efford et al., 2016).

In New Zealand's beech forest and alpine grassland systems, populations of house mice, ship rats and mustelids undergo sporadic irruptions following pulses of food resource released during heavy masting events (synchronous production of large amounts of seed) (Wardle, 1984; Wilson and Lee, 2010; Walker et al., 2019). These periodically high population densities are likely associated with smaller values of σ. For spatially decaying detection functions there is also a correlation between g_0 and σ, with increases in σ (i.e. increasing home-range size) corresponding to decreases in g_0 (Ramsey et al., 2005; Sweetapple and Nugent, 2018). This is explained by an animal with a larger home range having a lower chance of encountering a device at its home-range centre because it spends less time there on average than an animal with a smaller home-range.

Estimates of g_0 and σ are reported in the literature (primarily in SECR studies), usually for individual pest species at a single study site. To date, there has been no attempt to collate detectability estimates for all of New Zealand's mammalian pest species across a variety of surveillance techniques (though see single-species reviews by (Glen and Byrom, 2014). In this work, we conduct a comprehensive review of studies reporting spatially-explicit detection parameter estimates, for key small mammal pest species in New Zealand. We compute summary values and quantify the dependencies between g_0, σ and density for application in future modelling (e.g. as model priors). We also assess how detectability varies under different biological, environmental and surveillance conditions, to provide insight into pest behaviour and efficacy of different surveillance methods. Finally, we identify critical knowledge gaps to help prioritise future research.

2.2 Methods

We collated information from New Zealand studies on spatial detectability parameters g_0 and σ for brushtail possum (*Trichosurus vulpecula*), four rodent species (ship rat, *Rattus rattus*; Norway rat, *R. norvegicus*; kiore, *R. exulans*; and house mouse, *Mus musculus*), three mustelid species (stoat, *Mustela erminea*; ferret, *M. furo*; and weasel, *M. nivalis*), feral cat (*Felis catus*) and European hedgehog (*Erinaceus europaeus*). We included all studies where detection probability g_0

and spatial-decay parameter σ were estimated by fitting SECR models to capture-recapture data. We also included studies reporting empirical measures of g_0, based on field observations of pest behaviour in close proximity to detection devices (see e.g. Nathan (2016)), or estimates of home-range size, typically obtained from telemetry data using minimum convex polygons (MCP) or kernel density estimation (KDE). Home-range size estimates were converted to a corresponding σ value using:

$$\text{HR size (in m}^2) = \pi(2.45\sigma)^2, \tag{2.2}$$

where HR size is the radius of circular home-range area occupied by an average animal 95% of the time.

We reviewed published studies, unpublished contract reports, unpublished datasets, and theses. From each study, we extracted estimated mean or median values and associated uncertainty for g_0, σ and density. For studies that mentioned but did not report g_0 or σ, authors were contacted to request estimates. We also extracted information on the sex of the animal, dominant habitat type (classified as beech (*Fuscopora* and *Lophozonia* spp.) forest, mixed beech/podocarp-broadleaved forest, podocarp-broadleaved forest, kauri forest, exotic plantations, alpine grassland, open-country, urban, wetland, braided riverbed), device type (live ground traps, tracking tunnels, hair-snag tubes, snap trap tunnel, bait station, or camera traps), season, location, study type (SECR or home-range size), detection function (half-normal, negative exponential, hazard rate or uniform), and the software/model method used. For studies in New Zealand beech forest or alpine grassland systems, we recorded whether the study was conducted during or following a "mast year" to indicate whether populations were likely to be at low or high density. Where it was available, we also recorded details of the detection device model, device layout and spacing, bait/lure type, study location and the survey month/year.

Extracted values were pooled across studies to calculate summary statistics. For species with sufficient data, we used SECR estimates to quantify the relationships between g_0 and σ, and between population density and σ. We also assessed the

effects of habitat and seasonality on g_0, and of sex on σ, by pooling g_0 and σ across habitats, seasons and sex, and comparing their means. For consistency, if multiple detection functions were used to estimate g_0 and σ values within the same study, we always retained the parameter values reported for the half-normal function, which was most commonly applied across all studies. Where multiple models were fitted repeatedly to the same dataset and parameter values reported for each, we selected only the best model, as determined by AIC. If AIC was not reported, we chose the estimates from the null M_0 model (Otis et al., 1978) using the maximum likelihood closed-population estimator of population size, for pooling across studies so as not to violate statistical independence assumptions.

2.3 Results

Our literature search yielded 21 New Zealand studies reporting spatial detectability parameters for the selected key pest species, resulting in 178 estimates of g_0 and σ. An additional 58 studies provided a further 158 estimates of σ or home-range size (which we converted to σ, see Methods) only. A full list of studies and their attributes is provided in Supplementary Material and summarised in Table 2.1.

Table 2.1 shows the means and ranges of g_0, σ, and density estimates reported in each study for the ten pest species, along with the detection method and habitat type. Possums (24 studies) and ship rats (16 studies) were most commonly studied. We found only a few home-range size studies for Norway rats (4 studies), kiore (1 study) and weasels (1 unpublished study), and no SECR studies for these species to provide an estimate for g_0. Over all studies and species, the vast majority of detectability parameters were reported for live ground traps, though device models, spacings and baits/lures varied widely. We also found two SECR studies for camera traps (for cats and hedgehogs), three for tracking tunnels (ship rats and stoats), and one for bait stations and snap trap tunnels (ship rats). However, representation of devices and habitat types within species was uneven and sparse. Urban environments were under-represented across all species: we found no studies providing g_0 estimates, and three studies reporting home-range sizes for possums, one for ship rats and one for Norway rats. No SECR studies were conducted in

wetland habitats.

Table 2.1: Summary of mean estimates of spatial detectability parameters g_0, σ (metres), and density (animals per ha) for New Zealand's key small mammal pest species for different detection methods and habitat types. Estimates were extracted from SECR studies or home-range size studies (home-range size estimates were converted to σ). Where only one estimate was provided, we reported its value in the "mean" field, and left "range" empty. Where more than one estimate was provided, we reported the mean and the range of all estimates. Reported values were pooled across sexes.

Species	g_0 mean	g_0 range	σ (m) mean	σ (m) range	Density (ha^{-1}) mean	Density (ha^{-1}) range	Study type	Detection method	Habitat	Reference
Possum	0.05	-	63	-	-	-	SECR	LGT	OC/B	(Ball et al., 2005)
	0.22	0.12-0.35	27.88	24.55-34.39	10.81	8.33-15.91	SECR	LGT	B/PB	(Efford and Cowan, 2004)
	0.23	0.16-0.26	48.49	47.90-48.70	1.88	1.67-2.45	SECR	LGT	E	(Efford et al., 2005)
	0.17	-	35	-	-	-	SECR	LGT	OC	(Ramsey et al., 2005)
	0.11	0.03-0.19	40.5	31-50	-	-	SECR	LGT	PB	(Ramsey et al., 2005)
	0.11	0.08-0.13	29	27-31	-	-	SECR	LGT	B/PB	(Ramsey et al., 2005)
	0.24	-	50	-	-	-	SECR	LGT	E	(Ramsey et al., 2005)
	0.10	0.05-0.17	42.64	26.53-63.70	5.42	3.63-9.39	SECR	LGT	B/PB	(Richardson et al., 2017)
	0.07	0.04-0.09	116.42	104.53-146.75	0.62	0.44-0.94	SECR	LGT	OC	(Rouco et al., 2013)
	0.13	-	97.00	-	1.05	-	SECR	LGT	OC/PB	(Sweetapple and Nugent, 2018)
	-	-	38.01	28.48-47.53	-	-	Home-range size		U	(Adams et al., 2014)
	-	-	127.07	125.92-128.22	-	-	Home-range size		OC	(Brockie et al., 1987)
	-	-	60.33	47.19-73.47	-	-	Home-range size		OC	(Byrom et al., 2008)
	-	-	25.14	23.03-27.25	-	-	Home-range size		E	(Clout, 1977)
	-	-	18.44	16.28-20.6	-	-	Home-range size		B/PB	(Crawley, 1973)
	-	-	32.27	24.5-40.05	-	-	Home-range size		U	(Fitzgerald and Innes, 2017)
	-	-	106.36	98.51-114.22	-	-	Home-range size		B/PB	(Green and Coleman, 1986)
	-	-	31.20	21.85-40.55	-	-	Home-range size		OC	(Jolly, 1976)
	-	-	24.55	21.85-27.25	-	-	Home-range size		OC	(Paterson et al., 1995)
	-	-	56.45	38.26-73.55	-	-	Home-range size		B	(Pech et al., 2010)
	-	-	42.26	30.03-54.49	-	-	Home-range size		OC	[Ramsey]*
	-	-	29.00	26.26-31.74	-	-	Home-range size		E	(Triggs, 1982)
	-	-	19.27	19.27-19.27	-	-	Home-range size		E	(Warburton, 1977)
	-	-	41.30	37.13-45.48	-	-	Home-range size		B/PB	(Ward, 1978)
	-	-	53.70	25.23-79.77	-	-	Home-range size		E	(Whyte et al., 2013)
	-	-	33.02	28.2-37.84	-	-	Home-range size		U	(Winter, 1963)
Ship rat	0.05	0.04-0.05	23.99	19.50-28.82	12.68	12.10-13.41	SECR	LGT	B/PB	(Carpenter, 2020)
	0.40	0.29-0.51	8.32**	6.05-10.6	27.75	21.6-33.9	SECR	LGT	B	(Efford and Hunter, 2018)
	0.29	0.20-0.40	18.6**	13-23	5.82	4.1-10.5	SECR	LGT	B/PB	(ManaakiWhenua, 2020)
	0.12	0.09-0.18	18.75**	12-25	3.43	2.3-5.7	SECR	LGT	B	(ManaakiWhenua, 2020)
	0.14	0.05-0.25	14.67**	13-23	5.77	4.1-10.5	SECR	LGT	PB	(ManaakiWhenua, 2020)
	0.12	0.02-0.28	16.42	9.80-12.04	13.30	9.2-20.0	SECR	LGT	K	(Nathan, 2016)
	0.27						SECR	TT	K	(Nathan, 2016)
	0.29						SECR	BS	K	(Nathan, 2016)
	0.01						SECR	STT	K	(Nathan, 2016)
	0.03	0.02-0.04	31.57	27.80-37.40	6.33	5.4-8.7	SECR	LGT	B/PB	(Wilson et al., 2007)
	-	-	8.14	-	-	-	Home-range size		PB	(Daniel, 1972)
	-	-	21.42	-	2.90	-	Home-range size		K	(Dowding and Murphy, 1994)
	-	-	10.03	9.68-10.38	-	-	Home-range size		U	(Fitzgerald and Innes, 2017)
	-	-	10.09	9.11-11.08	-	6.52-11.60	Home-range size		PB	(Harper and Rutherford, 2016)
	-	-	16.64	-	-	1.8-2.3	Home-range size		PB	(Hickson et al., 1986)
	-	-	23.09	-	6.20	-	Home-range size		PB	(Hooker and Innes, 1995)
	-	-	18.85	-	-	-	Home-range size		PB	(Innes and Skipworth, 1983)
	-	-	11.51	-	-	6.73-22.43	Home-range size		W/PB	(Latham, 2006)
	-	-	18.75	12-25	3.43	2.3-5.7	Home-range size		B	(ManaakiWhenua, 2020)
	-	-	18.60	13-23	5.82	4.1-10.5	Home-range size		B/PB	(ManaakiWhenua, 2020)
	-	-	14.67	11-18	5.77	2-11	Home-range size		PB	(ManaakiWhenua, 2020)
	-	-	16.42	9.8-23.04	13.30	9.2-20	Home-range size		K	(Nathan, 2016)
	-	-	41.34	11.97-70.72	-	-	Home-range size		B	(Pryde et al., 2005)
Norway rat	-	-	53.76	52.16-55.36	-	-	Home-range size		OC	(Bramley, 2014)
	-	-	14.70	14.04-15.37	-	-	Home-range size		U	(Fitzgerald and Innes, 2017)
	-	-	31.57	17.08-46.06	-	0.17-0.21	Home-range size		PB	(Hickson et al., 1986)
	-	-	25.23	20.60-30.90	-	2.6-4.2	Home-range size		PB	(Moors, 1985)
Kiore	-	-	9.20	3.99-12.82	-	-	Home-range size		OC	(Bramley, 2014)

* Unpublished dataset from Table 3.1 of Montague (2000)
** Negative exponential detection function instead of half-normal used
Detection Method: BS - Bait Stations, CT - Camera Traps, LGT - Live Ground Traps, STT - Snap Trap Tunnels, TT - Tracking Tunnels
Habitat: AG - Alpine Grassland, B - Beech forest, BR - Braided Riverbed, E - Exotic plantation, K - Kauri forest, OC - Open Country, PB - Podocarp-Broadleaved forest, U - Urban, W - Wetland

Table 1: (CONT.) Summary of mean estimates of g_0, σ and Density for different small mammal species. The "home range size" studies correspond to studies that estimate home-range size using telemetry or trapping techniques to detect animal locations. Where only one estimate was provided, we reported its value in the "mean" field, and left "range" empty. Where more than one estimate was provided, we reported the mean and the range of all estimates. Reported values were pooled across sexes.

Species	g_0 mean	g_0 range	σ (m) mean	σ (m) range	Density (ha^{-1}) mean	Density (ha^{-1}) range	Study type	Detection method	Habitat	Reference
House mouse	0.38	0.08-0.62	26.06	9.10-75.80	31.19	5.2-71.0	SECR	LGT	OC	(Efford, 2004)
	0.34	0.09-0.67	-	-	78.3	14.6-156.7	SECR	LGT	PB	(Goldwater, 2007)
	0.21	0.10-0.28	28.3	17.7-37.7	0.52	0.02-1.77	SECR	LGT	B	(Wilson and Lee, 2010)
	0.29	0.08-0.75	14.83	10.0-20.3	12.41	0.32-55.93	SECR	LGT	AG	(Wilson and Lee, 2010)
	0.09	0.03-0.15	16.44	13.16-21.29	-	-	SECR	LGT	PB	(Wilson et al., 2018)
	-	-	16.14	11.16-19.37	1.42	0.54-2.93	Home-range size		B/PB	(Fitzgerald et al., 1981)
	-	-	11.62	11.04-12.19	13.03	13.03-13.03	Home-range size		OC	(MacKay et al., 2011)
	-	-	-	8-10	>150	-	Home-range size		PB	(MacKay et al., 2019)
	-	-	-	17-25	19.20	-	Home-range size		OC	(MacKay et al., 2019)
	-	-	18.90	14.2-23.6	-	5.0-28.0	Home-range size		B/PB	(Wilson et al., 2007)
Stoat	0.13	-	397	-	0.48	-	SECR	TT	B/PB	(Clayton et al., 2011)
	0.06	0.02-0.11	299.67	162-482	0.03	0.02-0.03	SECR	TT	B	(Efford et al., 2009)
	0.03	0.02-0.05	623.5	521-726	1.30	1.0-1.6	SECR	LGT	AG	(Smith et al., 2008)
	0.06	0.04-0.08	660	429-891	1.15	0.8-1.5	SECR	LGT	B	(Smith et al., 2008)
	-	-	283.57	169.22-414.51	-	-	Home-range size		B	(Alterio, 1998)
	-	-	106.34	63-160	-	-	Home-range size		AG	(Cuthbert and Sommer, 2002)
	-	-	307.0402258	248.02-407.41	-	-	Home-range size		BR	(Dowding and Elliott, 2003)
	-	-	222.9081584	65.13-332.91	-	-	Home-range size		K/PB	(Gillies et al., 2007)
	-	-	254.1734681	126-490	-	-	Home-range size		E	(Miller et al., 2001)
	-	-	245.8067069	130.27-337.66	-	-	Home-range size		OC	(Moller and Alterio, 1999)
	-	-	255.74	103-442	-	-	Home-range size		OC/B/PB	(Murphy and Dowding, 1994)
	-	-	199	163-236	-	-	Home-range size		B	(Murphy and Dowding, 1995)
	-	-	211.1738063	94.95-365.56	-	-	Home-range size		AG/B	(Smith et al., 2003)
	-	-	165.6508178	145.64-185.66	-	-	Home-range size		PB	(Young, 1998)
Ferret	0.08	0.01-0.22	466.09	305-791	3.71	0.8-6.9	SECR	LGT	OC	(Efford and Norbury, 2005)
	-	-	223.27	-	-	-	Home-range size		OC	(Baker, 1989)
	-	-	167.7106866	-	-	-	Home-range size		OC	(Byrom et al., 2008)
	-	-	492.04	349.24-634.84	-	-	Home-range size		OC	(Caley and Morriss, 2001)
	-	-	238.20	-	-	-	Home-range size		OC	(Dymond, 1991)
	-	-	280.78	267.56-294	-	-	Home-range size		OC	(Moller and Alterio, 1999)
	-	-	216.66	200.75-232.57	-	-	Home-range size		OC	(Norbury et al., 1998)
	-	-	316.71	242.62-390.8	-	-	Home-range size		OC	(Pierce, 1987)
	-	-	184.02	154.48-213.55	-	-	Home-range size		OC	(Ragg, 1997)
	-	-	176.88		-	-	Home-range size		OC	(Ragg, 2002)
	-	-	274.94	229.13-320.74	-	-	Home-range size		OC	(Spurr et al., 1997)
	-	-	236.65	166.06-307.23	-	-	Home-range size		OC	(Yockney et al., 2013)
	-	-	255.24	205.97-282.97	-	-	Home-range size		OC	(Young, 1998)
Feral cat	0.07	-	188.21	-	-	-	SECR	CT	OC	(Nichols, 2018)
	0.13	0.01-0.22	152.83	96.5-182.5	-	-	SECR	CT	OC	(Nichols and Glen, 2015)
	-	-	269	220.06-317.31	-	-	Home-range size		OC	(Baker, 1989)
	-	-	336.58	291.29-381.88	-	-	Home-range size		K/PB	(Dowding, 1997)
	-	-	157.86	156.18-159.54	-	-	Home-range size		OC	(Dowding, 1998)
	-	-	237.02	201.57-272.46	-	-	Home-range size		OC/B/PB	(Fitzgerald and Karl, 1986)
	-	-	368	249.09-486.32	-	-	Home-range size		K/PB	(Gillies et al., 2007)
	-	-	908.94	766.88-1051	-	-	Home-range size		OC/PB	(Harper, 2007)
	-	-	282.01	219.67-356.01	-	-	Home-range size		OC	(Langham and Porter, 1991)
	-	-	305.73	280.15-331.32	-	-	Home-range size		OC	(Moller and Alterio, 1999)
	-	-	339.98	316.58-363.38	-	-	Home-range size		OC	(Norbury et al., 1998)
	-	-	595.87	580.29-611.44	-	-	Home-range size		OC	(Pierce, 1987)
	-	-	766.56	610.03-923.08	-	-	Home-range size		OC/B/E	(Recio et al., 2010)
	-	-	514.11	253.31-800.7	-	-	Home-range size		OC	(Recio and Seddon, 2013)

Detection Method: BS - Bait Stations, CT - Camera Traps, LGT - Live Ground Traps, STT - Snap Trap Tunnels, TT - Tracking Tunnels
Habitat: AG - Alpine Grassland, B - Beech forest, BR - Braided Riverbed, E - Exotic plantation, K - Kauri forest, OC - Open Country, PB - Podocarp-Broadleaved forest, U - Urban, W - Wetland

2.3.1 Brushtail possum (*Trichosurus vulpecula*)

Our search yielded seven published studies of possum detection probabilities, reporting 63 estimates of both g_0 and σ, for a range of different habitats. A further 16 studies reported possum home-range size which we converted to σ. The range of all extracted estimates of g_0 range from 0.03 and 0.35; σ estimates ranged from 24.55 to 155 m, and density estimates were between 0.18 and 15.91 possums/ha (Table 2.1). The highest value of $g_0 = 0.35$ was reported during winter in mixed beech-podocarp-broadleaved forest, using wire mesh traps baited with apples and flour, where the estimated average density was 10.0 possums/ha and $\sigma = 25.3$ metres (Efford, 2004). In the following winter, g_0 decreased to 0.13 and possum density increased to 14.0 possums/ha, with $\sigma = 32.6$ metres. This inter-annual variation was possibly due to possums ranging further afield to exploit food resources during heavy fruiting of *Nothofagus truncata* and *Elaeocarpus dentatus* tree species in that year (Efford, 2004). The lowest value of $g_0 = 0.03$, with $\sigma = 50$ metres, was found in a study conducted in podocarp-broadleaved forest on Rakiura/Stewart Island using leg-hold traps [Ramsey - unpublished dataset from Table 3.1 of Montague (2000)].

Largest σ estimates, corresponding to large home-range size, were found in studies conducted in habitat dominated by modified open-country where possum densities were low. For example, Rouco et al. (2013) reported $\sigma = 131.2$ metres, with an average density of 0.44 possums/ha and $g_0 = 0.074$, at a low-elevation trial site in highly modified semi-arid grassland/shrubland in Central Otago, using Grieve wire cage traps baited with apple and powdered sugar.

The significant relationships between g_0 and σ ($p < 0.0001$) and between density and σ ($p < 0.0001$) were described well by a decaying exponential functions (Adjusted R^2=44.3% and 90.7% for g_0/σ and density/σ respectively), reflecting the known inverse correlations between home-range size and both g_0 and population density (Figure 2.1). However, there was high variability in g_0 for low values of sigma.

2.3.2 Rodents

2.3.2.1 Ship rat (*Rattus rattus*)

We found three studies (Efford and Hunter, 2018; Nathan, 2016; Wilson et al., 2007) and two unpublished capture-recapture datasets (Carpenter, 2020; ManaakiWhenua, 2020) reporting detectability in ship rats, using live ground traps in all four forest types (in both mast years and non-mast years for beech or mixed beech forest), and using tracking tunnels, bait stations, and snap-trap tunnels in kauri forest (Nathan, 2016). A further 11 studies reported ship rat home-range size which we converted

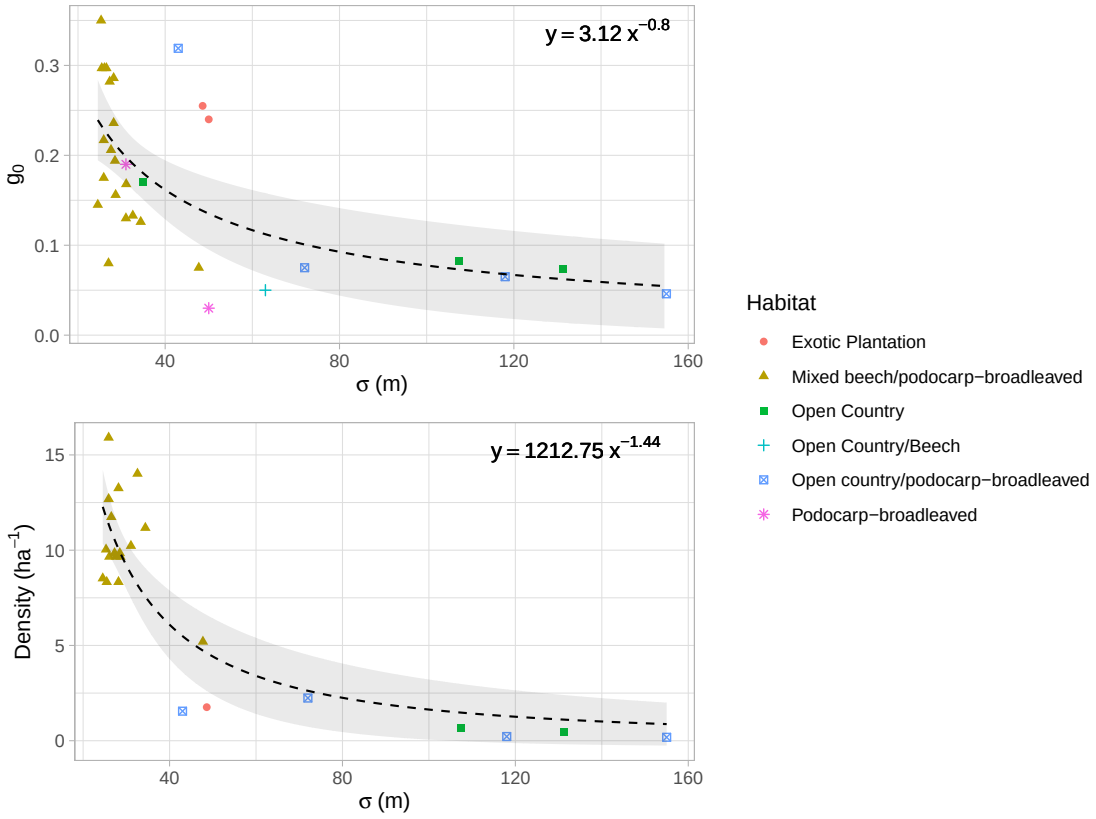

Figure 2.1: Relationship between g_0/σ and density/σ for possums. Estimates of g_0 versus σ (top) and density versus σ (bottom) for possums, labelled for dominant habitat type, and power law linear regression lines (dashed, equations in top right corners) with 95% confidence intervals shaded in grey.

to σ.

The extracted SECR-modelled estimates for g_0 ranged between 0.01 and 0.4, σ between 9.8 m and 37.4 m, and density between 2 and 20 rats/ha (Table 2.1).

The significant relationships between g_0 and σ ($p = 0.0002$) was described well by a decaying exponential functions (Adjusted R^2=35.7%), reflecting the known inverse correlations between home-range size and both g_0. A significant relationship ($p = 0.03$) between density and σ was also found, but the high variability of g_0 resulted in a low R^2 (=12.4%) for our fitted line (Figure 2.3).

Analysis of g_0 values over different seasons, over all habitats combined, showed a higher mean detectability in spring than in autumn and winter (Figure 2.3). However, the data found was too scarce to detect any differences in detectability between mast and non-mast years.

One study reported home-range sizes of ship rats in urban gullies in Hamilton, corresponding to $\sigma = 9.7$ (SE=1.25) m in spring for male rats and $\sigma = 10.4$ (SE=0.55) m for females (Fitzgerald and Innes, 2017).

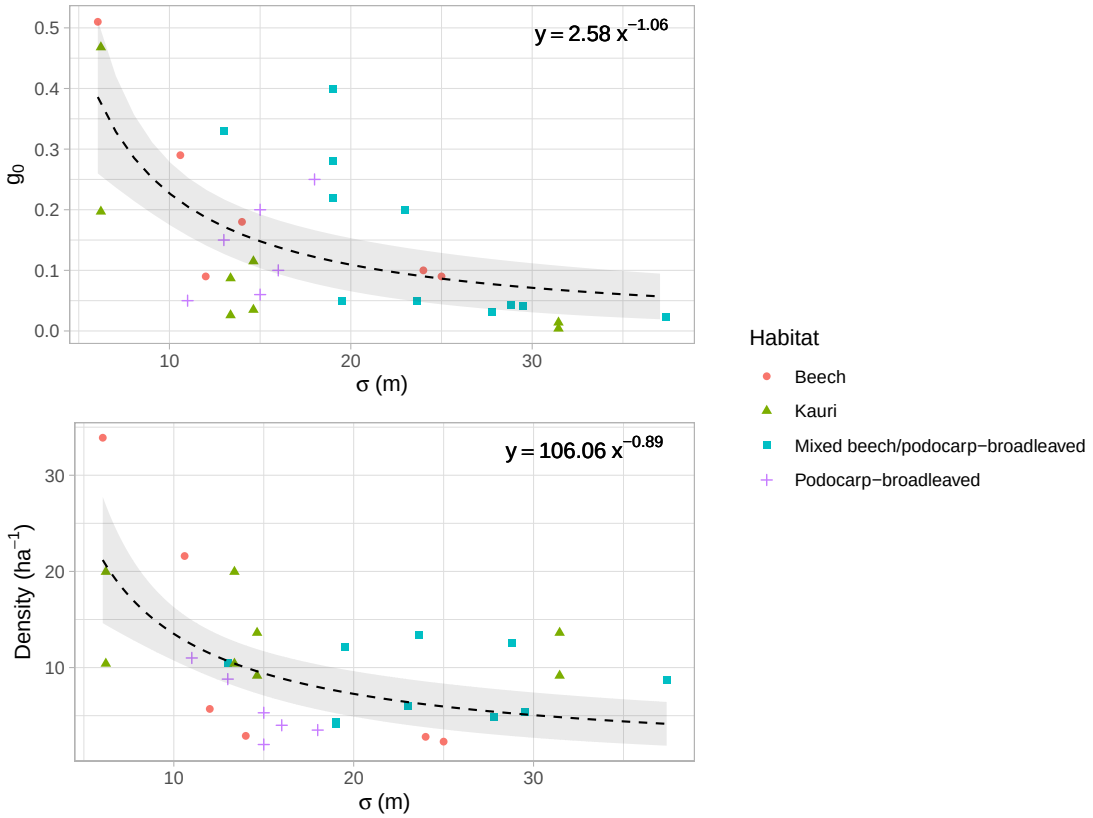

Figure 2.2: Relationship between g_0/σ and density/σ for ship rats. Estimates of g_0 versus σ (top) and density versus σ (bottom) for possums, labelled for dominant habitat type and log-log linear regression lines (dashed) with 95% confidence intervals shaded in grey.

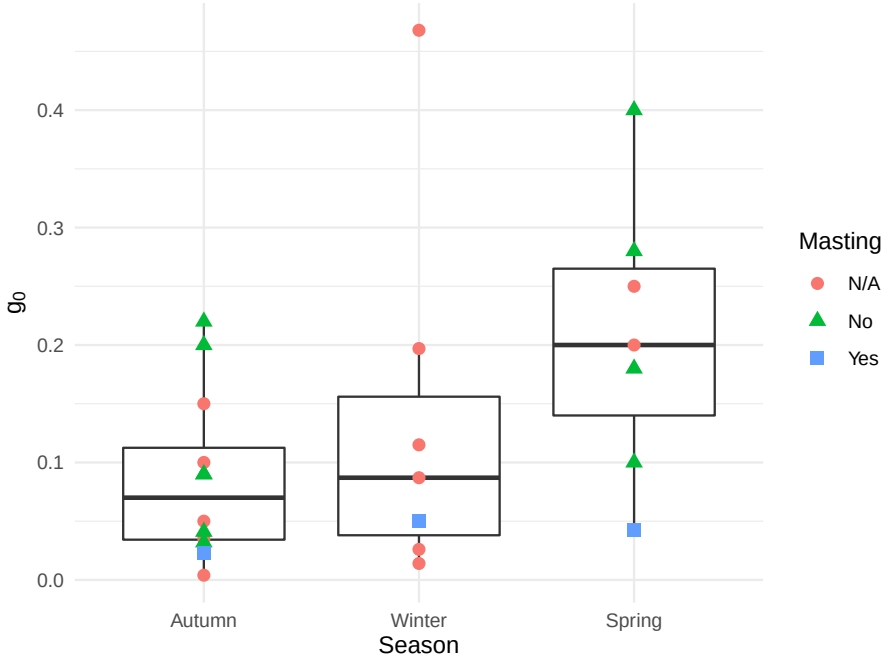

Figure 2.3: Summary of ship rats' g_0 values by season.
Boxplot labelled for masting status. "N/A" corresponds to cases where masting status was not stated in the paper or where it didn't affect the habitat where the study was conducted. We don't display the boxplot for summer as we had too few data.

A further ten studies reporting home-range size for ship rats (Fitzgerald and Innes, 2017; Harper and Rutherford, 2016; Nathan, 2016; Latham, 2006; Pryde et al., 2005; Hooker and Innes, 1995; Dowding and Murphy, 1994; Hickson et al., 1986; Innes and Skipworth, 1983; Daniel, 1973), which were converted to σ values using Equation 2. These values ranged from 8.14 m in podocarp-broadleaved forest (an average over seasons and sex) to 70.72 m for male rats in early autumn in masting beech forest (Eglinton Valley, Fiordland). Three of these studies previously showed that home-range sizes are roughly similar for male and female rats in winter, but increase in size for males in the breeding season (Pryde et al., 2005; Dowding and Murphy, 1994; Hooker and Innes, 1995). Nathan (2016) also found that g_0 and σ estimates were higher for males than females. Furthermore, they suggested that some estimates may be negatively biased due to high levels of trap saturation from non-rat species and false triggers.

2.3.2.2 Norway rat (*R. norvegicus*) and kiore (Pacific rat, *R. exulans*)

We found no studies reporting g_0 values for Norway rats and only one study for kiore. Four studies provided home-range sizes for Norway rats (Fitzgerald and Innes, 2017;

Bramley, 2014; Moors, 1985; Hickson et al., 1986) which we converted to values of σ (one in open country, one in an urban environment and two in podocarp-broadleaved forest, see Table 2.1).

We also found one study presenting home-range sizes for kiore in winter-spring, in a high-density population living in open country habitat on Kapiti Island (Bramley, 2014). Converting these values gave estimates of σ = 8.6 m (ranging from 4.0 m to 12.6 m, n=6) for males and σ = 9.8 m (ranging from 5.2 m to 12.8 m, n=5) for females.

2.3.2.3 House mouse (*Mus musculus*)

We found four SECR studies (Wilson et al., 2018; Wilson and Lee, 2010; Goldwater, 2007; Efford, 2004) reporting estimates for density and associated detection parameters for house mice in New Zealand, all conducted using live ground traps. Of all species, house mice showed the greatest variation in g_0 and population density. Over all seasons and habitat types, estimates for g_0 ranged from 0.03 to 0.75, σ estimates were between 9.1 m and 75.8 m (corresponding to home-range areas from 0.16 ha to 10.83 ha, respectively), and associated densities were between 0.02 mice/ha and 156.7 mice/ha (Table 1).

A significant power law relationship was found between g_0 and σ (p = 0.0001) and between density and σ (p = 0.0006) (Figure 2.4). The high variability of g_0 and density resulted in moderate adjusted R^2 values (26.9% and 41.9% for g_0/σ and density/σ respectively). Our results are in agreement with Efford (2004), who also reported a strong negative exponential relationship between density and σ, indicating mice have smaller home-range sizes at higher population densities. High mouse densities arise in New Zealand during masting events (King, 1983; Wilson and Lee, 2010) or as a result of meso-predator and competitor release in areas where other pest species have been eradicated (Wilson et al., 2018).

Comparing detectability over different seasons (over all habitats combined), the average g_0 was higher in autumn than in other seasons (Figure 2.5). The high mouse densities occurring during population irruptions, predominantly over autumn in mast years (King, 1983), could be contributing to this seasonal effect.

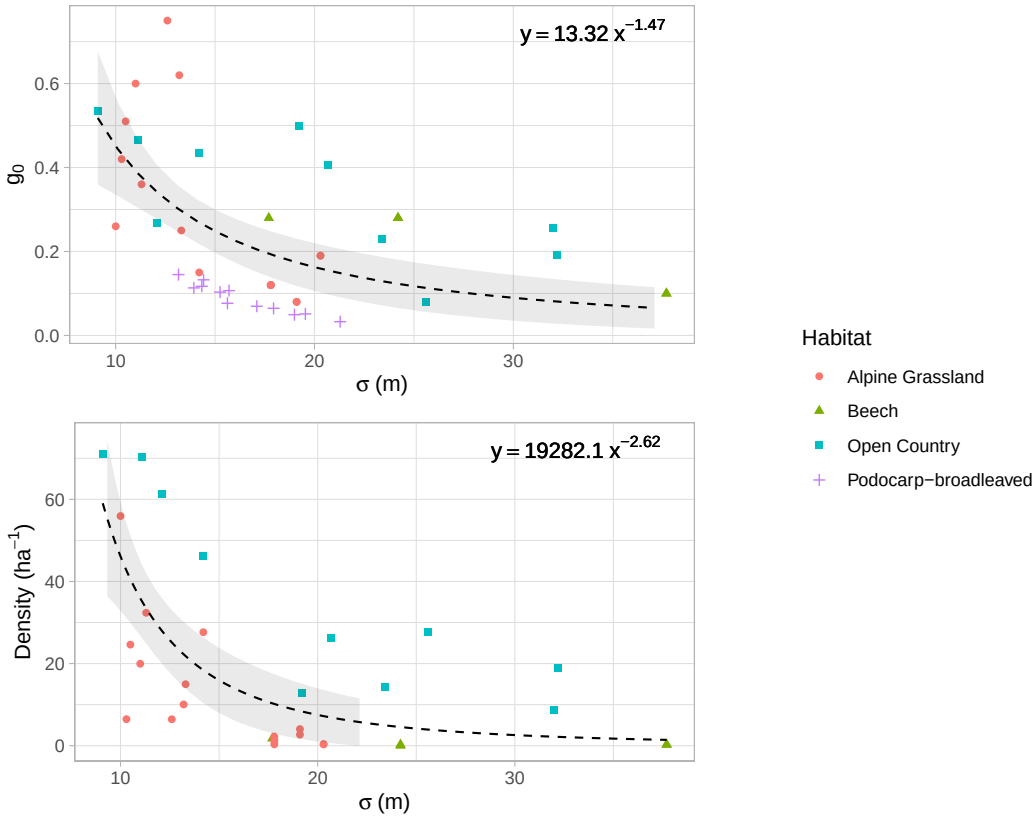

Figure 2.4: Relationship between g_0/σ and density/σ for house mice. Estimates of g_0 versus σ (top) and density versus σ (bottom) for possums, labelled for dominant habitat type, and power law regression lines (dashed) with 95% confidence intervals shaded in grey.

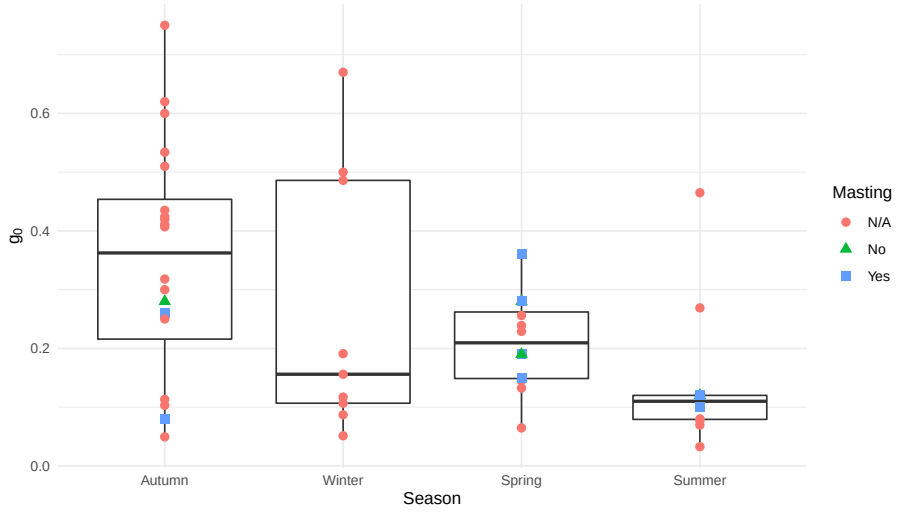

Figure 2.5: Summary of house mouse's g_0 values by season. Boxplot labelled for masting status. "N/A" corresponds to cases where masting status was not stated in the paper or where it didn't affect the habitat where the study was conducted.

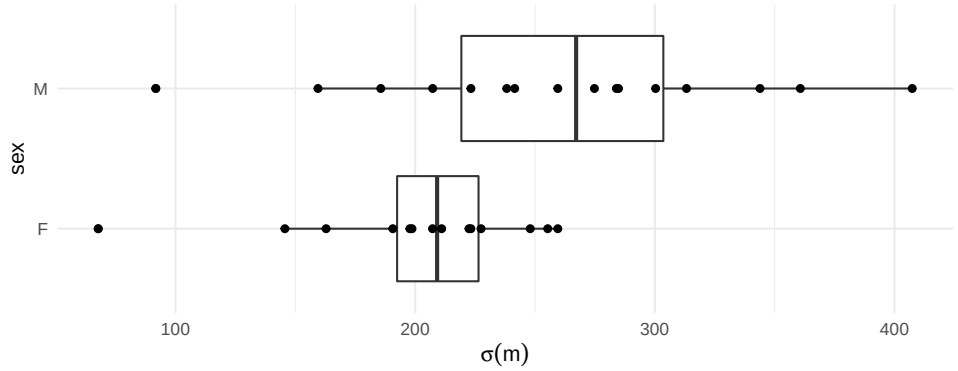

Figure 2.6: Summary of stoat's σ values by sex.
Boxplot of data coming from 10 home-range size studies (Table 2.1).

2.3.3 Mustelids

2.3.3.1 Stoat (*Mustela erminea*)

Three SECR studies reported stoat detectability parameters for live ground traps and hair-snagging tunnels (Gleeson et al., 2010) and one further study performed Bayesian inferential modelling of kill-trap capture data to estimate g_0 and σ. Studies were conducted in alpine grassland (Smith et al., 2008) and beech (Smith et al., 2008; Efford et al., 2009) or mixed beech/podocarp-broadleaved forest (Clayton et al., 2011; Anderson et al., 2016). Values for g_0 ranged between 0.016 and 0.113, σ estimates ranged between 162 m and 891 m, and density ranged between 0.0048 and 0.026 stoats per ha. We found no correlation (at the α=0.05 significance level) between g_0 and σ or between density and σ. The lowest estimate of $g_0 = 0.016$ was found by Anderson et al. (2016), along with high heterogeneity in trappability on Resolution Island. This stoat population had been managed under a 6-year kill-trapping programme so trap avoidance or differences in trapping methodologies could be behind this lower capture probability.

Male stoats typically occupy larger home ranges than females and during spring can travel large distances in search of females (King and Forsyth, 2021). Home range sizes extracted from 10 studies across different habitats, gave σ values ranging from 68 to 407 m (average σ= 233 m). The σ values for female stoats (μ = 201 m, s.d. = 50.2, n = 14) were significantly lower (t(df=25.7) = 2.5, p = 0.019) than males (μ = 261m, s.d. = 79, n = 16) (Figure 2.6).

Stoat home range size depends on population density and distribution of prey. In masting beech forest, high stoat densities occur during the summer following a mast year, due to high prey abundance and a delayed breeding season (White and King, 2006; King, 1983). During these periods, stoats occupy smaller home ranges (Mur-

phy and Dowding, 1995), however associated estimates of g_0 remain a knowledge gap. King et al. (2003) reported a non-spatially explicit probability of first capture (0.17 (95% CI 0.12-0.24)) for a high density stoat population in a post-seedfall year in beech forest. After the first capture, there was evidence of a reduction in trappability for both adults and young, likely due to trap avoidance. Young-of-the-year female stoats had the lowest recapture probability (0.07 (0.04-0.11)), while young-of-the-year males showed little change in trappability.

2.3.3.2 Ferret (*Mustela putorius furo*)

We found only one study reporting g_0 estimates for ferrets in New Zealand (Efford and Norbury, 2005), in a capture-recapture trial conducted in Central Otago farmland using live ground traps. All studies were conducted in open-country habitat, the favoured habitat of ferrets in New Zealand (King and Forsyth, 2021). Estimates for g_0 ranged between 0.014 and 0.216, σ values were between 305 m and 791 m, and density estimates were between 0.8-6.9 ferrets/ha. Efford and Norbury (2005) reported an inverse relationship between g_0 and σ, but found no correlation between g_0 and density. A previous review by Byrom et al. (2015) found 12 studies reporting home-range areas for ferrets, which we converted to estimates for σ (Table 2.1).

The Efford and Norbury (2005) trial was conducted in summer and autumn (February to May 2003). Ferrets are known to have a seasonal pattern of trappability, with highest capture rates in summer and autumn, and lowest in late winter and spring, especially for females (NPCA, 2009; King et al., 2009). We would therefore expect lower g_0 estimates for ferrets in winter-spring but did not find any studies conducted over these seasons to assess the effect of season.

King et al. (2009) found clear evidence of individual variation in ferret interactions with traps and bait dispensers on pastoral farmland, likely related to gender, activity and prior experience. Some ferrets demonstrated active avoidance of devices, or alternatively, avoidance of the infra-red illumination emitted by cameras used for field observations. Additionally, some individuals lacked the opportunity to interact with a device; there was either insufficient time for animals to encounter a device or for them to overcome their neophobia.

2.3.3.3 Weasel (*Mustela nivalis*)

There have been no New Zealand studies reporting g_0 for weasels. One unpublished study measured home-range areas for four weasels in podocarp-broadleaved forest when mouse abundance was low (Dr. E. Murphy pers. comm.), yielding an average $\sigma = 239.4$ (SE=27.84) m for males ($n = 3$) and $\sigma = 176.9$ m for females ($n = 1$).

Studies in other countries have shown that weasels expand their home-ranges during periods of low prey availability (Jędrzejewski et al., 1995).

2.3.4 Feral cat (*Felis catus*)

We found two studies reporting on detectability of feral cats in New Zealand. Both studies were conducted using camera traps in open country habitat (Nichols, 2018; Nichols and Glen, 2015). In the pre-removal monitoring period of both experiments, g_0 vales ranged between 0.002 and 0.449, σ values were between 58.67 m and 478.97 m, and density estimated were between 0.01-0.26 cats/ha. We extracted σ estimates from a further 12 studies of home-range size in open-country and forest, which ranged from σ = 156 m to 1051 m. For these studies, we compared the σ values of female cats (μ = 418 m, s.d. = 225, n = 15) with those of male cats (μ = 444 m, s.d. = 237, n = 17) and found no statistically significant difference between the two.

2.3.5 European hedgehog (*Erinaceus europaeus*)

There are no published studies reporting both g_0 and σ for hedgehogs in New Zealand. Six studies reporting home-range areas, mainly in open country or braided riverbed habitats, were converted to 16 estimates for σ, yielding an average σ = 76.17 (SE=14.21, n=16) m. Home-range areas of male hedgehogs are known to be generally larger than females, and both sexes expand their home-ranges in spring-summer compared to autumn-winter (King and Forsyth, 2021). Across all studies, adult males had a larger but not statistically different average σ (mean=104.57 m, SE=29.77 m, n=6), ranging from 20.6 m to 323.13 m, compared to σ for females (mean=71.32 m, SE=21.37 m, n=5), which ranged from 23.03 m to 197.83 m. Moss (1999) compared home-range areas in different seasons, corresponding to an average σ = 187.66 m (SE=35.61 m, n=2) in spring-summer and σ = 109.76 m (SE=32.01 m, n=2) m in late summer-autumn.

2.4 Discussion

The ability to predict residual pest density or probability of eradication is critical for determining the success of invasive mammalian pest control in New Zealand. Obtaining accurate model predictions requires reliable estimates of spatial detection parameters and their associated uncertainty. Our comprehensive review of the literature, collates all g_0 and σ values reported to date for detectability of New Zealand's key small mammal pests, to provide an easily accessible reference for parameterising future models. Current population density estimation methods strongly rely on

correct input values for g_0 and σ. In addition, previous literature (Efford, 2004) highlights how population density estimates using g_0 and σ are likely to be affected by non-circular home-ranges and individual variation in g_0. In addition, while these methods assume animals to spend most of their time around a central den in the middle of their home-range, some animals might behave differently. For example, they might display a more "patchy" space use and travel across several dens scattered throughout their home-range. We explore the effect that different space use modalities can have on probability of encounter in Chapter 4 of this thesis.

As well as SECR models, our literature search also yielded studies presenting results obtained through occupancy modelling (MacKenzie et al., 2002). This alternative approach employs a "probability of detecting a species given it is present at a site", i.e. a detection probability of at least one animal being present (Efford and Dawson, 2012). This parameter is not spatially explicit, and the concept of detection probability in occupancy models is highly problematic as it depends on density. These studies were not included in our collated dataset but also offered insight into detectability.

Our review revealed some important knowledge gaps. Overall, extracted values of g_0 and σ varied greatly, both within species and between species. In general, there was insufficient representation and replication of studies to draw reliable conclusions about the effects of different habitats or other covariates on detection parameters. We found a statistically significant negative correlation between g_0 and σ for possums, mice and ship rats, in line with previous findings that a larger home-range size corresponds to a lower trappability at the home-range centre.

There were no SECR studies (only home-range studies) reporting detectability for feral cats in forest habitats, few studies for any species conducted in an urban environment and no SECR studies conducted in wetlands. One of the key knowledge gaps we identified was for pest detectability in and following mast years in masting beech systems. Where studies had been conducted in beech or mixed beech forest, most were conducted in inter-mast years or did not provide information on seed-fall density. While there were insufficient studies comparing detection parameters for mast and non-mast years to permit a statistical analysis of the extracted values, we did observe higher mean g_0 values for house mice (suggesting high mouse densities) in autumn, when the amount of seed-fall in beech forest and alpine grassland systems typically reaches its maximum during mast years. Research conducted on yellow-necked mice (*Apodemus flavicollis*) in masting forests in Europe indicate a reduction in space use through increased population density caused by masting events (Stradiotto et al., 2009; Mazurkiewicz and Rajska-Jurgiel, 1998), or an in-

crease in home-range size together with a higher spatial overlap among neighbours in post-mast years (Bogdziewicz et al., 2016). If the house mice in New Zealand have a similar behaviour, we would expect a similar reduction in home-range size, or a higher spatial overlap following mast events. Although we did not find enough data to compare detection parameters for mast and non-mast years on ship rats, previous research suggests that ship rat populations irrupt following heavy masting events in beech forest, due to the highly abundant food resource (seed and house mice prey) available during autumn and early winter (King, 1983). These ship rat irruptions typically peak in the spring following a heavy mast event and densities can remain high until the following winter-spring when food supply is exhausted and the population crashes (Elliott and Kemp, 2016).

In addition to seasonality, other factors - such as weather, neophobia, sex, age, size, food supply and population history - affect detectability in pest species. Our collation of studies reporting stoat home-range sizes reinforces previous findings that home-range size is, on average, significantly larger for male stoats than female. Stoat home-range size is also known to vary depending on season and availability of prey. Using occupancy modelling, Christie et al. (2014) showed that, on average, increased rainfall was associated with a higher probability of detecting rats in tracking tunnels. Neophobic behaviour towards new devices is likely a key factor affecting g_0 for ship rats (Cowan and Barnett, 1975) and Norway rats (Byers et al., 2019; Inglis et al., 1996). In the early stages of trapping, large adult rats have higher trappability than smaller juveniles (Byers et al., 2019), therefore age and size are additional factors that affect their detectability.

Nearly all the reviewed literature described studies conducted using live ground traps, with only two studies reporting detectability for camera traps, two studies for tracking tunnels and one study for bait stations and snap trap tunnels. Advances in camera technology, along with a reduction in cost, mean that camera traps are becoming an increasingly popular detection tool globally (Green et al., 2020). Obtaining reliable detection parameter estimates for camera traps, for the full suite of invasive pests in a range of habitats and seasons, should therefore be a priority for future research.

CHAPTER 3

Effects of heterogeneous trappability on pest management

The previous chapter presented differences in detectability traits found between populations of New Zealand's invasive small mammal species, and we highlighted the knowledge gaps around the detectability of certain species and habitats.

In this chapter, we explore different scenarios of a pest eradication programme under the assumption of a behaviourally heterogeneous population. We simulate individuals with different levels of trap-shyness and different distributions of personalities within a population, highlighting the impact that this heterogeneity can have on eradication success.

3.1 Introduction

Invasions by mammalian predators pose a serious threat to biodiversity in many of the world's ecosystems (Blackburn et al., 2004; Mack et al., 2000; Salo et al., 2007; Vitousek et al., 1997). Worldwide, control and eradication of these pests is carried out using monitoring devices, poisonous baits and traps set across the landscape (Courchamp et al., 2003; Gillies et al., 2003). Most successful pest eradications have been completed in restricted or isolated areas (e.g. small islands and fenced eco-sanctuaries), whereas open pest populations pose a much greater challenge and eradication efforts are seldom successful. In most cases, the traps set in the predators' territories can only capture some of the population, and as soon as control pressure is released the pests' populations gradually return to their original densities (Anderson et al., 2014). Furthermore, some individuals seem to be less likely

than others to interact with control devices, a phenomenon known as "trap-shyness" (King et al., 2003; Robertson et al., 2016b). Note that this term is sometimes associated with the change in behaviour *after* initial capture, but we will use it throughout this thesis to refer to the probability of interaction with a device, with no assumption of previous capture.

Most trapping models are built on the foundational assumption that all individuals within a population behave in the same way when confronted with a trap. Most models of control effort for mammal pests include juvenile survival, breeding success and immigration (Morgan et al., 2006), but rarely behavioural heterogeneity. However, there is a growing recognition that animals show significant and consistent behavioural differences within a population (Dingemanse et al., 2010). These differences could influence a number of population-level processes and ecological interactions, such as population responses to disturbance, success of reintroduction, harvest and control, and resource selection (Merrick and Koprowski, 2017). In a similar way, they could affect the success of a control or eradication programme.

It has already been shown that most "random" samples of animals are systematically biased due to consistent variations in behaviour (Biro, 2013), and that individual heterogeneity can affect foraging patterns, spatial dynamics (Spiegel et al., 2017) and collective behaviour (Aplin et al., 2014). Previous work has explored intra-specific differences in behaviour (Dall et al., 2004; Fogarty et al., 2011), highlighting the presence of behavioural syndromes in animals and their ecological and evolutionary implications (Sih et al., 2004).

Several papers have explored the relationship between personality and trappability (Brehm and Mortelliti, 2018; Boyer et al., 2010; Garamszegi et al., 2009). The results of these studies suggest that this relationship is complex, and while a correlation between the two has been found by some authors (Boyer et al., 2010; Le Cœur et al., 2015), others studies found that trappability was not repeatable (Brehm and Mortelliti, 2018), suggesting that trap-happiness and trap-shyness are labile and can change within an individual. In this study, we consider trappability to be constant over time within an individual, but more or less variable across a population.

Researchers have proposed several techniques to introduce individual heterogeneity in their capture-recapture models. In particular, a number of methods have been developed to estimate population size from capture-recapture data whilst allowing for heterogeneity in individual probability of capture. These include the jackknife estimator (Burnham and Overton, 1978), the generalised removal estimator (Otis et al., 1978) and the sample coverage approach (Lee and Chao, 1994; Chao et al.,

1992), as well as some likelihood-based methods (Yang and Chao, 2005; Pledger, 2000; Norris and Pollock, 1996; Yip et al., 1995; Agresti, 1994; Huggins, 1991), bayesian probability models (Anderson et al., 2016; Mäntyniemi et al., 2005) and mixture models (Dorazio and Royle, 2003). Most of these methods are based on the heterogeneous population models firstly described by Otis et al. (1978), and some of them are used in modern software for density estimations from mark-recapture or capture-recapture data (Efford et al., 2004).
Chao and Chang (1999) published a summary of homogeneous and heterogeneous models and their estimators, as well as proposing a class of catch-effort models allowing for heterogeneous removal probabilities. Other studies (Russell et al., 2017; Anderson et al., 2016; Samaniego-Herrera et al., 2013) presented spatial-survey models applied to eradication confirmation that included variability in the animals' probability of capture.

However, when unequal trappability is taken in consideration, modellers use a single parameter to describe the probability of capture, aggregating the probability of encountering a trap and the probability of interaction-given-encounter, with heterogeneity typically modelled on this combined capture probability. In our model, we disentangle the probability of encounter (derived from the distance between traps and the animals' average diffusion coefficient) from the probability of interaction-given-encounter, and model heterogeneity specifically on the latter probability. Note that this clear distinction is only possible in an artificial scenario where we consider a device to be encountered if an animal comes within a defined distance from it. It is quite challenging to disentangle encounter and interaction in real life when they can manifest in such similar ways (an animal walking towards a device could be interpreted as both the animal randomly walking in that direction, or as the animal deciding to explore a previously perceived device).

Furthermore, no explicit comparison between simulated homogeneous and heterogeneous populations has yet been carried out in the specific case of pest eradication programmes.

The aim of this work is to develop a simulation and an analytical model of animal movements within their home range and their encounters and interactions with traps. We investigate the effect of individual heterogeneity in the simulated populations on the prediction of population size during a trapping session and test different methods of modelling pest movements and decision-making. We also give an example of how to fit our model to animal capture data in order to detect and measure heterogeneity in a population. This study does not aim to create a new, ready-to-use estimator for population abundance during eradication, but rather it highlights

the effects of different levels of individual heterogeneity on model predictions for the pest population size.

Theoretical models such as this can provide pest managers with valuable information on the possible effect of individual heterogeneity on the outcome of an eradication programme, as well as highlighting the need for a better understanding of the effect of animal personalities on trappability.

3.2 Methods

We use a stochastic, spatially-explicit, individual-based model of animal movement and trapping. Individuals move according to a simple random walk on a regular spaced lattice with lattice size δ and time step τ for 12 hours every day (corresponding to the pests' active foraging times). Individuals always start at the centre of the lattice (representing the home-range centre) and their position is reset to the centre at the end of every 12-hour period. This ensures that the animal spends the most time around the centre of its home-range and increasingly less time in locations further from it.

We consider a grid of regularly spaced traps (with distance between traps d). For Sections 3-5, we keep the distance home-range centres and traps (and therefore the probability of encountering a trap) constant in order to isolate the effect of individual heterogeneity on an animal's probability of interacting with a trap. For the more applied approach described in Section 6, we consider a set of randomly placed home-ranges. The distance x between each home-range centre and the closest trap is randomly drawn (see Appendix for details).

A single trap is placed a fixed number of cells away from the home-range centre and the individuals perceive a trap only when entering the cell containing it. It is assumed that the trap is always active and ready to spring (*i.e.* traps are checked and cleared every day). For simplicity, we assume there is no interaction between individuals, no overlap of home-ranges and exactly one trap in each individual's home-range. Although this is not the most realistic model, it allows to isolate the effect of trappability on the decline in population size over time and on the probability of eradication success.

We set a step length δ of 10 m and a number of steps per hour of 100, which give a time step $\tau = 36$ s and a diffusion coefficient $D = 1.39$ m^{2}s^{-1}. The diffusion coefficient describes the rate at which the animal disperses from its home-range centre. The values chosen for our simulation allow individuals to travel up to 1 km

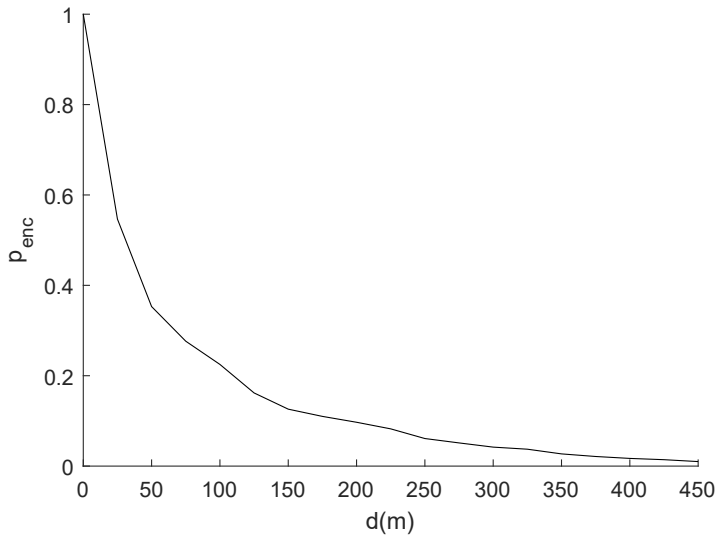

Figure 3.1: Probability of encounter for increasing trap distances. The probability of encounter p_{enc} as a function of the distance between the trap and the animal's home-range centre for a step length $\delta = 10$ m and a diffusion coefficient $D = 1.39$ m^2 s^{-1}.

Simulation parameters		
Parameter	Symbol	Value
Mean p_{int}	μ	0.5
Initial population size	N	50
Diffusion coefficient	D	1.39 m^{2}s^{-1}
Grid spacing	δ	10 m
Time step	τ	36 s
Distance between traps	d	300 m

Table 3.1: Parameter values used in our random walk simulations.

h^{-1}, which is a reasonable speed for a small mammal.

Because the simulated animal always starts its random walk at the home-range centre, the probability p_{enc} of encountering a trap in a given 12 hour period is a decreasing function of distance d between the home-range centre and trap (Fig.3.1), and depends on the value of the diffusion coefficient.

Individual heterogeneity can affect a great number of behavioural traits: movement rate and pattern, social interactions, foraging behaviour (Spiegel et al., 2017; Aplin et al., 2014). For this model, it is assumed that all individuals move and behave the same way (the random walk parameters are the same for all individuals), except when confronted with a trap. The only source of heterogeneity is the animals' probability of interaction parameter (p_{int}), indicating how likely an animal, having encountered a trap, is to interact with it (and hence get captured). This probability

includes the effects of attractants (baits, olfactory lures). There is no behavioural response to encounter (the animal does not change its behaviour after encountering a trap and not interacting with it).

When an individual interacts with a trap it is killed and removed from the population. We assume there is no birth, natural mortality, immigration or emigration during the trapping session, so the only cause of change in population size is trapping mortality. Each realisation of the simulation outputs the population size $N(t)$ of individuals at each time t up to the point where there are no individuals left. Multiple realisations of the simulations give an average $N(t)$, which can be plotted to observe the decrease of the average population size and the mean time required for eradication, hereafter referred to as "eradication time".

Simulations were run for both heterogeneous and homogeneous populations. Individuals in the homogeneous populations all have the same $p_{int} = \mu$, whereas those in the heterogeneous populations have a p_{int} drawn from a β-distribution with shape and scale parameters that give a mean μ. The heterogeneous populations are therefore composed of individuals with different levels of "trap-shyness".

The parameters of the β-distribution, α and β, can be adjusted to obtain the desired proportion of shy and bold individuals. While several studies provide numerical values for the probability of capture of an animal, we have only found one (Ball et al., 2005) giving an explicit value of 0.44 for the "intrinsic trapping probability" of a small mammal, which in our case corresponds to the probability of interaction with a trap, given encounter has occurred. We therefore arbitrarily choose to use a β-distribution with mean $\mu = 0.5$ for all our heterogeneous populations, which requires $\alpha = \beta$. Decreasing the values of α and β increases the variance of the distribution of interaction probabilities p_{int}, resulting in a more heterogeneous population. The homogeneous population is a limiting case of the β-distribution, with $\alpha, \beta \to \infty$.

We model variation in behaviour in two different ways: in the first approach, we decide whether each animal will interact with the trap or not (depending on the animal's p_{int}) every time the animal encounters the trap during its random walk. Each decision is independent of decisions made on previous encounters, and this model allows for multiple opportunities for an animal to interact with the trap in a single 12 hour period. We refer to this model as **inconsistent daily behaviour**, as it implies that animals may make different decisions on the same night.

The second approach to model the probability of interaction is to decide whether an animal will interact with the trap the first time it encounters the trap in a 12

hour period. Animals that choose not to interact with the trap will keep to this decision for the rest of the night, even if multiple encounters occur. Behaviour in different 12 hour periods is still assumed to be independent. We refer to this model as **consistent daily behaviour**, as it implies that animals stay consistent with their initial decision throughout each 12 hour period. For the consistent daily behaviour model, random-walk simulations are not necessary, as the probability p_c of capturing an animal in a 12 hour period does not depend on the number of encounters and is given by $p_c = p_{enc}p_{int}$.

For most of our simulations, we make the assumption that the distance between the animals' home-range centres and the traps - and therefore the probability p_{enc} of encountering a trap - is constant. In the last section of this paper, we test our model using random values of p_{enc} to explore the effect of its variability on our estimates of population heterogeneity.

3.3 Effects of individual heterogeneity on the decline of population size

Fig.3.2 shows time series for the average population size and the average value of p_{int} for a homogeneous population and for two populations with different degrees of heterogeneity. The initial population size was set to be $N(0) = 50$ and results are averaged over 1000 realisations. At the beginning of each simulation, all pest populations have the same average p_{int}. While members of the homogeneous population are all behaviourally identical (*i.e.* have the same p_{int}), the p_{int} of the members of the heterogeneous populations take different values.

The simulation results (Fig.3.2) corroborate the general intuition that very trap-shy individuals in the heterogeneous populations (red, blue curves in Fig.3.2), considerably slow the decrease in population size relative to the homogeneous population with the same mean interaction probability (green curve in Fig.3.2). The higher the degree of heterogeneity, the slower the population decline, *i.e.* the larger the eradication time. Over time, the individuals with high p_{int} (the "bolder" individuals) tend to be captured, leaving a greater proportion of "shy" individuals in the free population and causing a reduction in the average p_{int}, as shown in Fig.3.2.

The consistent behaviour model (dashed curves in Fig.3.2) results in a longer eradication time than the inconsistent behaviour model (solid lines) for the same degree of heterogeneity. This is due to the fact that the inconsistent behaviour potentially allows animals multiple chances to interact with a trap in a single 12 hour period,

which increases the probability of capture.

3.4 Effects of individual heterogeneity on the probability of eradication

The consistent daily behaviour model, described in the previous section, can be approached analytically. As the animal does not change its initial decision as to whether to interact with a trap, the probability of capture p_c in a given 12 hour period is equal to $p_{enc}p_{int}$ and is independent of the number of encounters with the trap. As shown in Fig.3.1, the probability of encounter p_{enc} depends on the distance between home-range centre and trap, and the diffusion coefficient D of the animal. D is kept constant, but the distance between home-range centre and trap is random, therefore p_{enc} is also random.

For an individual i with capture probability $p_{ci} = p_{enc}p_{int_i}$, the probability of being captured by night k is given by:

$$P(i \text{ captured by night } k) = 1 - (1 - p_{enc}p_{int_i})^k \tag{3.1}$$

For a population of initial size N, each individual i will have its own probability of interaction p_{int_i}, which could take any value between 0 and 1 with a probability density function (PDF) denoted by $f(p_{int})$. The expected value of the probability of eradication of the whole population by night k will therefore be:

$$\begin{aligned} E(P(\text{eradication by night } k)) &= E\left(\prod_{i=1}^{N} 1 - (1 - p_{enc}p_{int_i})^k\right) \\ &= \prod_{i=1}^{N} E\left(1 - (1 - p_{enc}p_{int_i})^k\right) \\ &= \left(\int_0^1 f(p_{int})(1 - (1 - p_{enc}p_{int})^k)dp_{int}\right)^N \end{aligned} \tag{3.2}$$

Fig.3.3 shows time series of the probability of eradication (by night k) obtained using both the analytical method above and simulations of the consistent behaviour model, for different levels of heterogeneity. As expected, increasing the variance of the β-distribution reduces the eradication probability. Moreover, the simulation results for the consistent behaviour method correspond closely to the analytical results, which validates our analytical method. The inconsistent behaviour model is harder to approach analytically, so we only show the simulation results for comparison.

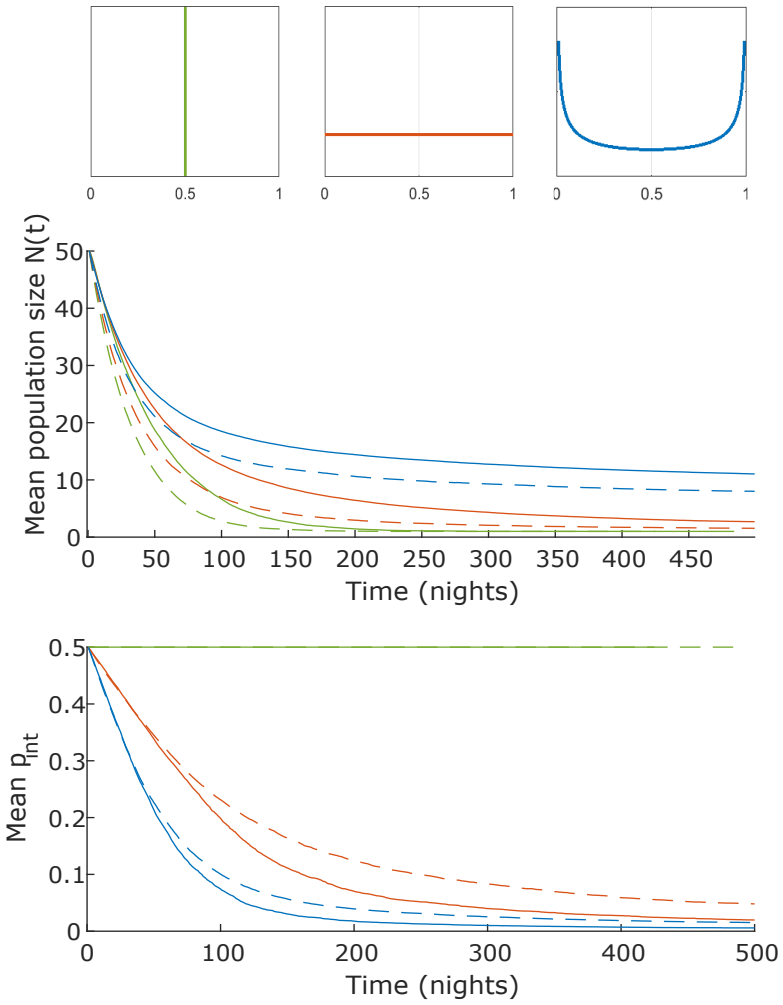

Figure 3.2: A more heterogeneous population corresponds to a longer eradication time. Decline of population size $N(t)$ (top) and average p_{int} over time (bottom) for different levels of heterogeneity. The p_{int} values for each individual in the population were drawn from the β-distributions (shown above, with parameters $\alpha = \beta = [\infty, 1, 0.5]$ respectively for the green, red and blue graphs). For each distribution, 1000 simulations were run using the simulation parameters shown in Table 3.1. Both models - consistent (solid line) and inconsistent (dashed line) daily behaviour - were used to produce these results. The graphs show the average values, across all simulations, obtained for each day.

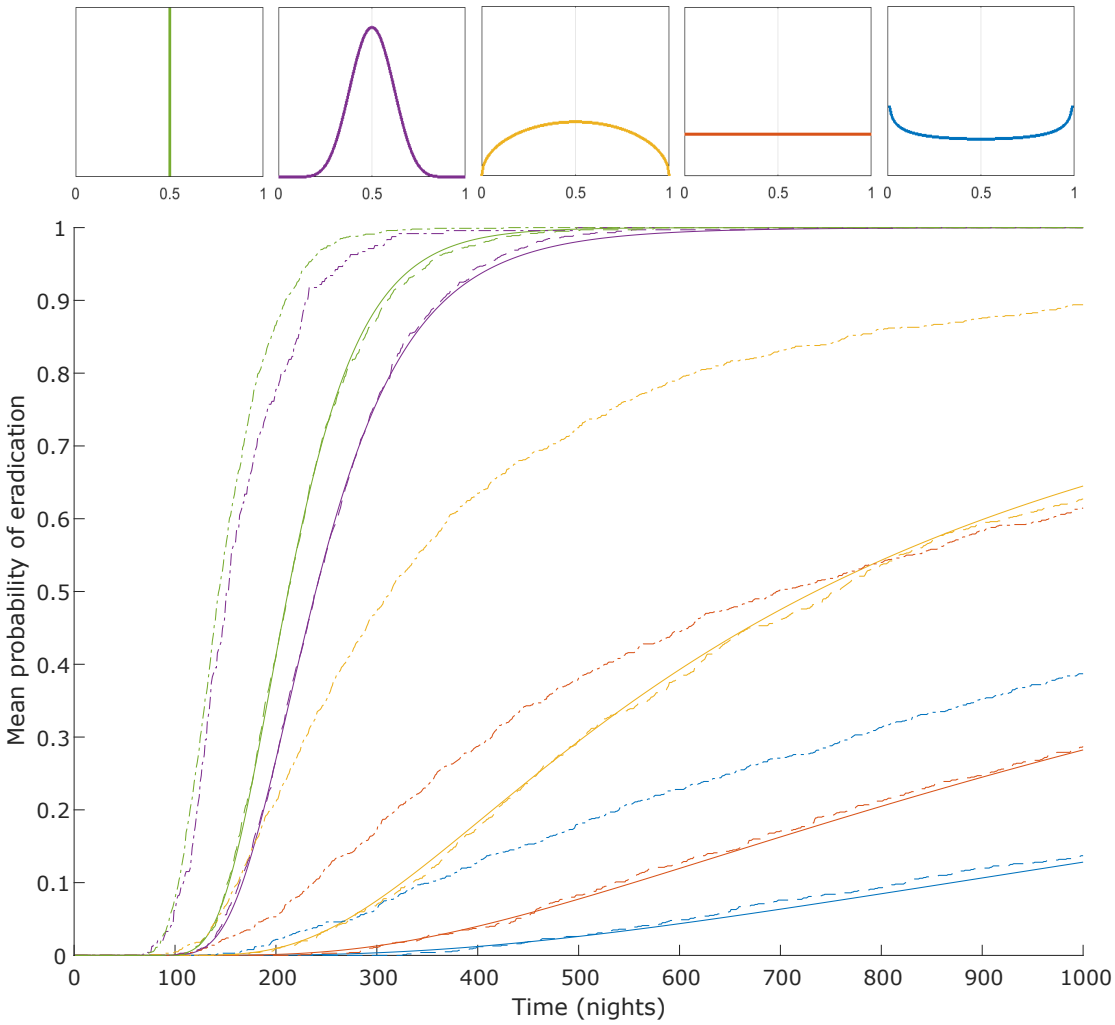

Figure 3.3: The higher the heterogeneity level in a population, the lower the probability of eradication after k nights. Analytical results (full lines) and simulation results (dashed lines for the consistent behaviour method, point-dashed line for the inconsistent behaviour method) of the eradication probability over time for different β-distributions (shown above, with parameters $\alpha = \beta = [\infty, 10, 1.5, 1, 0.8]$ respectively for the green, purple, yellow, red and blue graphs). The probability of encounter used for the analytical results was $p_{enc} = 0.04$, and the initial population was $N(0) = 50$. The simulation results correspond to the mean eradication probability over 1000 simulations.

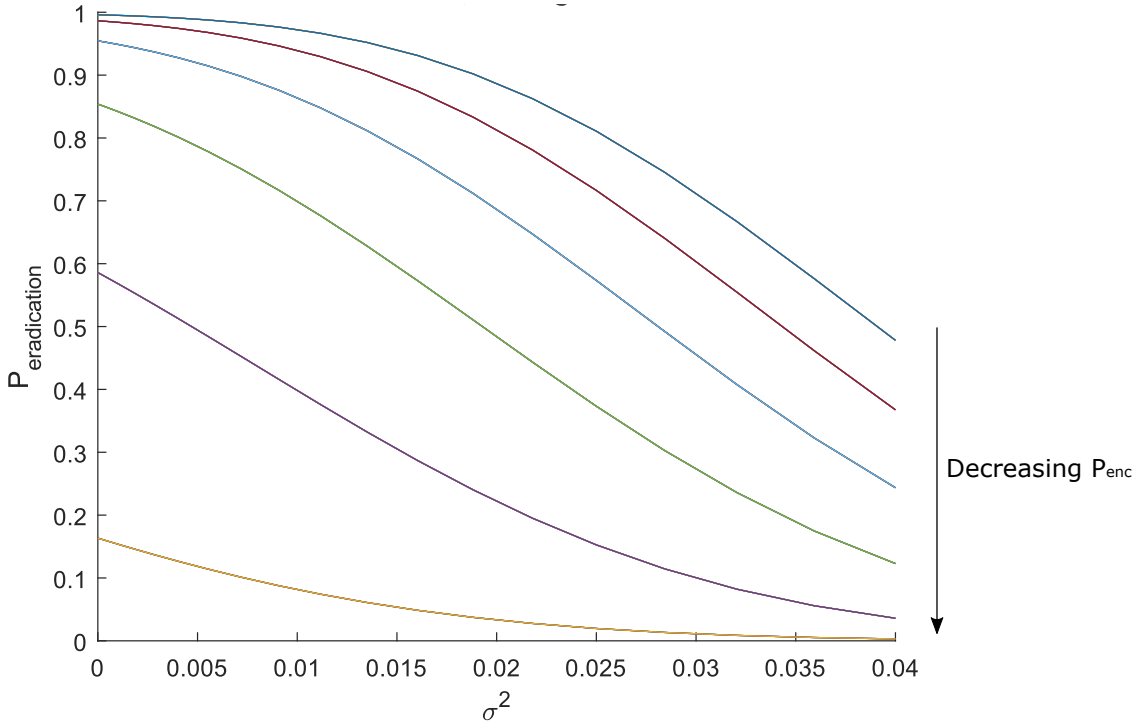

Figure 3.4: The probability of eradication decreases with increasing heterogeneity in p_{int} and decreasing p_{enc}. Mean probability of eradication for a population of 100 individuals after 400 nights, as a function of the level of heterogeneity in the population (expressed as the variance σ^2 of the β-distribution from which the individuals' p_{int} are drawn) and for different encounter probabilities (from top to bottom, p_{enc} = [0.05, 0.044, 0.038, 0.032, 0.026, 0.02]). The mean eradication time results were produced using the "consistent daily behaviour" model with parameter values equal to those in Table 3.1. The means are calculated over 1000 simulations. The probability of eradication results were produced analytically.

The higher the proportion of trap-shy individuals in a population, the higher the time needed for eradication. By increasing the variance of the β-distribution for the individuals' probability of interaction p_{int}, we observe a rapid increase in the eradication time, as well as a decrease in the probability of eradication (Fig.3.4).

3.5 Effects of heterogeneity on eradication assessment

A key question in most pest eradications is, at what point can the eradication session be declared "successful"? More specifically, after a given number of consecutive "quiet nights" (*i.e.* nights in which no animals were captured), how certain can we be that the population has been fully eradicated. Most managers aim for a 95%

certainty threshold, *i.e.* an eradication is declared successful upon reaching a 95% probability that every member of the population has been trapped (Anderson et al., 2017; Russell et al., 2017; Samaniego-Herrera et al., 2013). Correctly estimating the time when this threshold is met can be quite challenging when the population includes trap-shy, undetectable individuals (García-Díaz et al., 2017; Rout et al., 2014).

We ran simulations for both homogeneous and heterogeneous populations and calculated the probability of full eradication as a function of the number of consecutive nights since last animal captured (Fig.3.5). Simulation results show a considerable difference between the two populations. When individual heterogeneity is not considered (homogeneous population), the 95% threshold was reached at around 200 quiet nights, whereas for the heterogeneous populations the 95% threshold was not attained at any point during the 1000 first nights. This means that when dealing with heterogeneous populations, because of the presence of a few very shy individuals, we require much greater trapping efforts to be certain of the success of an eradication.

3.6 A framework for detecting heterogeneity using capture data

A useful application of the models described above would be using them to detect and quantify heterogeneity in a real population. To give an example of how this could be done, in this section we fit the model to synthetic animal capture data by maximum likelihood and estimate the heterogeneity parameters.

We then use the estimate of the variance in the individuals' probabilities of interaction to estimate and detect the level of heterogeneity in the population.

We assume the available data consists of n_k, the number of individuals caught on night $k \in [1, 2, ..., k_{max}]$, and n_{tot}, the total number of individuals caught.

3.6.1 Constant probability of encounter p_{enc}

We study a few different scenarios to explore our model's sensitivity to the different parameters. In this section, we fix the probability of encounter p_{enc} to 0.2, which corresponds to a distance home-range centre/trap of approximately 120m (see Fig. 3.1). In the next section, we will use random p_{enc} drawn from a $\beta-$distribution and we analyse how an increasing variability in p_{enc} affects our estimates of population

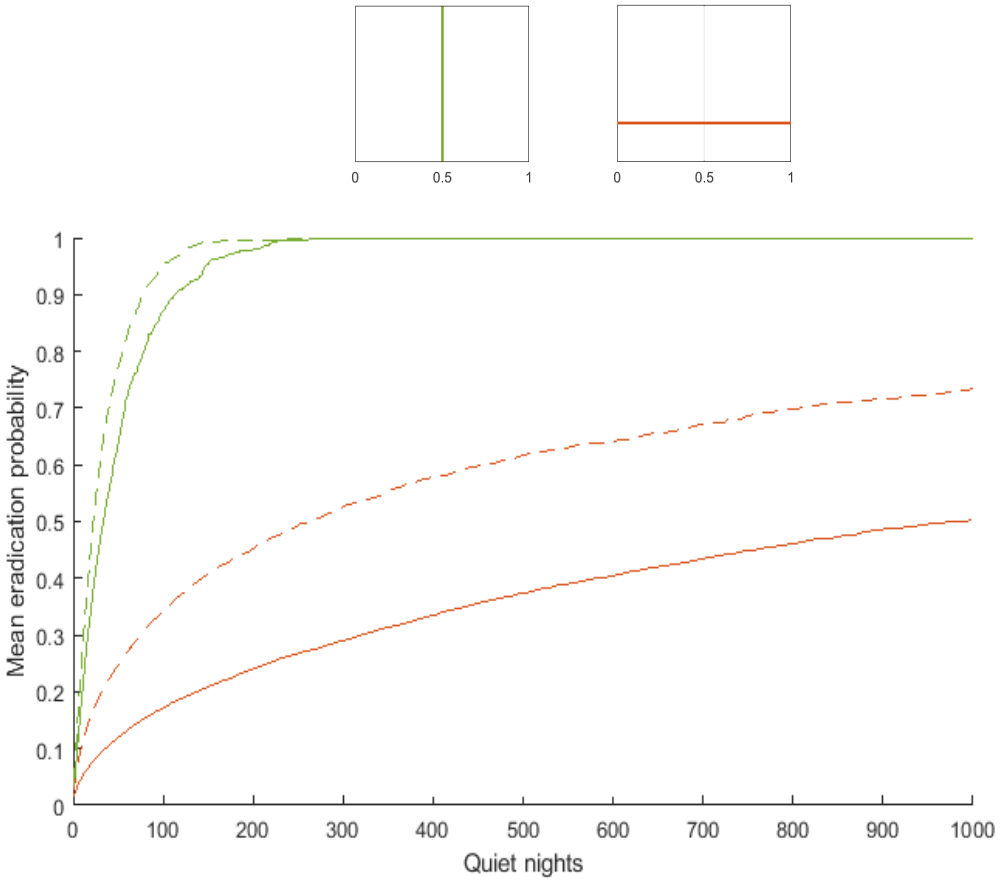

Figure 3.5: The number of consecutive "quiet nights" required for a high probability of eradication success increases with the level of heterogeneity. Probability of successful eradication depending on the number of "quiet nights" since the last captured animal for both the consistent behaviour method (full line) and the inconsistent behaviour method (dashed line). We compare results for a homogeneous population (green line) and a heterogeneous population (red line).

heterogeneity.

In real-life eradication programs, the real value of population size N is unknown and must be estimated. In this section, we simulate capture data using $N = 300$, and we then fit our models to the data using different guesses for N.

We assume that individuals behave in the manner described for the consistent daily behaviour model. First, we use the model to generate nightly capture data for a trapping session of k_{max} nights. We then fit our model to the data as follows.

The probability P_{n_k} of capturing n_k individuals on night k is given by the probability of not having captured those individuals on the first $k-1$ nights, times the probability of capturing them on night k. Under the assumption of a homogeneous population with interaction probability p_{int}, this is given by:

$$P_{n_k} = \left(p_{enc}p_{int}(1 - p_{enc}p_{int})^{k-1}\right)^{n_k} \tag{3.3}$$

Similarly, we can calculate the probability of not having captured the remaining $(N - n_{tot})$ individuals in the population by the last night k_{max}. The likelihood L of the data under this model is then given by:

$$\begin{aligned}\ln(L) = &\left(\sum_{k=1}^{k_{max}} n_k \ln\left(p_{enc}p_{int}(1 - p_{enc}p_{int})^{k-1}\right)\right) + \\ &(N - n_{tot})\ln\left((1 - p_{enc}p_{int})^{k_{max}}\right)\end{aligned} \tag{3.4}$$

where p_{enc} is the probability of encountering a trap, which in this scenario is kept constant at $p_{enc} = 0.2$.

Under the assumption of a heterogeneous population, with distribution of p_{int} specified by PDF $f(p_{int})$, the probability of capturing n_k individuals on night k is given by:

$$P_{n_k} = \left(\int_0^1 f(p_{int})p_{enc}p_{int}(1 - p_{enc}p_{int})^{k-1}dp_{int}\right)^{n_k} \tag{3.5}$$

The likelihood L of the data under this model is then given by:

$$\begin{aligned}\ln L = &\left(\sum_{k=1}^{k_{max}} n_k \ln\left(\int_0^1 f(p_{int})p_{enc}p_{int}(1 - p_{enc}p_{int})^{k-1}dp_{int}\right)\right) + \\ &(N - n_{tot})\ln\left(\int_0^1 f(p_{int})(1 - p_{enc}p_{int})^{k_{max}}dp_{int}\right)\end{aligned} \tag{3.6}$$

In the heterogeneous population model, $f(p_{int})$ is the β-distribution, and we find the values of the mean μ and variance σ^2 of the β-distribution that maximise $\ln L$. Note that the homogeneous population model is a special case of the heterogeneous population one. It is obtained when $f(p_{int})$ is a $\delta-$function centred at μ, or in the limit case with distribution parameters α, $\beta \to \infty$. We therefore find the values of μ and σ that maximise $\ln L$ by fitting our model to the capture data. When fitting the heterogeneous population model to data coming from a homogeneous population, we expect our estimate of the variance σ^2 to be close to zero.

To evaluate the sensitivity of this approach, we simulated capture data from a homogeneous population ($\sigma = 0$), a weakly heterogeneous population ($\sigma = 0.18$), and a strongly heterogeneous population ($\sigma = 0.29$). All populations had the same mean capture probability ($\mu = 0.5$). We then used the method described above to try to recover the parameters used for the simulation, as well as to determine whether the population was homogeneous or heterogeneous.

Fig. 3.6 shows the results of the model fitting procedure for different guesses of population sizes N.

We can see how as our guesses of population size N deviate further from the true value of 300, our estimates for p_c, μ and σ become less accurate. In particular, an overestimate of population size by 10 or more individuals resulted in the erroneous detection of heterogeneity ($\sigma \geq 0.2$) when there was none (Fig. 3.6, row 1, col 2). From this we can conclude that an accurate estimate of population size is necessary to properly detect heterogeneity in the population using this method.

We have tested the sensitivity of our model to the population size N and to the mean μ and standard deviation σ of the β-distribution from which the individual p_{int} values are randomly drawn. We have used the same heterogeneous population model (Eq. 5 and 6), under the assumptions of constant and known probabilities of encounter $p_{enc} = 0.2$. Table 7.1 in the appendix summarises our results.

As mentioned before, prior knowledge of N and p_{enc} usually results in accurate estimates of the population's heterogeneity level. Only in the case of very high heterogeneity levels ($\sigma_{th} = 0.289$), our model seemed to consistently underestimate both the mean μ and the standard deviation σ of the β-distribution (Table 7.1). When both the population size N and the population variance σ_{th} are high (resulting in a large number of very trap-shy individuals), the model erroneously estimated σ to be equal to zero (no heterogeneity) and μ to be much lower than its real value.

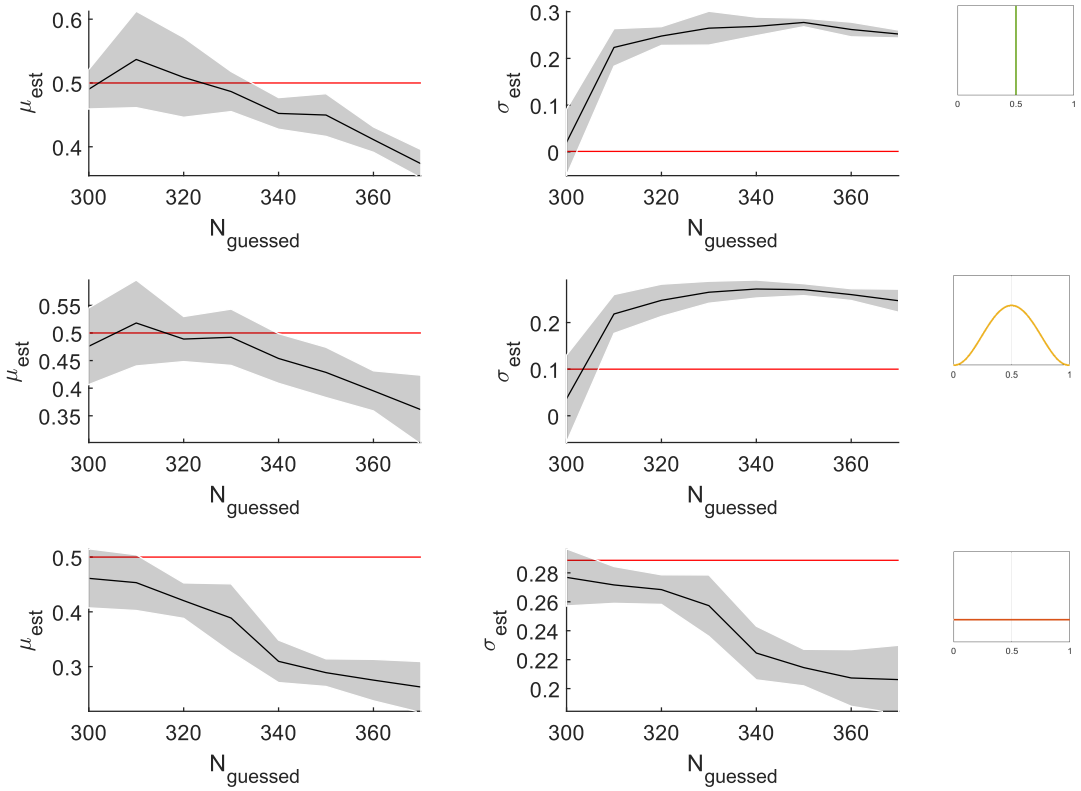

Figure 3.6: Heterogeneity can be accurately detected and evaluated with a good enough estimate of population size. For simulated data using three different distributions of interaction probability p_{int} (right corner insets) and constant encounter probability $p_{enc} = 0.2$, we compare the estimates of the two unknown parameters of our model: mean μ and variance σ^2 of the distribution of capture probability. The red lines represent the real parameter values used to simulate the data, the black line represents the mean value estimated by our model across 500 repeated simulations, and the greyed area corresponds to $\pm$ 2 standard deviations from the mean estimates. Note that y-axes scales differ between plots.

3.6.2 Random probability of encounter p_{enc}

In this section, we simulate capture data using the same parameter values as before, but this time we use the more realistic scenario of having random probabilities of encounter p_{enc}. We analyse how increasing variance in the distribution of p_{enc} affects our guesses of the population heterogeneity.

The previous equations for the log-likelihood are now adapted to include all the possible values of p_{enc}:

$$P_{n_k} = \left(\int_0^1 g(p_{enc}) p_{enc} p_{int} (1 - p_{enc} p_{int})^{k-1} dp_{enc} \right)^{n_k} \tag{3.7}$$

The likelihood L of the data under this model is then given by:

$$\begin{aligned} \ln(L) = &\left(\sum_{k=1}^{k_{max}} n_k \ln \left(\int_0^1 g(p_{enc}) p_{enc} p_{int} (1 - p_{enc} p_{int})^{k-1} dp_{enc} \right) \right) + \\ &(N - n_{tot}) \ln \left(\int_0^1 g(p_{enc}) (1 - p_{enc} p_{int})^{k_{max}} dp_{enc} \right) \end{aligned} \tag{3.8}$$

where p_{enc} is the probability of encountering a trap, which depends on the random distance between the animal's home-range centre and the closest trap. The random probabilities of encounter are drawn from a $\beta-$distribution with mean $\mu_{p_{enc}} = 0.2$ and changing variance.

Under the assumption of a heterogeneous population, with distribution of p_{int} specified by PDF $f(p_{int})$, the probability of capturing n_k individuals on night k is given by:

$$P_{n_k} = \left(\int_0^1 \int_0^1 g(p_{enc}) f(p_{int}) p_{enc} p_{int} (1 - p_{enc} p_{int})^{k-1} dp_{int} dp_{enc} \right)^{n_k} \tag{3.9}$$

The likelihood L of the data under this model is then given by:

$$\begin{aligned} \ln L = &\left(\sum_{k=1}^{k_{max}} n_k \ln \left(\int_0^1 \int_0^1 g(p_{enc}) f(p_{int}) p_{enc} p_{int} (1 - p_{enc} p_{int})^{k-1} dp_{int} dp_{enc} \right) \right) + \\ &(N - n_{tot}) \ln \left(\int_0^1 \int_0^1 g(p_{enc}) f(p_{int}) (1 - p_{enc} p_{int})^{k_{max}} dp_{int} dp_{enc} \right) \end{aligned} \tag{3.10}$$

Figure 3.7 shows how our estimates of the mean $\mu_{p_{int}}$ and variance $\sigma_{p_{int}}$ of the p_{int} distribution become less accurate as the variance $\sigma_{p_{enc}}$ of the p_{enc} distribution

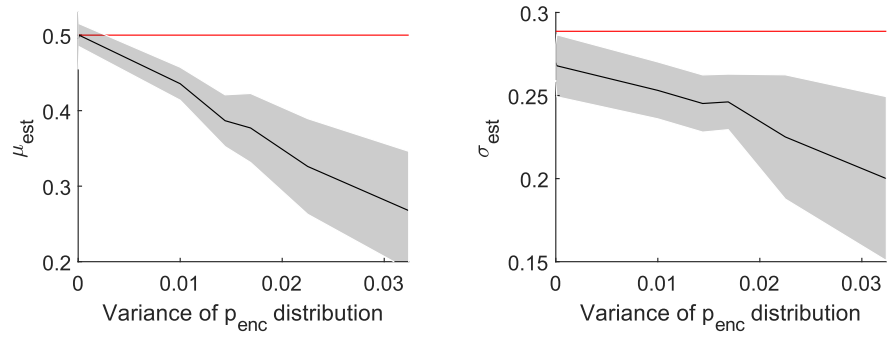

Figure 3.7: Heterogeneity can only be accurately evaluated when individuals have a similar probability of encounter p_{enc}. For simulated data using $N = 300$, $\mu = 0.5$, $\sigma = 0.289$ and a range of values for the variance of the distribution of encounter probabilities p_{enc}, we compare the estimates of the two unknown parameters of our model: mean μ and standard deviation σ of the distribution of capture probability. The red lines represent the real parameter values used to simulate the data, the black line represents the mean value estimated by our model across 500 repeated simulations, and the greyed area corresponds to $\pm$ 2 standard deviations from the mean estimates.

increases. With zero variance (*i.e.* the model described in Section 6.1, our estimates are closed to the real values used to simulate our data. As $\sigma_{p_{enc}}$ gets bigger, our estimates are more and more negatively biased.

Even with a high variance in the distribution of p_{enc}, however, our estimates of the the parameter σ (the measure of how heterogeneous our population is) are not too far from the theoretical values (up to 20% difference in the worst case scenario). This means that our model still detects heterogeneity (although its measure is biased) even when the distance between the animals' home-range centre and the traps is completely random.

3.7 Discussion

We have developed a model to investigate the influence that individual heterogeneity has on the success and the efficiency of trapping operations. Overall, our results demonstrate a strong effect of heterogeneity on model predictions of population size decline, showing that even relatively weak heterogeneity increases the average time needed for eradication. In line with previous studies (see *e.g.* Mäntyniemi et al. (2005); Pledger and Efford (1998)), our results also showed that estimates of population size are markedly biased when heterogeneity is not included in the model.

These simulations add to a growing corpus of research showing that animals' different behavioural profiles are a key component in the modelling of population dynamics. Particularly, it is interesting to explore the applications of these kinds of models to the control of invasive pest populations, where consistent behavioural variation could ultimately determine the success or failure of an eradication attempt.

These results could be used as a guide for managers designing and tracking progress of an eradication procedure. For example, identifying the threshold time at which the rate of decrease in population size starts to considerably slow, could provide an indicator to inform managers that only highly trap-shy individuals are remaining. A change to a more intensive and targeted eradication method could be introduced at this time to capture the rest of the trap-shy population. For example, different types of olfactory lures can be used as attractants for the management of invasive mammalian predators (Price et al., 2019). A change of lure could increase the probability of interaction with the trap for the more trap-shy individuals in the population.

Also, in our proposed framework to detect heterogeneity we showed that it is possible to gain important information about the population of interest early on in the eradication process. This step can help design trapping or detection procedures that are better tailored to the population type we are dealing with. The proposed method, however, rests on the model assumptions described earlier (population closure, non-overlapping home-ranges, consistent daily behaviour), which are all simplifications of the real population dynamics and which are only valid in a few specific cases, such as that of rapid eradication programmes in relation to the species' life history. Furthermore, the sensitivity analysis presented in section 6 shows that the accuracy of the estimates obtained with this method relies on previous knowledge of the population size, which is not always easy to measure. This model is an example of how we could use available data to infer likely heterogeneity in the animals' trappability, and would need to be calibrated to the population of interest in order to give realistic results.

While there is some evidence to suggest personality traits could be genetically transmitted from one generation to the next (Dochtermann et al., 2015), many animal species are known to have developed social learning skills, allowing them to acquire new behaviours via knowledge transmission from their parents or other members of their population (Nicol, 1995; Griffin, 2004). Our results suggest that during eradication of a heterogeneous population, the few individuals left at the end of a trapping session will be dominated by the most "trap-shy" individuals. Knowledge transfer from these individuals could lead to a new generation of "super pest" with a much

lower average probability of interaction than the original parent population (King et al., 2003). On the other hand, if the proportion of very trap-shy individuals was low enough, the removal of a sufficiently large portion of the population could still lead to eradication due to Allee effects (Liebhold and Bascompte, 2003). The population thinning during the removal of pests might also change the way animals use their territory: lower densities would increase home-range sizes, and if the animals diffused at a higher rate because of the population thinning, then the probability of encountering a trap would increase, therefore accelerating the eradication process.

As mentioned before, we model probabilities of capture as the product of two separate probabilities, probability of encounter (which mostly depends on external factors, such as the distance between traps and trap attractiveness, but also the animal's rate of diffusion and propensity to explore) and probability of interaction (which is mostly related to internal factors, such as the animal's personality and life history). Because we model these separately, the model could be extended to explore vertical/horizontal transmission of personality traits, once these parameters have been calibrated using field data.

Future research could be devoted to the investigation and measure of personality traits that could affect the population's trappability (*e.g.* the aforementioned propensity to explore and interact with a novel object, but also aggressive behaviour and activity level), and to the vertical and horizontal transmission of these personality traits across members of a population. Our model could also be extended for animal movement in a heterogeneous environment, including landscape features, other animals' home-ranges, and urban activity zones.

CHAPTER 4

Personality Transmission: like parent, like child

In the introduction of this thesis, we discussed the different factors that could influence an individual's personality. In this chapter we focus specifically on vertical transmission of a personality trait: trap-shyness. We expand the model of small mammal pest population dynamics presented in Chapter 3 to include reproduction and density-dependent home-ranges.

4.1 Introduction

In some species, individuals display behaviour that mimic that of their parents. We call this phenomenon "vertical" personality transmission. Vertical personality transmission happens when offspring exhibit similar behavioural responses as those of their parents, when subject to same stimuli or environmental cues. Whether this transmission happens at the genetic level or during an individual's upbringing is unclear and will not be discussed here.

In this study we present a simulation model built to explore different scenarios of vertical personality transmission. Specifically, we simulate the vertical transmission of trap-shyness (as defined in Chapter 3). We use the example of possum eradication in a New Zealand forest, with a simulated grid of traps overlaying the home-ranges of a the possum population.

In this chapter we also explore the relationship between probability of encounter and home-range size, by considering two scenarios of den use: multiple dens use (common in brushtail possums) and single central den use. We then present the differences

and similarities in eradication success and duration between the two scenarios.

Our results suggest that vertical transmission of trap-shyness strongly impacts the probability of eradication of the pest population and the time to complete an eradication, and that a poorly designed eradication programme may lead to populations of super-pests with very low average trappability.

4.2 Modelling framework

We use a stochastic individual-based model of animal trapping. We expanded the model presented in Chapter 3 by including density-dependent reproduction, mortality, density-dependent home-range radii, random distances to the nearest traps and vertical transmission of personalities.

4.2.1 Landscape

We assume a homogeneous landscape of arbitrarily fixed area A (Table 4.2). We chose a carrying capacity per hectare K from the values allocated to New Zealand land cover classes by Warburton et al. (2009). The value we chose corresponded to a non-controlled population of possum in a mixed beech/podocarp-broadleaved forest, and is the highest carrying capacity measured amongst all habitats mentioned in that study.

At the beginning of each simulation, the coordinates of each animal's home-range centre are randomly drawn from an array of possible locations. This position is used to calculate the distances to all traps within the home-range. The distances are then converted to probabilities of encounter p_{enc} as described in Section 4.2.3. These calculations are done independently for each animal and we assume no overlap of home-ranges (each animal's p_{enc} is not affected by the other animals' home-range positions).

4.2.2 Density-dependent reproduction and natural mortality

Possum populations show density-dependent effects on fecundity (King and Forsyth, 2021; Ramsey et al., 2002). We model the birth rate at time t as

$$B_t = \left(\alpha - \frac{\gamma}{KA} N_{t^*}\right) f(t) \tag{4.1}$$

where α is the constant annual birth rate, γ is the constant annual growth rate, K is the carrying capacity, and A is an arbitrarily chosen study area (see Table 4.2). To account for the gestation period we update the density dependent term by using the number of alive adults at time t^*, the beginning of the reproduction season. $f(t)$ corresponds to the normal distribution function used to model the reproduction season, evaluated at day t. Brushtail possums in New Zealand have been observed to have one major breeding season starting at the end of summer and lasting for 3-4 months (King and Forsyth, 2021; Lustig et al., 2019; Crawley, 1973). A small portion of females have a second breeding season in spring. For simplicity, we ignored the second breeding season and we modelled reproduction season as a normal distribution with a 20 days standard deviation.

Natural mortality is modelled as a constant per capita mortality rate per unit time using the formula

$$M = 1/l \tag{4.2}$$

with l being life expectancy.

The expected number of newborn and natural deaths on a given day $t + 1$ is then calculated as

$$\begin{aligned} J_{t+1} &\sim Bin(N_t, B_t \delta t) \\ D_{t+1} &\sim Bin(N_t, M \delta t) \end{aligned} \tag{4.3}$$

where $\delta t = 1$ is the time step.

Newborns do not affect the density-dependent fecundity until they are one year of age, but they can die naturally or from trapping at the same rates as adults.
In the absence of trapping, personality has no effect and the model behaves like a stochastic density-dependent individual-based model with seasonal reproduction (Figure 4.1).

4.2.3 Density-dependent probability of encounter

The way animals move in their home-range vary from species to species. Understanding the movement patterns of the modelled population is crucial, as these patterns determine how likely an animal is to be found at a given location. In this section, we present two modelling approaches for the calculation of density-dependent probability of encounter.

Firstly, we present a model of multiple dens use, which is common in brushtail possums (Whyte et al., 2014). This model will be calibrated with $g_0 - \sigma$ data

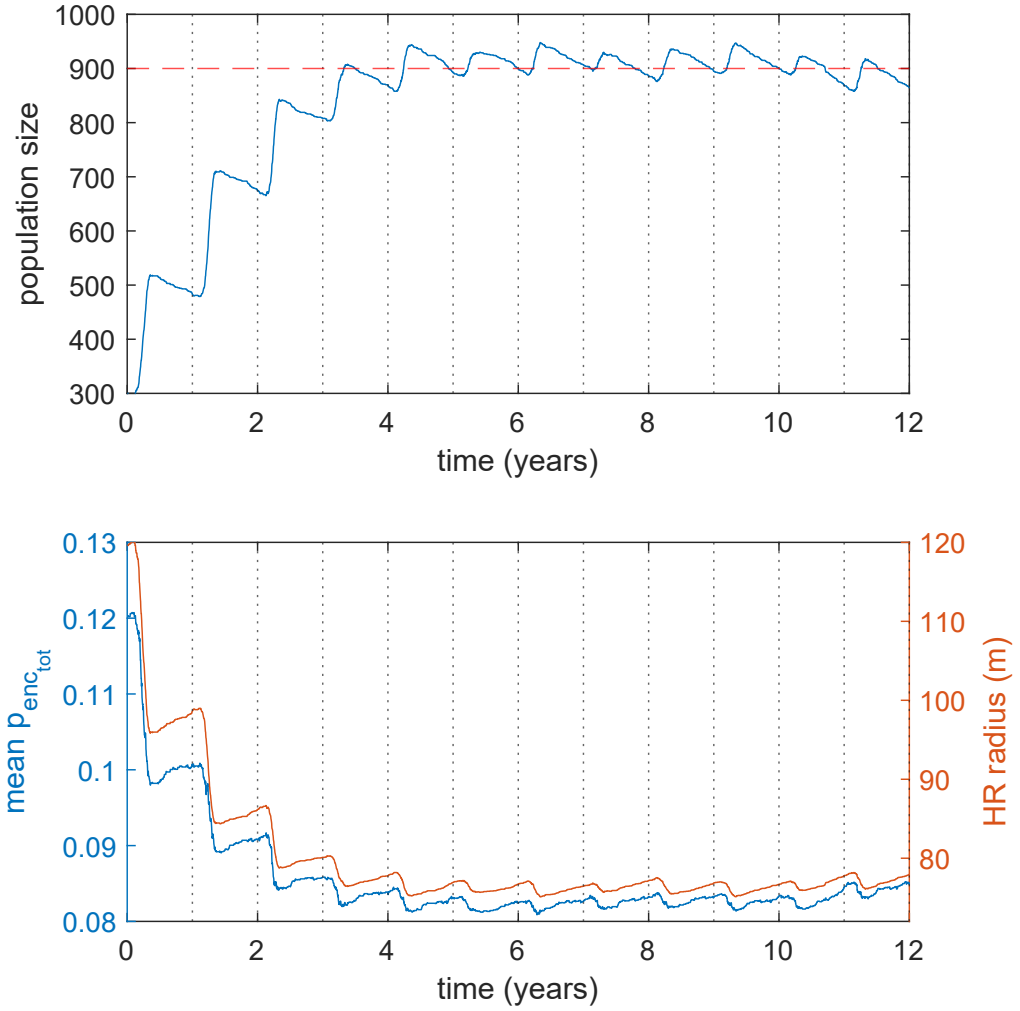

Figure 4.1: Population dynamics with seasonal reproduction and natural mortality in the absence of trapping, simulated using parameter values in Table 4.2 and for an initial population $N_0 = 300$. **Top:** Change in population size over time. The red horizontal line corresponds to carrying capacity. **Bottom:** Change in mean total probability of encounter $p_{enc_{tot}}$ (blue; as defined in Equation 4.6) and density-dependent home-range radius (red; as defined in Section 4.2.3.1) over time. The reduction in encounter probability is a direct consequence of the reduction in home-range radius.

from the meta-analysis of New Zealand pest detectability presented in Chapter 2. We then consider a model of single central den use, where animals always return to their home-range centre at the end of each day. We use a simulated random walk to explore the relationship between the probability of encountering a trap within the animal's home-range, the home-range radius, and the distance between traps (assuming a regularly spaced grid of traps). Both submodels take home-range radius and trap grid spacing as inputs, and output the total nightly probability of encountering a trap from the grid of traps.

4.2.3.1 Multiple den use - the brushtail possum example

The pest detectability literature review we presented in Chapter 2 highlights a negative correlation between σ (a spatial-decay parameter related to the circular area that animal occupies 95% of the time, with HR area = $\pi(2.45\sigma)^2$) and the population density of New Zealand's small mammal pest species. In other words, as these populations grow larger, each individual has less space to move in, *i.e.* a smaller home-range, and vice versa.

The relationship between home-range size σ and density D for brushtail possum in New Zealand is well described by the power law $D/D_0 = 1212.75(\sigma/\sigma_0)^{-1.44}$ (where $D_0 = 1\text{ha}^{-1}$ and $\sigma_0 = 1\text{m}$, see Figure 2.1), which can be rearranged into $\sigma/\sigma_0 = 76.14(D/D_0)^{-0.4}$. In our model, all individuals in the population have the same home-range size, which is updated at every time step (every day) with the new population density using the function above.

The relationship between the probability of encounter and the home-range size for brushtail possums is not well explored in the literature. This relationship depends on a number of factors: the trap grid spacing, the animal's denning behaviour, movement rate and perception distance. In addition, as shown in Chapter 2, most studies do not make the distinction between probability of encounter and probability of detection given encounter. Instead, they report the nightly detection probability by one device set at a distance d from the animal's home-range centre as

$$p_{detect}(d) = g_0 e^{-d^2/2\sigma^2} \tag{4.4}$$

where g_0 is the nightly probability of detection at the home-range centre.

We assume $p_{detect}(d) = p_{enc}(d)p_{int}$, where p_{int} is the probability of interaction with the device, given encounter. Therefore, the probability that an individual i with home-range size σ_i encounters a single trap set at a distance d from their home-

range centre can be derived as:

$$p_{enc}(d) = \frac{g_0(\sigma_i)}{p_{int}} e^{-d^2/2\sigma_i^2} \tag{4.5}$$

where $g_0(\sigma_i)$ is the relationship between g_0 and σ, which for brushtail possums in New Zealand is best described by the power law $g_0 = 3.12(\sigma_i/\sigma_0)^{-0.8}$, with $\sigma_0 = 1$m (Figure 2.1). Note that reasonable values of σ are sufficiently large that using this function will always result in $g_0 \leq 1$.

Ideally, we would have a measure of g_0 for each individual in the population, to account for individual differences in trappability. However, as the values of g_0 we collected do not distinguish between individuals, we assume $p_{int} = \mu_0$ in Equation 4.5, with μ_0 being the average initial p_{int} of our simulated population.

Equation 4.5 describes the probability of encountering a single trap in the animal's home-range. However, our simulated animals can have more than one trap within their home-range. We define "total probability of encounter" $p_{enc_{tot}}$ the probability of encountering *any* of the traps within the home-range on a given day. This probability is updated every time the home-range radius changes with population density using the formula

$$p_{enc_{tot}} = 1 - \prod_{j=1}^{T} (1 - p_{enc}(d_j)) \tag{4.6}$$

where $p_{enc}(d_j)$ is the probability of encountering trap j at a distance d_j from the home-range centre, evaluated using Equation 4.5, and T is the total number of traps.

4.2.3.2 Single central den use

We now present a random-walk simulation to explore the effects of different home-range radii and trap grid spacings on the probability of encounter in the single central den scenario, *i.e.* that of animals that always returns to their home-range centre at the end of each day.

To our knowledge, no previous study has provided an explicit measure of the probability of encounter in a grid of equally-spaced traps, for the specific case of animals using a single central den of unknown position and for different home-range radii. This knowledge gap inspired the simulation work presented in this section.

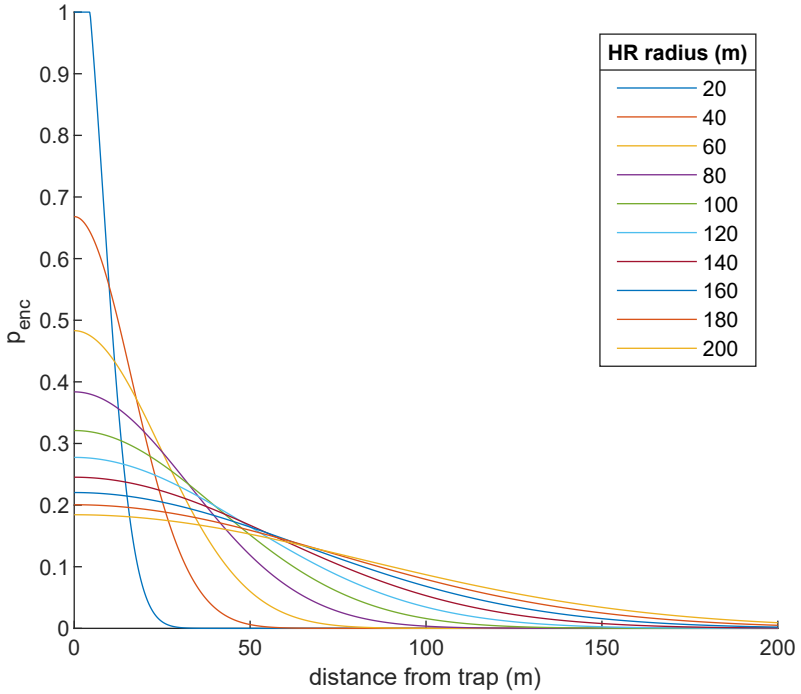

Figure 4.2: Relationship between the probability of encounter p_{enc} and the distance d between trap and home-range centre. Plots produced using Equation 4.5 for different values of σ (which was converted to HR radius using the formula σ =HR radius/2.45, in accordance with the definition of σ).

Table 4.1: Parameter values used for the random walk simulations used to extract the total probability of encounter $p_{enc_{tot}}$ for different home-range radii and trap grid spacings.

Parameter	**Value**
Step size (m)	2
Number of steps per day (12h)	480
Perception distance (m)	10
Trap grid spacings (m)	[40, 60, 80, ..., 200]
Home-range radii (m)	[20, 40, 60, ..., 200]

We used a spatially-explicit, individual-based model to measure how home-range radius and grid spacing affect the total probability of encounter in a grid of equally spaced traps. Each simulated individual has a home-range centre randomly drawn in an "infinite" grid of traps (the home-range centre was always surrounded by traps on all sides). The simulated animal would start a lattice-free, unbiased simple random walk (Codling et al., 2008) at its home-range centre, its movement was parametrised using the values in Table 4.1. We considered a successful "encounter" the instance where the animal came within view (<10m away) of a trap during its 12-hour long walk. An example of this random walk can be seen in Figure 4.3.

$p_{enc_{tot}}$ was found to be independent of home-range radius (Figure 4.4), so long as the home-range radius was at least half as big as the distance between traps (at least one trap within the home-range). This result seems reasonable, as $p_{enc_{tot}}$ mostly depends on the distance between home-range centre and trap, and we calculated an average $p_{enc_{tot}}$ for randomly drawn home-range centres. For home-range radii smaller than half the distance between traps, the average $p_{enc_{tot}}$ is smaller, as there may or may not be a trap within the home-range. Figure 4.4 also shows a negative relationship between $p_{enc_{tot}}$ and grid-spacing: a small distance between traps corresponds to a high probability of encounter, for similar home-range radii.

These simulations were based on the assumptions that the animals always return to the home-range centre at the end of each 12 hour period, and that their movements can be characterised by a diffusion coefficient that doesn't change with home-range radius. A constant diffusion coefficient means that the animals can only cover so much ground within one day. For small home-range radii, this results in the animals having a high probability of covering the entirety of their home-range each day. For big home-range radii, this results in the animals not using all the space available, as the walk always starts at the centre of their home-range.

Another possible scenario is a diffusion coefficient proportional to home-range radius: in that case, an increase in home-range radius would corresponds to the animal

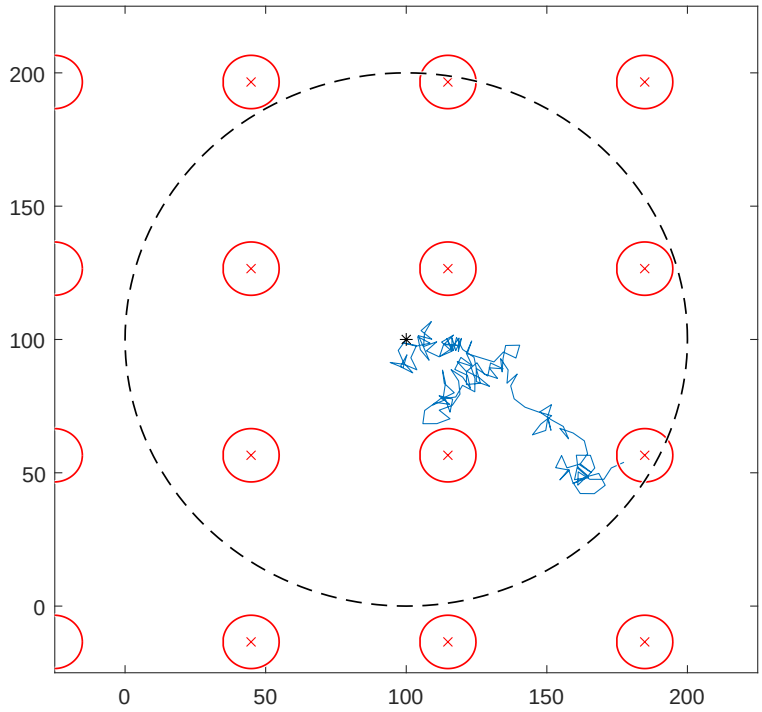

Figure 4.3: Example of random walk in a grid of traps. Example of a single simulation of a lattice-free, unbiased simple random walk in a grid of traps. The black dashed circle represents the boundaries of the animal's home-range. The red crosses and circles represent the traps and the perception radii, respectively.

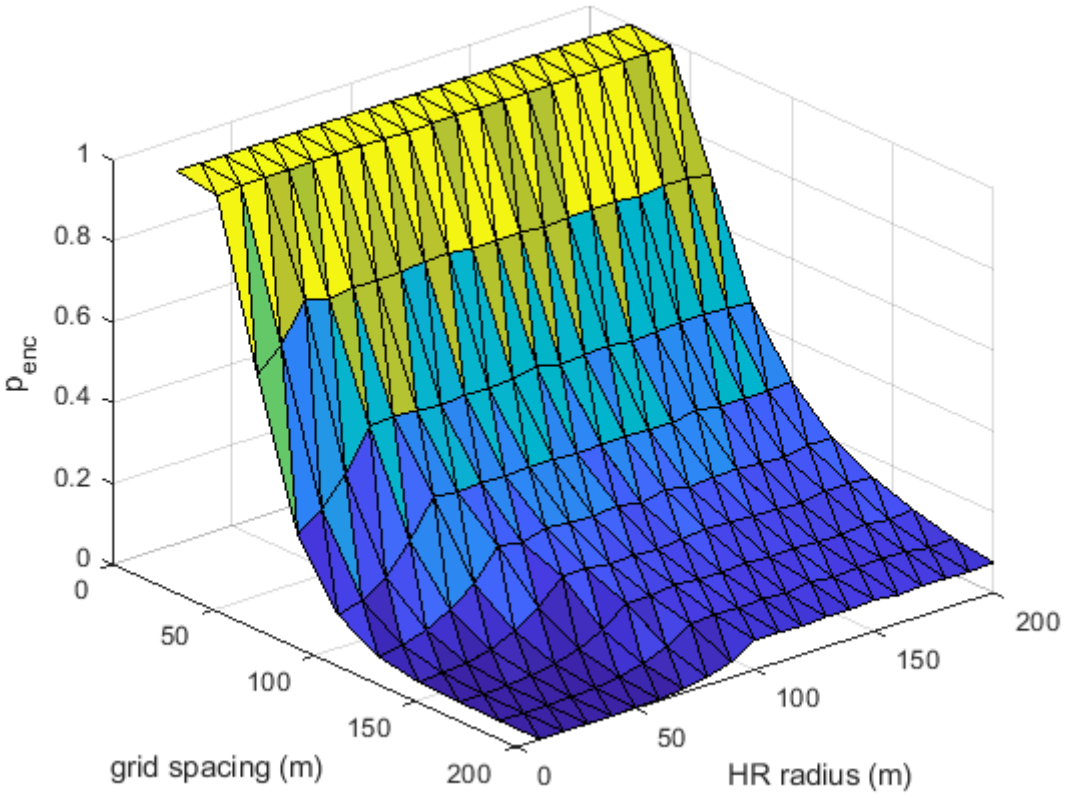

Figure 4.4: $p_{enc_{tot}}$ **is negatively related to with grid spacing but doesn't depend on home-range radius, as long as the home-range contains at least one trap and the animal always returns to the centre at the end of each night.** Relationship between $p_{enc_{tot}}$, home-range radius and grid spacing for 15 different values of home-range radius. Each point is the average of 10k simulations, run using parameter values presented in Table 4.1.

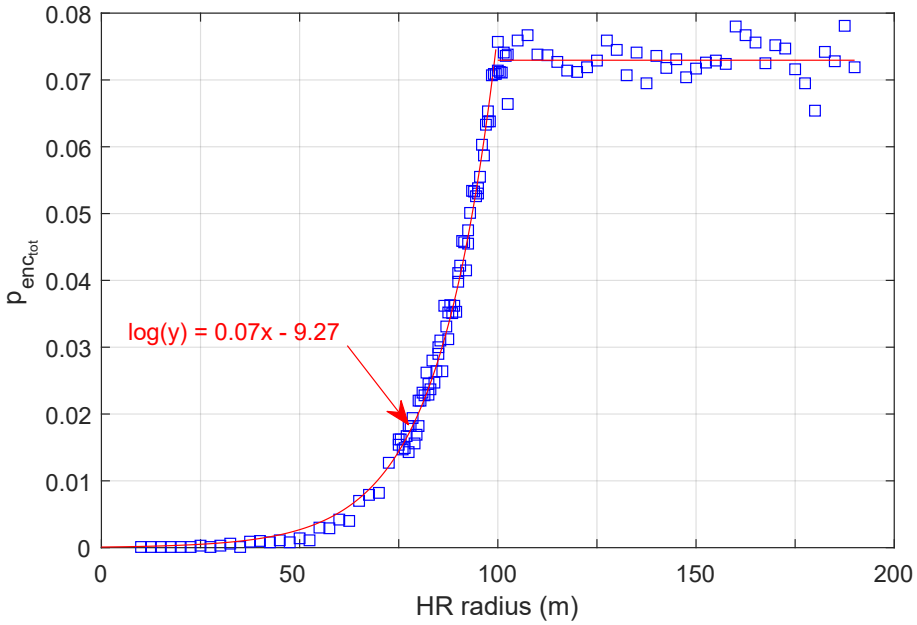

Figure 4.5: Total daily probability of encounter as a function of home-range size, for a trap grid spacing = 200 m, for animals returning to their home-range centre each night. Simulation results obtained using the simple random walk described in Section 4.2.3.2. Each blue dot represent the probability of encountering a trap over 10k simulations for a given home-range radius. The red lines are the fitted functions used to update $p_{enc_{tot}}$ in the population dynamics simulations of animals returning to their home-range centre.

covering a larger area in the same amount of time, and vice-versa. This would result in a higher $p_{enc_{tot}}$ for higher home-range radii.

In our simulations for single den use, we set the trap grid spacing to 200 m. The density-dependent probability of encounter is updated using the function presented in Figure 4.5, which is a slice through Figure 4.4. As we can see, the probability of encountering a trap on any given night increases exponentially as the home-range radius increases towards the trap grid spacing of 200 m. For home-range radii of 100 m and above, each animal's home-range contains at least one trap and $p_{enc_{tot}}$ remains constant at 0.073.

4.2.4 Trapping and probability of interaction

Each individual has a daily probability of capture $p_c = p_{enc_{tot}} p_{int}$, with $p_{enc_{tot}}$ being the total daily probability of encounter, and p_{int} being the probability of interacting with a trap, given encounter.

We model population heterogeneity at the individual level, by assigning a different probability of interaction p_{int} to each individual. The p_{int} of the initial population are drawn from a beta distribution with mean μ_0 and standard deviation σ_0.

The probability of encounter $p_{enc_{tot}}$ depends on the trap grid spacing, the animals' home-range centre and home-range radius, the latter being density dependent (see Section 4.2.3), and on whether we consider a single central den or a multiple den use.

4.2.5 Vertical transmission of personality

We model the vertical transmission of the p_{int} personality trait. Every newborn has a probability v to have the same p_{int} as their parent (for simplicity, as reproduction probability is assumed homogeneous, p_{int} drawn from the distribution of the *current* population distribution), and a probability $(1 - v)$ to have a random p_{int} (drawn from the original distribution, described by μ_0 and σ_0).

4.2.6 Simulations

We calculated the probability of eradication within 1000 days, by averaging results over 1000 simulations. Our initial population is at carrying capacity. We tested three different values of μ_0 (the initial population's mean p_{int}), 11 different values of σ^2 (the variance of the initial population's p_{int}, a measure of heterogeneity), and 11 different values of the vertical transmission parameter v (see Table 4.2).

4.3 Results

4.3.1 Multiple den use

Figure 4.6 shows three examples of simulated population dynamics for animals using multiple dens across their home-range, *i.e.* animals not returning to their home-range centre each night (see Section 4.2). These figures show how different distributions of trap-shyness and different levels of vertical transmission can greatly affect the outcome of an eradication program.

Of the three simulations shown in Figure 4.6, only the one corresponding to the "best" case scenario (high trappability, low heterogeneity, no vertical transmission) resulted in eradication in less than 1000 days. The other two simulated populations survived after 1000 days. In particular, the population corresponding to the "worst" case scenario (low trappability, perfect vertical transmission), after an initial period

Table 4.2: Parameter values used in the population dynamics simulations for the exploration of the effects of vertical transmission of trap-shyness on pest eradication.

Parameters	**Symbol**	**Value**	**Comments/references**
LANDSCAPE			
Study area	A	100 ha	
Trap grid spacing		200 m	
Carrying capacity	K	9 ha^{-1}	(Warburton et al., 2009), value corresponding to populations of possum in New Zealand's mixed beech/podocarp-broadleaved forests
POPULATION			
Trap perception distance		10 m	
Life-span	l	13 years	(Cowan, 2001)
Annual birth rate	α	0.77	Calculated as annual growth rate in King and Forsyth (2021) + annual mortality rate from Eq. 4.2.
Maximum home-range radius		380 m	Corresponding to the maximum value of σ (155 m) found in our literature review, see Chapter 2
SIMULATIONS			
Time step	dt	1 day	
First day of trapping	t_0	1^{st} Jan	
First day of reproduction season	t^*	1^{st} Feb	
Number of simulations		1000	
Initial opulation's mean p_{int} distribution tested	μ_0	[0.3, 0.4, 0.5, 0.6, 0.7]	
Initial population's variance of p_{int} distribution tested	σ_0^2	[0, 0.01, 0.02, ..., 0.1]	
Vertical transmission levels tested	v	[0, 0.1, 0.2,..., 1]	

where the few trap-happy individuals got captured, saw an increase in population size as very trap-shy newborn appeared during reproduction season (Figure 4.6, second graph down of the left column). This suggests the possibility of a population of "super pests" appearing if the most trap-shy individuals are left to reproduce, and if trap-shyness is transmitted to their offspring.

We then ran simulations using a range of possible values for the population's initial mean probability of interaction μ_0, the population's initial level of heterogeneity σ_0, and the level of vertical transmission v, as defined in the methods section of this chapter. Figure 4.7 shows a summary of our simulation results, obtained using the parameter values presented in Table 4.2. We show the eradication probability for each combination of parameter values tested, as well as the average eradication time, and the average population size after 1000 days for the populations that were not eradicated.

It appears that the probability of eradication is negatively affected mostly by low mean initial p_{int} and high levels of heterogeneity, but not so much by the level of vertical transmission v of trap-shyness. However, the level of vertical transmission affects the mean final population size for the simulations where the population was not eradicated, meaning that while surviving populations with little or no vertical transmission of trap-shyness leave behind only a small population of trap-shy individuals, a surviving population with high vertical transmission can result in a much higher number of very trap-shy "super pests".

The shortest eradication time (around 120 days from the beginning of trapping) was obtained for the least heterogeneous population with no or very little vertical transmission of trap-shyness, and for high values of the mean initial p_{int}.
In the simulations where eradication was not achieved after 1000 days, the population settled to an equilibrium population size ranging from 1-2 individuals to over 500. Figure 4.6 suggests that these survivor populations could have a mean p_{int} as low as 0.001.

These results seem reasonable, as a high level of vertical transmission means that offspring are more likely to inherit their parents' level of trap-shyness. Over time, the most trap-shy individuals are left, and when they reproduce they create new populations of "super-pests" with very low levels of p_{int}, provided that the level of vertical transmission is high enough, and that there are some trap-shy individuals to begin with.

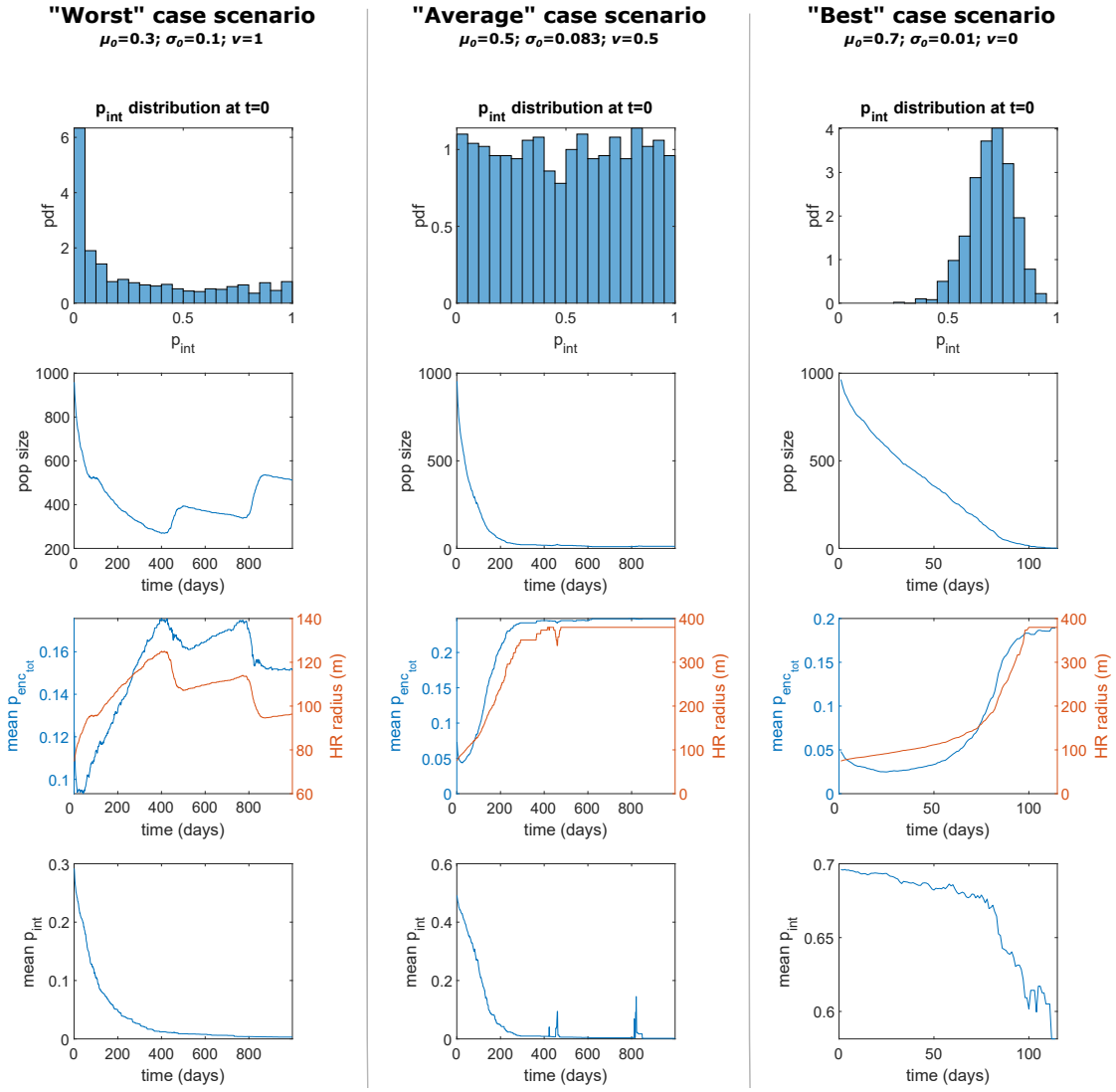

Figure 4.6: Three examples of simulated population dynamics during an eradication program, under different scenarios of personality distributions and vertical transmission, for animals *not* returning to home-range centre.

Left - "worst" case scenario: a majority of trap-shy individuals in the initial population (average initial $p_{int} = \mu_0 = 0.3$), high heterogeneity ($\sigma_0 = 0.1$), and perfect vertical transmission ($v = 1$, all newborns inherit their parents' trap-shyness). **Centre - "average" case scenario:** a majority of original individuals having an average level of trap-shyness (average initial $p_{int} = \mu_0 = 0.5$), average heterogeneity ($\sigma_0 = 0.083$), and a vertical transmission index $v = 0.5$ (about half of all newborns inherit their parents trap-shyness). **Right - "best" case scenario:** a majority of trap-happy individuals (average initial $p_{int} = \mu_0 = 0.7$), low heterogeneity ($\sigma_0 = 0.01$), and no vertical transmission of trap-shyness.

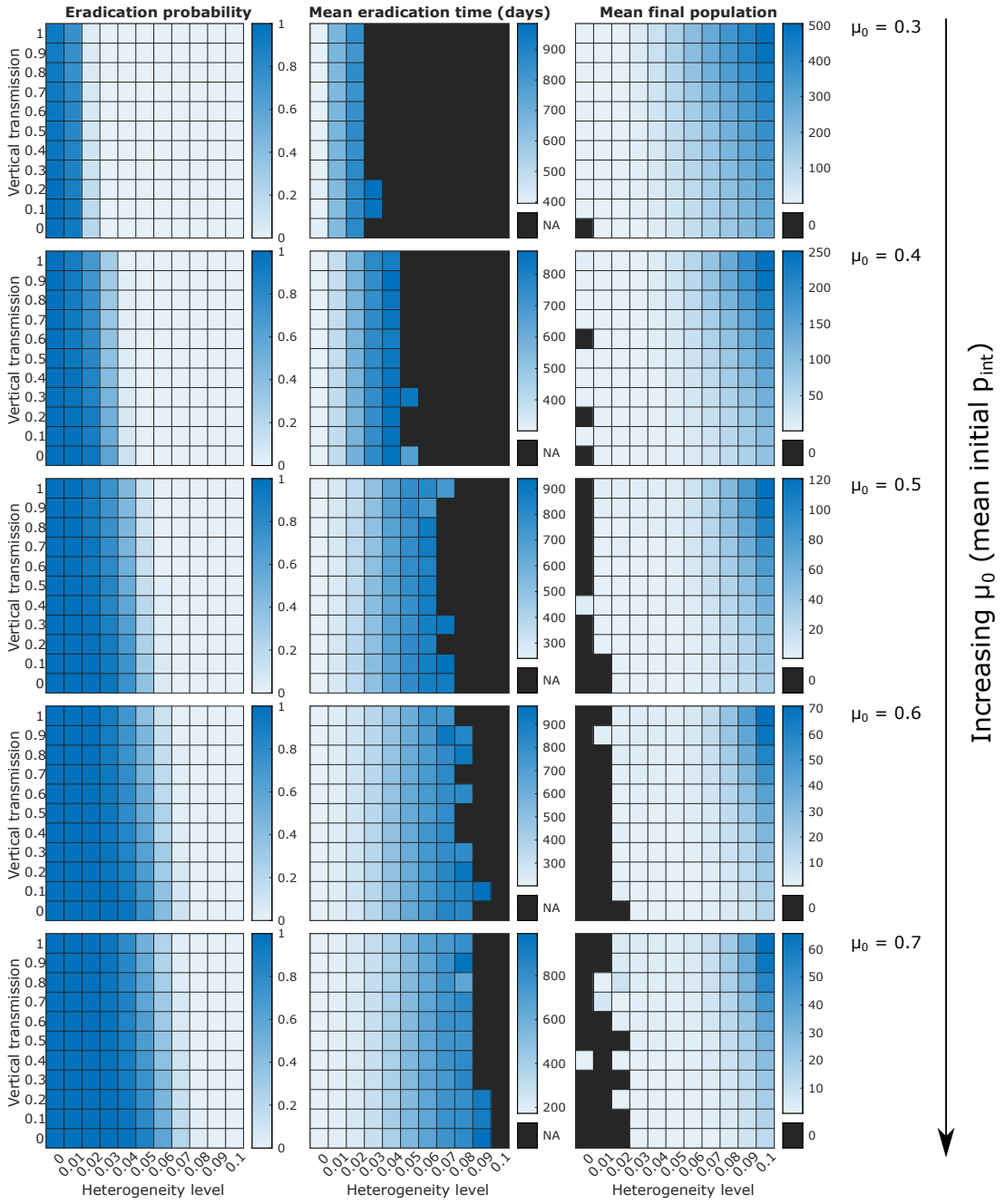

Figure 4.7: Eradication probability and duration for different populations, for animals *not* returning to their home-range centre each night. Heatmaps of the probability of eradication, the mean eradication time, and the mean final population for different levels of initial behavioural heterogeneity (different means μ_0 and heterogeneity level expressed as standard deviations σ_0 of the beta distribution used to draw individual p_{int}), and different levels of vertical transmission of trap-shyness. The "heat" in the graphs corresponds to the eradication probability after 1000 days over 1000 simulations (left column), the mean eradication time in days (centre column), and the mean population size after 1000 days for the unsuccessful eradications (right column).

4.3.2 Single central den use

We now present simulation results obtained with our model of animals returning to a single central den each night. The only difference being the way we calculate the total daily probability of encounter $p_{enc_{tot}}$.

Figure 4.8 shows the same three examples of population dynamics under three different conditions. The results are very similar to those obtained in the "animal not returning to their home-range centre" scenario, with the only difference that $p_{enc_{tot}}$ now follows the relationship in Figure 4.5 and is in general lower than in the previous simulation scenario.

The heatmaps in Figure 4.9 show similar trends in the eradication probability, mean eradication time and mean final population as those described in Section 4.3.1 for the "multiple den use" scenario. The only difference being a slight decrease in eradication success for the single den users, whose $p_{enc_{tot}}$ never goes above 0.073 (whereas in the other model it could go as high as 0.25, see Figure 4.6). The higher maximum $p_{enc_{tot}}$ of single den users doesn't affect the eradication success much, as $p_{enc_{tot}}$ only goes that high when the population size is very low and comprising of only the most trap-shy individuals. These individuals' trap-shyness makes them very hard to catch, even for higher values of $p_{enc_{tot}}$.

4.4 Discussion

In this chapter we have developed a model to explore the effects of vertical transmission of trap-shyness on the success of eradication of a population of possums, under different scenarios of individual heterogeneity and space use.

Our results confirmed our findings of Chapter 3, showing that populations with lower mean trappability and higher heterogeneity are harder to eradicate. They also highlighted the role that vertical transmission can have on the state of the surviving population, in the case of unsuccessful eradications. Our findings are not surprising, but they demonstrate the importance of gaining information on animal personalities before and during any wildlife management programme where personalities can affect population dynamics.

In the specific case of invasive small mammals management in New Zealand, if these animals are able to teach or transmit trap-shyness to the rest of the population, pest eradication can become increasingly difficult if the population is allowed to reproduce. If enough surviving trap-shy individuals transmit their trap-shyness to

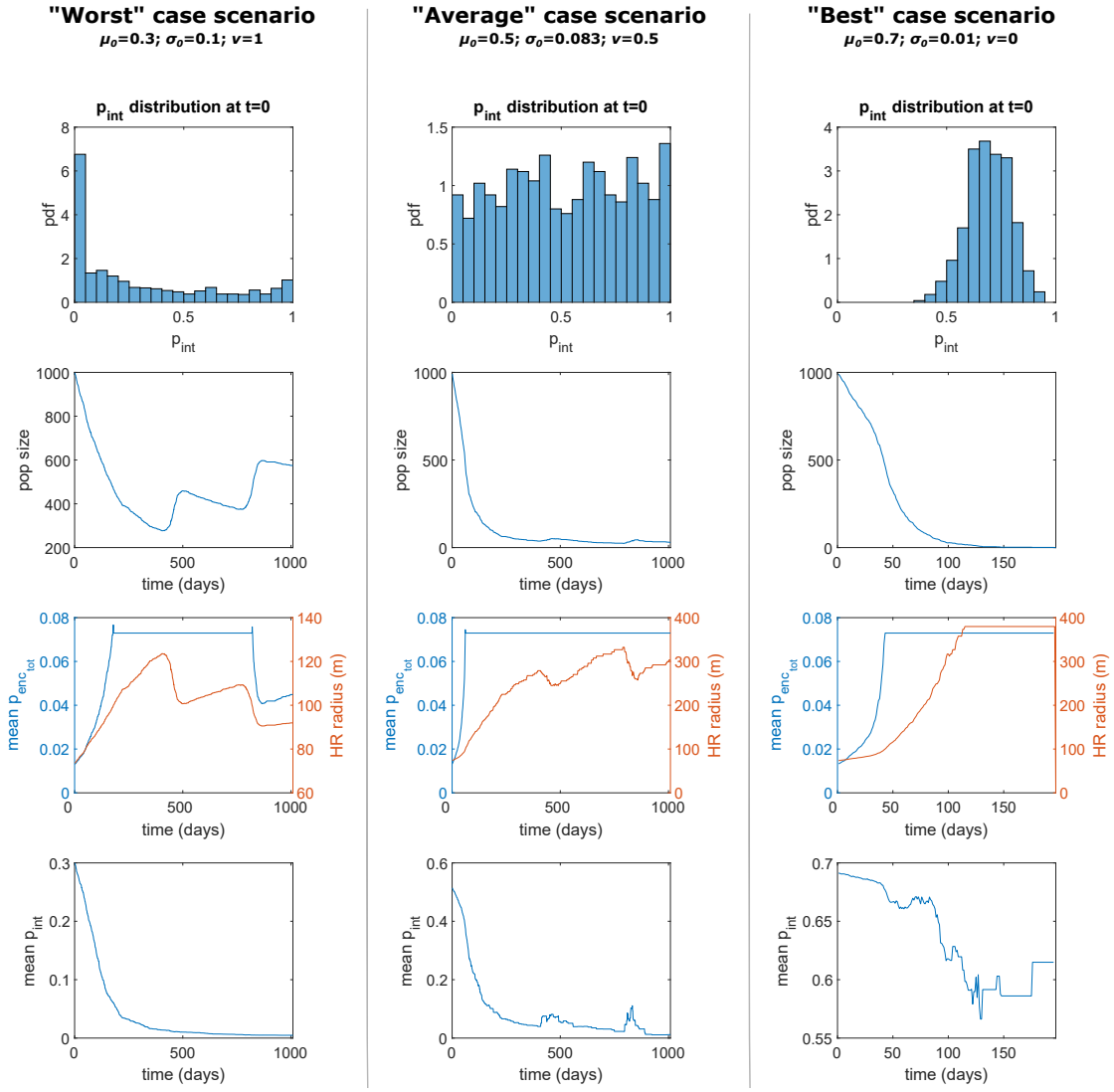

Figure 4.8: Three examples of simulated population dynamics during an eradication program, under different scenarios of personality distributions and vertical transmission, for animals returning to home-range centre.

Left - "worst" case scenario: a majority of trap-shy individuals in the initial population (average initial $p_{int} = \mu_0 = 0.3$), high heterogeneity ($\sigma_0 = 0.1$), and perfect vertical transmission ($v = 1$, all newborns inherit their parents' trap-shyness). **Centre - "average" case scenario:** a majority of original individuals having an average level of trap-shyness (average initial $p_{int} = \mu_0 = 0.5$), average heterogeneity ($\sigma_0 = 0.083$), and a vertical transmission index $v = 0.5$ (about half of all newborns inherit their parents trap-shyness). **Right - "best" case scenario:** a majority of trap-happy individuals (average initial $p_{int} = \mu_0 = 0.7$), low heterogeneity ($\sigma_0 = 0.01$), and no vertical transmission of trap-shyness.

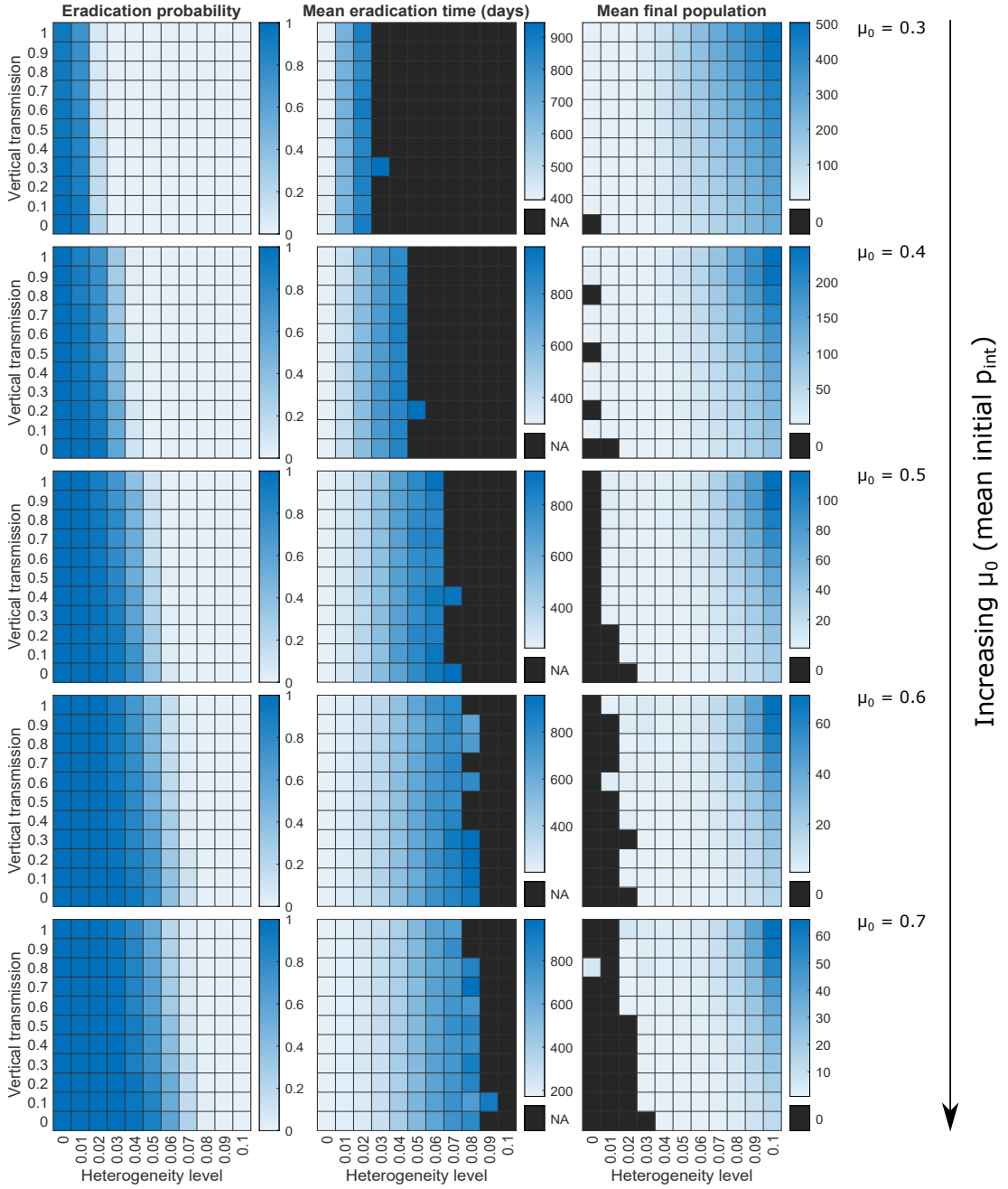

Figure 4.9: Eradication probability and duration for different populations, for animals returning to their home-range centre each night. Heatmaps of the probability of eradication, the mean eradication time, and the mean final population for different levels of initial behavioural heterogeneity (different means μ_0 and heterogeneity level expressed as standard deviations σ_0 of the beta distribution used to draw individual p_{int}), and different levels of vertical transmission of trap-shyness. The "heat" in the graphs corresponds to the eradication probability after 1000 days over 1000 simulations (left column), the mean eradication time in days (centre column), and the mean population size after 1000 days for the unsuccessful eradications (right column).

their offspring, the new population will become much more wary of traps and much harder to capture.

While there are many studies reporting small mammal pests' probability of capture (usually expressed as g_0, the daily probability of capture at the animal's home-range centre), few of them make the distinction between probability of encounter and probability of interaction. This can pose a few problems: (1) the lack of distinction between the two probabilities makes it hard to understand whether a low g_0 is due to a bad trap grid set-up (which would affect only p_{enc}), or to the animals' intrinsically low trappability, which could be met with a change of lure; (2) averaging the probability of capture over the whole population hides any between-individual differences in both space use and trappability, which, as we have shown in both this chapter and Chapter 3, can have a strong effect on the success and duration of an eradication programme.

In this chapter we also analysed the possible effects of population density and trap grid spacing on the probability of encountering a trap. Because we model probability of capture as the product of probability of encounter and interaction, the probability of encounter plays as big of a role in the eradication success as the level of trap-shyness: regardless of how trap-shy or trap-happy an animal is, if it hardly ever encounter a trap it will not get caught. This highlights the importance of ensuring animals have as many chances as possible to encounter an active trap for a successful eradication programme. In practice, this translate in a high trap density and in a regular trap checking and resetting.

The limitations of this study are mostly associated with the model calibration, the current knowledge gaps surrounding the way small mammal pests in New Zealand acquire their personalities, how or whether these personalities are transmitted between members of a population, and how these species move within their home-ranges.

This model could be extended by including other individual differences and mechanisms that could affect population dynamics, such as activity level, different home-range sizes and immigration. More complex random walk models could be used to extract probabilities of encounter in different scenario of trap grid set up, different home-range shapes and areas, and space use. The model could also be calibrated to a real-life treatment areas by introducing landscape features such as habitat types and resource availability.

CHAPTER 5

Measurement of wild North Island brown kiwi (*Apteryx mantelli*) personalities

In the previous chapter we introduced animal personalities in our theoretical models of population dynamics. One of the main challenges we faced was finding field data on the distribution of trap-shyness in wild populations to calibrate our models.

This chapter aims to shine more light on the challenges associated with the collection of field data on animal personalities. It is an example of how to differentiate between between-individual variance (linked to different personalities) and within-individual variance (corresponding to behavioural plasticity), as well as highlighting other potential sources of variance in the observed behaviour.

5.1 Introduction

5.1.1 Chapter organisation and aims

This chapter is divided in three separate studies, preceded by a general introduction on the biology of our species of interest, the North Island brown kiwi (*Apteryx mantelli*), the cultural importance of kiwi conservation, and the study site.

The first study presented is a statistical analysis of a dataset obtained in 2008/9 from a double-Y maze experiment aimed at identifying differences in brown kiwi reactions to three different sources of odour. This experiment was not designed with the aim of measuring animal personalities, but the data structure happens to be one that allows to distinguish between between-individual and within-individual

variance. The second study focuses on the analysis of a more recent field experiment aimed at measuring differences in the response to capture by human-habituated and non-human-habituated birds. Because of time constraints, only one measurement per bird was taken, which does not allow to distinguish between between-individual and within-individual variance. The third and last study presents the results of a power analysis aimed at identifying the kind of experimental data needed to detect personality differences.

While our main goal in this chapter is to examine what kind of data is needed and is useful for the detection of animal personalities, we took the opportunity to also learn as much as we could on the North Island brown kiwi behaviour from the available datasets.

5.1.2 The biology of North Island brown kiwi

Kiwi (*Apteryx spp.*) are nocturnal ground-dwelling insectivorous birds endemic to New Zealand. The experiments presented in this chapter were done on a population of North Island brown kiwi (*Apteryx mantelli*), one of the five species of kiwi. North Island brown kiwi are found in some areas of New Zealand's North Island, with an estimated total count of 25000 individuals in 2018 (Germano et al., 2018).

The behaviour of brown kiwi has been largely detailed by Cunningham and Castro (2011), but no study has yet tried to identify or quantify animal personalities in brown kiwi populations. Brown kiwi are social animals, and most individuals are part of either monogamous or cooperative relationships (*i.e.* where more than one male and one female breed as a group, with males sharing in copulations and the care of offspring) (Undin et al., 2021; Ziesemann, 2011). Brown kiwi roost in burrows which they excavate themselves, in natural subterranean tunnels, in hollows under fallen trees, thick vegetation, or inside logs, often returning to sites they had used previously (Ziesemann, 2011; McLennan et al., 1987).

Brown kiwi have a developed sense of smell, which Castro et al. (2010) hypothesised might be used as a mean of communication and to obtain information about their environment. Kiwi are the only birds with nostrils at the tip of their beak (Castro et al., 2010), which also contains a sensory organ used to gather information from their environment (Cunningham et al., 2013, 2007). Bill length is one of the measurements commonly used to identify brown kiwi's sex, as female kiwi have longer bills than male kiwi. Sexual dimorphism in this species is also found in size and weight, with female kiwi often being bigger and heavier than males (Mclennan et al., 2004). However, sex was never found to have any significant effect on different

aspects of kiwi foraging behaviour (Cunningham and Castro, 2011).

5.1.3 Kiwi conservation and cultural importance

North Island brown kiwi are classified as "At Risk" by the New Zealand Threat Classification System (Robertson et al., 2016a). The original decline of kiwi populations is attributed to predation and forest clearance, whereas the current decline is mostly attributed to predation by stoats, cats and dogs (Germano et al., 2018). However, this species has seen a shift from the "Threatened" category to the "At Risk" one thanks to successful conservation management programmes, and is currently being monitored as part of the Kiwi Recovery Plan by the New Zealand Department of Conservation (Germano et al., 2018).

A better understanding of kiwi behaviour and personality types could help wildlife managers make more informed management choices. For example, identifying personality types more likely to avoid encounters with predators, or less likely to disperse form managed areas, could inform on which individuals to translocate to a new area to start a new, more resilient population.

The importance of kiwi for *mana tangata* Kiwi have a high cultural importance for Maori, who have strong historic and spiritual association with these birds and who consider them a *taonga* (treasured) species. Kiwi are considered an older sibling of humans and therefore humans need to care for them. Kiwi feathers were used in weaving *kahukiwi* (kiwi feather cloak), reserved for people of high rank (Hartnup et al., 2011; Pendergrast, 1984).

For these reasons, *mana tangata* ("people with autority" - the Maori community) are particularly invested in their protection. The relationship between *mana tangata* and kiwi was formally recognised in their settlement claims in *Te Tiriti o Waitangi*, which contain specific details on kiwi recovery efforts.

Mana tangata possess an invaluable collection of knowledge surrounding kiwi (Lai, 2012), and have always taken an active role in many aspects of kiwi conservation efforts, including predator control, building of protection fences around conservation areas, and getting involved with kiwi translocations.

5.1.4 Study site

The two studies in this section were carried out on Ponui Island (Figure 5.1), the most eastern of the Inner Gulf Islands, Hauraki Gulf, New Zealand. About two thirds of the island is currently in pasture, farmed for beef and wool, and the rest

Figure 5.1: Topographic map of Ponui Island, from topomap.co.nz

is forested (Miles & Castro, 2000). The island is divided into three farms (South, Central and North Ponui). Our study area (approximately 150ha) is located in South Ponui farm and it is spread over three main gullies. The vegetation consists mainly of remnant broadleaf-kauri (*Agathis australis*) forest, regenerating kānuka (*Kunzea ericoides*) forest edges, and raupo (*Typha orientalis*) swamp (Brown 1979; Shapiro 2005).

North Island brown kiwi (*Apteryx mantelli*) were originally introduced to Ponui Island in 1964 at the request of the South Ponui farm owners. Six birds came from Hauturu-o-Toi (Little Barrier Island) and eight originated from Waipuoa Forest (Northland) (Miles and Castro, 1999). The kiwi population on the study site is estimated at one kiwi per hectare and considered one of the highest densities of the species today (Cunningham et al., 2007).

In 2004, the "Behavioural Ecology and Conservation" group of Massey University established a long-term study on Ponui Island to learn about North Island brown kiwi's biology and behaviour, to apply this knowledge to the conservation of brown kiwi populations. Since then, this group has closely monitored up to 50 brown kiwi through radio transmitters attached to the kiwi's legs, with at least one check-up a

year to monitor their weight, size, and overall health. Whenever one of these kiwi dies or loses its transmitter, a new kiwi is captured and a transmitter is attached.

In addition, some of these birds have taken part to some field experiments aimed at better understanding their behaviour. The data obtained from two of these experiments are presented and analysed in this chapter.

5.2 What's that smell? - the 2009 experiments

5.2.1 Introduction

Kiwi have a well-developed and functional sense of smell that they use in combination with remote touch to find prey underground (Castro et al., 2010; Cunningham et al., 2009, 2007). Castro et al. (2010) suggested that this sense is so important that it should be used in other areas of the bird's life such as in social situations. Other birds with smaller olfactory bulbs, and even without overt olfactory behaviours have been shown to use the sense of smell to recognise familiar conspecifics. In particular, brown kiwi produce faeces that are odorous and contain substances that are known to convey social messages in other species (Castro et al., 2010).

In this study, conducted between 2008 and 2009, Isabel Castro's team experimentally investigated in the field the response of wild adult brown kiwi to three sources of odour: kiwi faeces, sheep faeces, and banana skins. They expected that if faeces indicate a social message in kiwi, birds would show greater interest in them than other sources of odour. Sheep faeces are very commonly found on Ponui island, they were used in this experiment as a control treatment for faeces odour, kiwi were expected to show no interest in them. No study had explored kiwi's behavioural reaction to banana skin, but other studies showed that other species of birds responded to this odour even when exposed to it for the first time (Bang, 1971).

5.2.2 Methods

The data collected during this experiment are summarised in Table 5.1. In this chapter, we will explore individual differences in the "latency to approach" time t_0, the investigation time t_{inv}, and the total time in the maze t_{tot}, each used as a proxy of a personality trait, across all treatments and birds. We consider the "latency to approach" time t_0 and the total time in the maze t_{tot} to indicate kiwi's boldness/neophobia, and the investigation time t_{inv} to indicate kiwi's curiosity.

The four treatments are defined as follows:

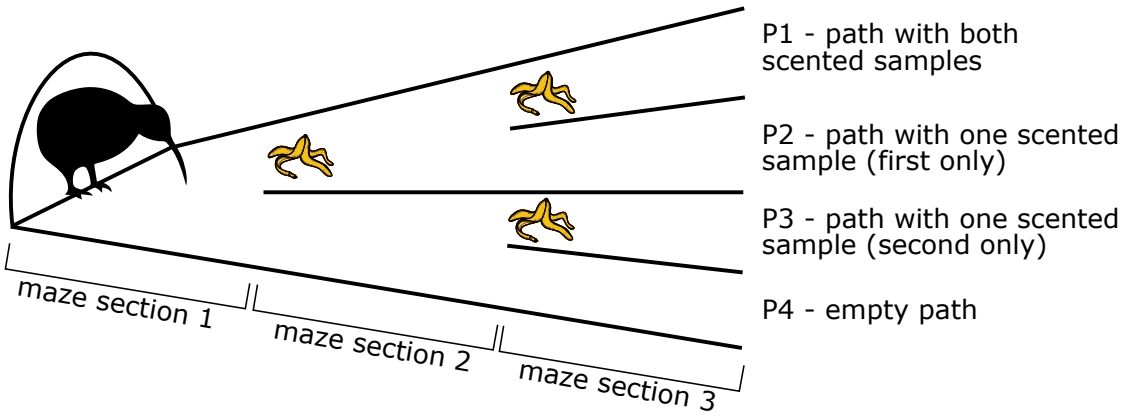

Figure 5.2: The double-Y maze set-up

- **T0 - control treatment**: an empty double-Y maze was set up in front of the kiwi burrow (as shown in Figure 5.2), with an empty leaf (randomly picked from the surrounding ground) placed where a sample should be, at either side (randomly chosen by coin toss) of each of the three intersections of the maze.
- **T1 - kiwi faeces**: a sample of kiwi faeces was placed on a leaf at either side (randomly chosen) of each of the three intersections of the maze.
- **T2 - sheep faeces**: a sample of sheep faeces was placed on a leaf at either side (randomly chosen) of each of the three intersections of the maze.
- **T3 - banana skin**: a sample of banana skin was placed on a leaf at either side (randomly chosen) of each of the three intersections of the maze.

Data were collected from 29 individuals from 11 different burrows (most brown kiwi roost alone or with one or two other kiwi partners). An individual bird was subjected to up to four treatments over the course of the experiment, during which its behaviour and choices were recorded. During the experimental period, each bird was repeatedly sampled for each treatment. Figure 5.3 clarifies the dependency structure in the experimental design.

5.2.3 Data analysis

Figures 5.4, 5.5 and 5.6 can help visualise the available data and formulate some hypothesis on the differences between kiwi responses to the experimental set-up.

Figure 5.6 shows differences in both the kiwi's mean reactions, with some kiwi spending a much longer time investigating the maze than others. It also suggests very different levels of behavioural plasticity, with some birds changing their behaviour

Parameter	Symbol	Description
Latency to approach	t_0	Time elapsed between the moment when the bird was first seen moving in the burrow and the moment when the bird's head came all the way out of the burrow entrance.
Time in maze section	$t_{1,2,3}$	Time the bird spent in each of the three maze sections (from burrow to first intersection, from first to second intersection, from second intersection to end of the maze, see Figure Figure 5.2) was measured when the whole body of the kiwi was in the next section.
Total time in maze	t_{tot}	Total time spent in the maze (excluding latency time).
Investigation time	t_{inv}	Total time the bird was seen inspecting the samples placed in the maze. The period spent investigating the item started when the kiwi bill got close to the item and finished when it first withdrew from it.
Path chosen	P	The path chosen by the bird to exit the maze. See Figure 5.2 for details.
Direction after maze	D	Direction the bird took after exiting the maze (left, centre-left, centre, centre-right, right, backwards).

Table 5.1: Data collected during the double-Y maze experiment.

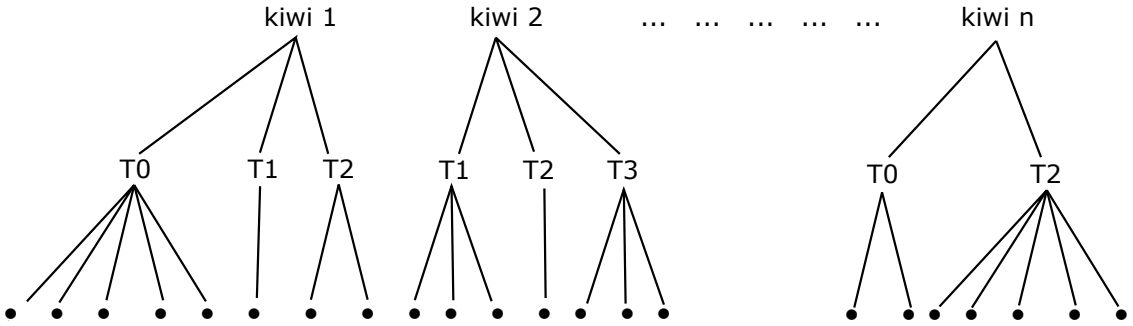

Figure 5.3: Nested structure for the double-Y maze experimental data Each kiwi goes through a maze (top row). For each treatment (second row), one or multiple repetitions of the experiment are made. Dots represent the repetitions. Not all birds were tested for all treatments, and number of repetitions varies across birds.

between repetitions. This observation can also be made from Figure 5.4. For example, the kiwi Salome, Daphnae and Valda all display high levels of plasticity, with a high variation in their responses to the same experimental set-ups, whereas kiwi such as Lance and Anna seem to exhibit a much more consistent response.

The bar plot in Figure 5.5 highlight a large number of null measurements for t_0 and t_{inv}: not all birds waited before entering the maze, and not all birds investigated the set-up.

Next, we will discuss outliers in our data, we will check independence of repetitions, and we will fit some gamma generalised linear models to our data to explore the possible sources of variation in the observed behaviour.

5.2.3.1 Outliers

Figure 5.6 shows 29 outliers (8 of which extreme) for the t_{inv} data, and 24 outliers (10 of which extreme) for the t_{tot} data. These unusually high measurements were attributed to 9 different kiwi. These birds were seen to either spend a long time preening after exiting their burrow, or sit down and look around.

The data on "latency to approach" time t_0 contains a very large number of zeros, which skews the distribution of times for each bird and results in most of the non-zero measurements to be counted as outliers. The birds with high values of t_0 were observed to stick their bill out of the burrow many times before exiting the maze.

In all the figures, all values surpassing 300 s were displayed at the 300 s mark for better visualisation. In the model fitting, we exclude all extreme outliers (data values which lie more than 3.0 times the interquartile range below the first quartile or above the third quartile), as including the extreme outliers affected the robustness of our models.

Assuming that these extreme outliers were not the result of measurement errors, they might be an indication of significantly different personalities in the kiwi that produced them compared to the other birds. Excluding these measurements from our analysis might decrease the within-individual variance for those individuals.

5.2.3.2 Independence of repetitions

Each treatment was tested multiple times on each bird, so an important step in the analysis was to check whether there was a trend in the change of mean behaviour across repetitions, for each treatment.

Figure 5.4: Kiwi birds exhibit different levels of variability when confronted with the same set-up. Plots of the latency to approach time t_0, the total investigation time t_{inv}, and the total time in the maze t_{tot} for each bird, each treatment, and each repetition of the experiment. The graph shows not only different mean behaviour for the same experimental set-ups, but also different levels of behavioural consistency or plasticity (some birds always exhibited the same behaviour, others changed their behaviour over different repetitions of the experiment). Extreme outliers (past 300 s) are shown at the 300 s mark for better visualisation.

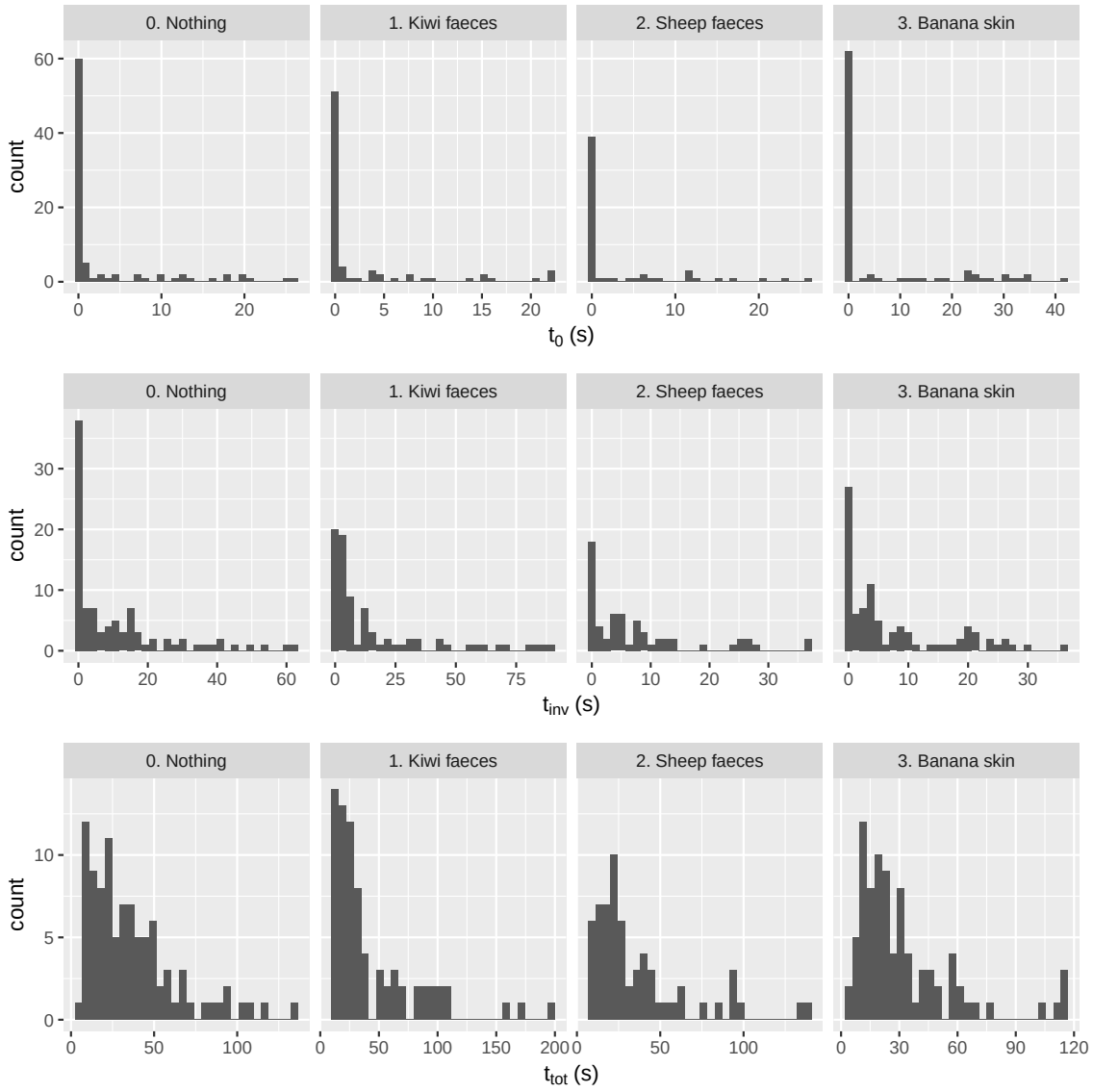

Figure 5.5: Distribution of t_0, t_{inv} and t_{tot} for each treatment, all birds and repetitions combined. Extreme outliers were excluded from this plot.

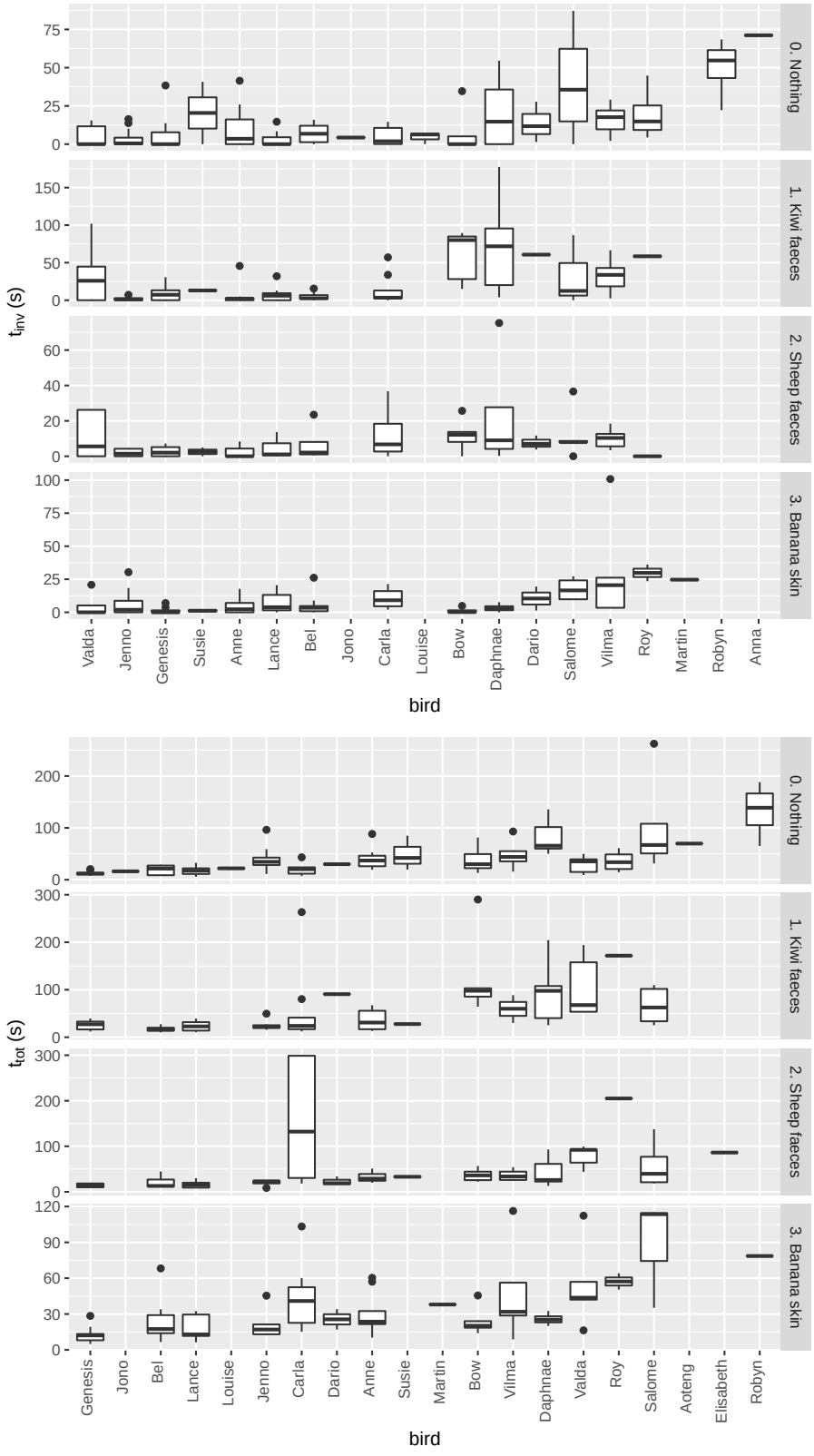

Figure 5.6: Different birds display different levels of curiosity and behavioural plasticity across treatments. Boxplots of investigation times t_{inv} (top) and total time in the maze t_{tot} (bottom) for each bird and treatment, showing that different birds spent different amounts of time investigating each maze. Outliers ($t_{tot} > 300$ s) are shown at the 300 s mark for better visualisation.

Visual inspection of Figure 5.7 suggests there might be a decrease of mean t_{inv} and t_{tot} over time for some of the treatments. The plot of t_0 was not informative because of the large number of null measurements and was not included.

To test whether there was an effect of repetition on the other two responses within each treatment (t_{inv} and t_{tot}), they were fitted with a Gamma Generalised Linear Mixed Model (GLMM) with a nested fixed effect of treatment:rep and a random effect of bird. We found a significant effect of repetition (p-value = 0.008) on the total investigation time t_{tot} for the sheep faeces treatment, indicating that kiwi might change their behaviour as they repeat their walk through this maze.

A pair-wise analysis of t_{tot} for the sheep faeces treatment only revealed significant differences between repetitions 1-3 and 1-5, indicating that the significant effect of repetition highlighted by the GLMM fit might have been due to higher measurements in the first repetition only. Indeed, when fitting the same model to the data, excluding repetition 1, the effect of repetition for the sheep faeces treatment was found to be non-significant (p-value = 0.061).

These higher measurements in the first repetitions could be due to the birds seeing he new set-up for the first time. Higher measurements of t_0, t_{inv} and t_{tot} are therefore expected for the first repetition. As we found no significant trend of repetition for any other treatment, from now on we will assume independence of repetitions.

Null measurements Some birds did not spend any time investigating, instead they walked straight through and out of the maze (Figure 5.8). Similarly, some birds did not wait any time before coming out of the maze ($t_0 = 0$). We tested if there was an effect of treatment and repetition on the probability $\mathrm{P}(t_{inv} = 0)$ of investigating versus not investigating and on the probability $\mathrm{P}(t_0 = 0)$ of the birds waiting some time before exiting their burrow versus not waiting.

We fitted a logistic regression model to both binary responses and found no significant effect of repetition or treatment on either probabilities $\mathrm{P}(t_0 = 0)$ or $\mathrm{P}(t_{inv} = 0)$. To include the null measurements in the models of these two responses, we fitted a zero-altered (hurdle) model to both (described in details in the next section).

5.2.3.3 Effect of treatment and sex

We tested models with two fixed covariates: treatment (categorical with four levels - nothing, banana skins, brown kiwi faeces, sheep faeces) and sex (categorical with two levels - male and female). To incorporate the dependency among observations of the same bird, we used bird ID as random effect.

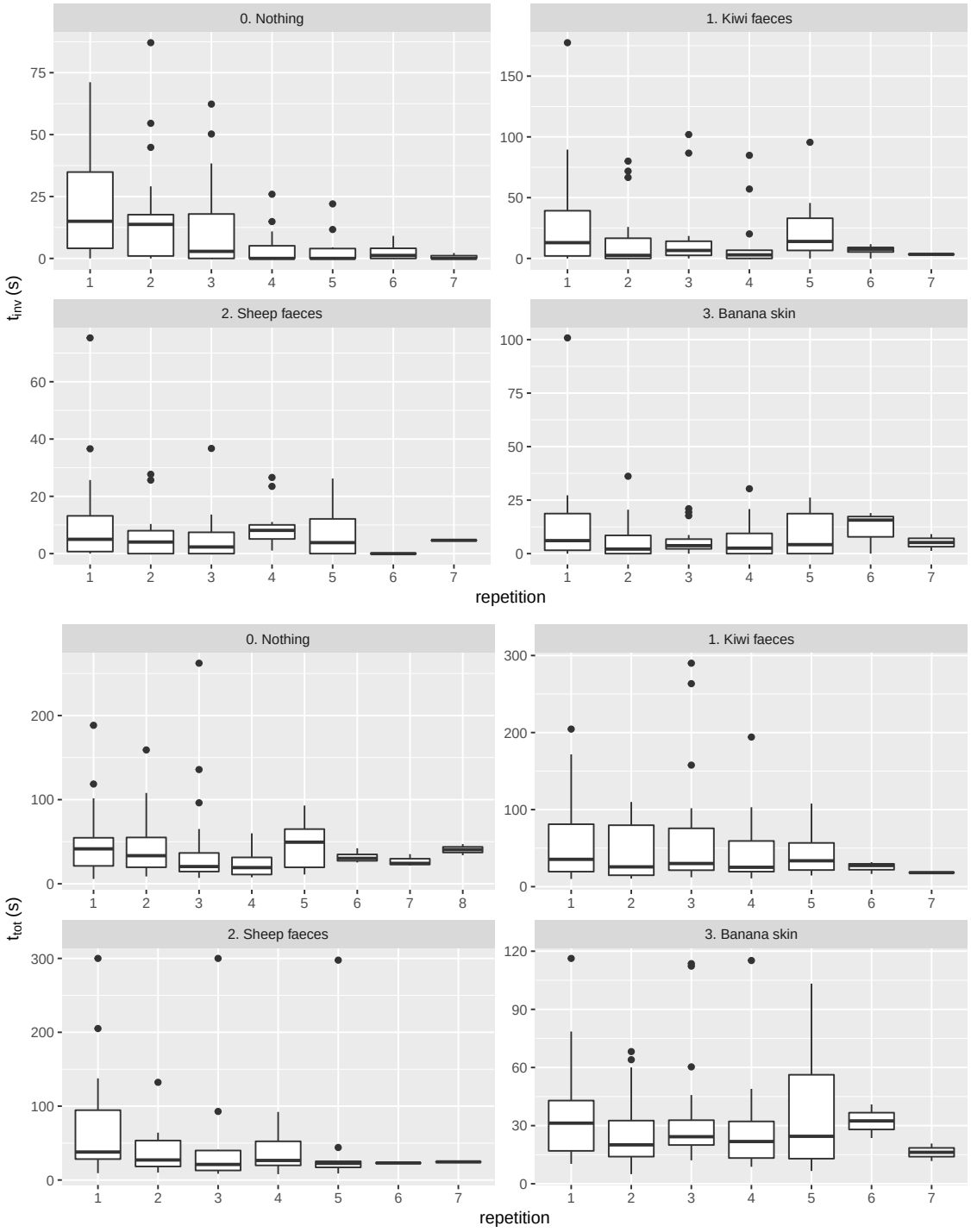

Figure 5.7: Kiwi do not significantly alter their behaviour on subsequent repetitions of the experiment. The boxplots of all investigation times t_{inv} and total times in the maze t_{tot}, pooled by treatment and repetition, suggest a decrease of t_{inv} over time for the control treatment, but no significant change for all other treatments.

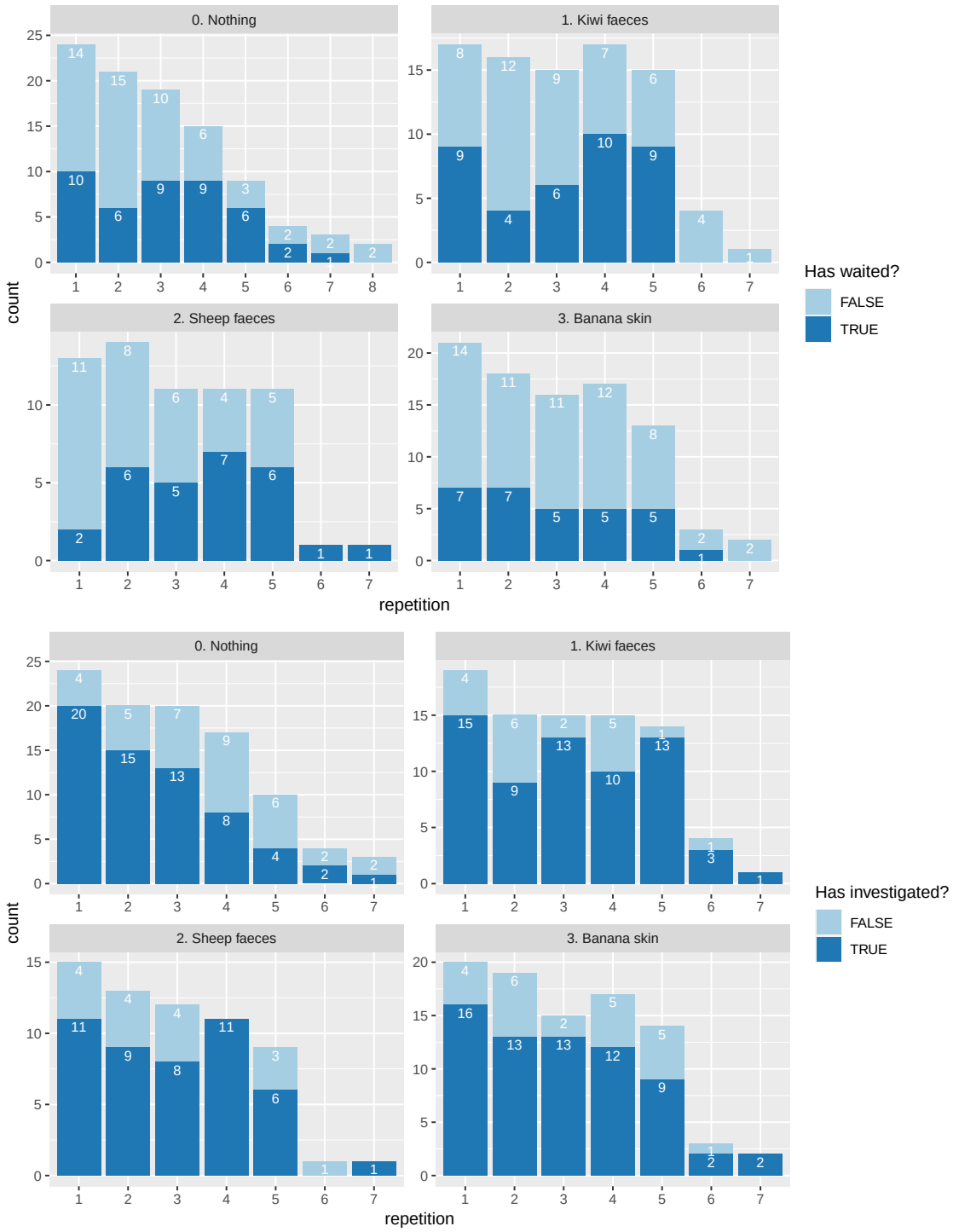

Figure 5.8: Top: proportions of birds having waited before exiting their burrow versus birds that did not wait. We define birds that have waited as birds that waited some time before exiting their burrow and entering the Y maze. **Bottom: proportions of birds having investigated the Y maze versus birds that did not investigate for each treatment and repetition.** We define birds that haven't investigated as birds that walked the maze without ever displaying any investigative behaviour.

The observations on the first two responses (t_0 and t_{inv}) were fitted with zero-altered (hurdle) Gamma GLMMs with log-link functions, t_{tot} was fitted with a Gamma GLMM with a log-link function:

$$
\begin{aligned}
&\text{has.waited}_i \sim \text{Bernoulli}(\pi_i) \\
&\text{logit}(\pi_i) = \beta_0 \\
&t_{0ij} | (\text{has.waited}_i = 1) \sim \text{Gamma}(k, \theta_{ij}) \\
&\mu_{ij} = k\theta_{ij} \\
&\log(\mu_{ij}) = (\beta_1 + \text{bird}_i) + \beta_2 \text{treatment}_{ij} + \beta_3 \text{sex}_{ij} + e_{ij} \\
&\text{bird}_i \sim N(0, V_{ind}) \\
&e_{ij} \sim N(0, V_e)
\end{aligned}
\tag{5.1}
$$

$$
\begin{aligned}
&\text{has.investigated}_i \sim \text{Bernoulli}(\pi_i) \\
&\text{logit}(\pi_i) = \beta_0 \\
&t_{invij} | (\text{has.investigated}_i = 1) \sim \text{Gamma}(k, \theta_{ij}) \\
&\mu_{ij} = k\theta_{ij} \\
&\log(\mu_{ij}) = (\beta_1 + \text{bird}_i) + \beta_2 \text{treatment}_{ij} + \beta_3 \text{sex}_{ij} + e_{ij} \\
&\text{bird}_i \sim N(0, V_{ind}) \\
&e_{ij} \sim N(0, V_e)
\end{aligned}
\tag{5.2}
$$

$$
\begin{aligned}
&t_{ij} \sim \text{Gamma}(k, \theta_{ij}) \\
&\mu_{ij} = k\theta_{ij} \\
&\log(\mu_{ij}) = (\beta_0 + \text{bird}_i) + \beta_1 \text{treatment}_{ij} + \beta_2 \text{sex}_{ij} + e_{ij} \\
&\text{bird}_i \sim N(0, V_{ind}) \\
&e_{ij} \sim N(0, V_e)
\end{aligned}
\tag{5.3}
$$

where t_{ij} is the j^{th} observation of bird i ($i = 1,\ldots, 29$); μ_{ij} is the mean time for bird i and repetition j; bird_i is the random effect of bird, which is assumed to be normally distributed with mean 0 and variance V_{ind}; e_{ij} is the residual error, assumed to be normally distributed with mean 0 and variance V_e. V_{ind} corresponds to the between-individual variance: the variance across random intercepts of individuals. V_e corresponds to the within-individual variance: the variance across random

Table 5.2: Comparison of model AIC and number of parameters for nested models fitted to the four responses measured in the "Y-maze" experiment.

	t_0		t_{inv}		t_{tot}	
Model	ΔAIC	*n.p.*	ΔAIC	*n.p.*	ΔAIC	*n.p.*
NULL	**0**	**4**	13.5	4	112.7	2
SEX	1.9	5	0.9	7	4.8	4
TREATMENT	3.7	7	0.9	7	2.7	6
TREATMENT + SEX	5.7	8	**0**	**8**	**0**	**7**

Table 5.3: Log-tranformed estimates of latency to approach (t_0), investigation time (t_{inv}) and total time in the maze (t_{tot}), together with standard errors, 95% confidence intervals and p-values for the linear regression models presented in Equations 5.1, 5.2 and 5.3.

	t_0				t_{inv}				t_{tot}			
Predictors	*Est.*	*SE*	*95% CI*	*p*	*Est.*	*SE*	*95% CI*	*p*	*Est.*	*SE*	*95% CI*	*p*
Intercept	3.05	0.43	2.20 – 3.90	**<0.001**	3.02	0.18	2.66 – 3.38	**<0.001**	3.87	0.14	3.59 – 4.15	**<0.001**
Sex (M)	0.18	0.61	-1.01 – 1.37	0.768	-0.38	0.22	-0.80 – 0.04	0.079	-0.43	0.18	-0.78 – -0.07	**0.018**
T1 - Kiwi faeces					0.17	0.18	-0.17 – 0.52	0.328	0.19	0.09	0.01 – 0.36	**0.043**
T2 - Sheep faeces					-0.52	0.19	-0.89 – -0.14	**0.007**	-0.08	0.1	-0.27 – 0.11	0.411
T3 - Banana skin					-0.4	0.18	-0.74 – -0.05	**0.024**	-0.09	0.09	-0.26 – 0.09	0.327
Zero-Altered Model												
Intercept	0.34	0.11	0.12 – 0.56	**0.002**	-0.91	0.12	-1.15 – -0.67	**<0.001**				
Random Effects												
V_{ind}	2.5				0.87				0.32			
V_e	0.88				0.13				0.14			
$V_{ind}/(V_{ind}+V_e)$	0.26				0.13				0.3			
N	20				18				20			
Observations	306				325				315			
AIC	142.1				1669.924				2725.779			

intercepts of individuals. The ratio $V_{ind}/(V_{ind}+V_e)$ corresponds to the sample's repeatability: the phenotypic variation attributable to differences between individuals (Dingemanse and Dochtermann, 2013).

Table 5.2 shows a comparison by AIC of different nested models with treatment and sex as covariates. This comparison of models of t_0 showed little support for the models including treatments. We therefore reported the estimated parameters for the model including only sex. The total time in the maze t_{tot} and the investigation time t_{inv} were both best fitted by the most complex model including both covariates (see Equations 5.2 and 5.3).

Summaries of the estimated regression parameters resulting from our model fittings can be found in Table 5.3.

The results presented in Table 5.3 and Figure 5.9 can be summarised as follows:

- **Effect of treatment:** kiwi spent a significantly shorter time investigating the mazes containing sheep faeces (41% lower t_{inv}, p-value=0.007) and banana skin (33% lower t_{inv}, p-value=0.024) than they did the empty maze. They also spent a significantly longer time overall (20% higher t_{tot}, p-value=0.043) in the

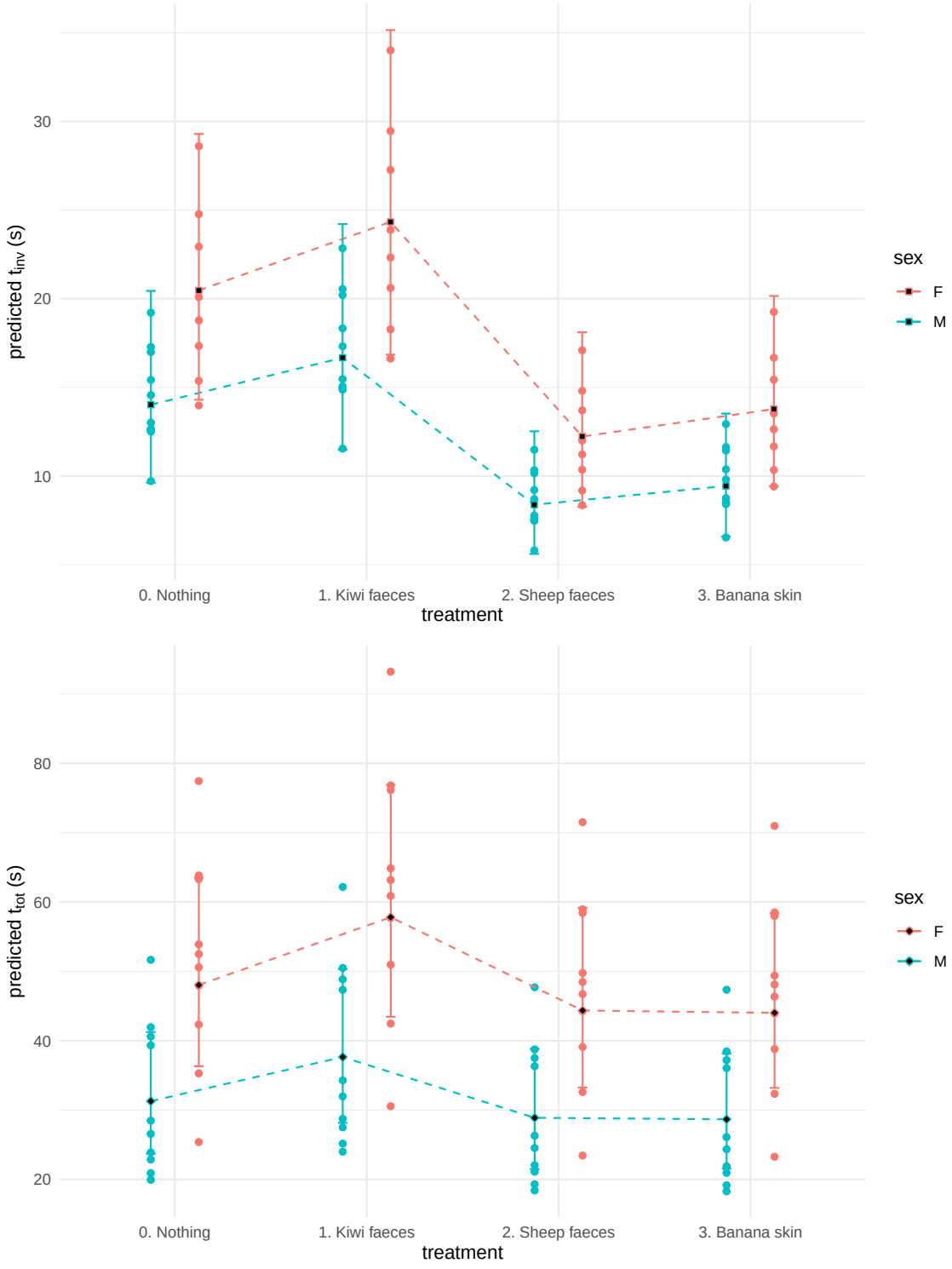

Figure 5.9: Predicted means and 95% confidence intervals for the dependent variables t_{inv} (above) and t_{tot} (below) for each treatment and sex, calculated using the estimated parameters presented in Table 5.3. Predicted means are shown as black dots, predicted random effects are shown in red and blue for females and males, respectively.

kiwi faeces maze than in the empty maze.

- **Effect of sex:** compared to females, male kiwi were found to spend significantly less time investigating (33% lower t_{inv}, p-value=0.018) and less time overall in the maze (35% lower t_{tot}, p-value=0.018). No significant differences in latency to approach time t_0 was found between sexes.

- **Repeatability measures:** The ratio $V_{ind}/(V_{ind} + V_e)$ indicates that the phenotypic variation attributable to between-individual differences (animal personalities) was 26% for t_0, 13% for t_{inv}, and 30% for t_{tot}, meaning that most of the observed variation came from within-individual variation (behavioural plasticity) rather than from differences in personalities. However, these are common levels of repeatability (Bell et al., 2009), and their being significantly different than zero suggests some level of personality variation.

The underlying model assumptions of independence, normality, homoscedasticity, and outliers were verified using the standard model diagnostics for all models presented in this section. The diagnostic plots can be found in Figure 7.1 in the Appendix of this thesis.

5.2.4 Discussion

The analysis revealed several interesting facts about the kiwi analysed. Firstly, we found a slightly higher time spent in the maze for the first repetition of the each experiment. This was attributed to kiwi experiencing the set-up for the first time. As this difference between first and subsequent repetition was found to be not statistically significant for all treatments except kiwi faeces, we assumed independence of repetitions and attributed any variation observed across repetition as behavioural plasticity. However, we recommend caution in including results of the first repetition(s) of such experiments in the analysis, as the behaviour exhibited at the first encounter with the experimental set-up might be different from the subsequent repetitions.

We have found significant differences in the birds' behavioural responses to different treatments. Individual kiwi spent the most time investigating and overall in the empty maze, and in the maze containing kiwi faeces compared to the other treatments. The fact that they spent more time in the kiwi faeces maze did not come as a surprise as previous studies have put forward the hypothesis of brown kiwi using olfactory stimuli as social cues (Castro et al., 2010). The lack of interest towards sheep faeces was also to be expected: sheep faeces are very commonly found on the

island, so kiwi are probably used to finding them on their path. We did not know what to expect from the banana skin treatment. Our analysis indicates that kiwi birds do not investigate the banana more than they do the sheep faeces (see Figure 5.9), and significantly less than they do the kiwi faeces. Interestingly, the birds spent quite some time investigating the empty maze. This could be due to the maze itself constituting a "novel" object which could cause some of the birds to become curious (or wary), and to take some time analysing it.

Our results on repeatability suggest some level of personality variation, although most of the observed variation is to be attributed to behavioural plasticity (or other external factors that weren't measured or included in our models). In addition, visual analysis of the data collected (Figure 5.6) suggested that some birds do not exhibit consistent behaviours when met with the same experimental conditions, while some others always display similar responses. This suggests different levels of behavioural plasticity between-birds.

The available data was only partially used in this analysis. Future research could use some of the other measurements (such as the path chosen and direction taken after the maze) to explore differences between birds and across treatments. In particular, exploring whether repeatability is consistent across treatment and sexes would answer the questions of whether kiwi show different personalities only when faced with specific situations, or whether sexes differ in repeatability.

In the next section of this chapter, we explore another experimental dataset from the brown kiwi of Ponui Island, this time focused on differences in stress responses to human handling between previously and newly handled birds.

5.3 Fight or flight - the 2020 experiments

5.3.1 Methods

These experiments were run on the same kiwi population of Ponui island as the 2009 experiments presented in the previous section. The field work was done between February and May 2020. This is the time when kiwi are not breeding so can be handled within legal requirements (Massey University Animal Ethics approvals 20/55 and 20/68. DOC permit 38796-FAU). Throughout this section, we make the distinction between "banded" and "new" birds. We define "banded" birds those that have a radio-transmitter attached to their tibia (using a taped plastic band) and had already interacted with humans before. These kiwi are part of a long-term study carried out by the "Behavioural Ecology and Conservation" group of Massey University (see Section 5.1.4). Birds wearing radio-transmitters are captured twice per year, once to replace transmitters (batteries last just a year) and a second time to check their health before the breeding season. Some birds may be captured more times if there are projects that require this. Note that some kiwi have been part of the project for longer than others, anywhere between 1 and 17 years. We define "new" birds those that had never interacted with humans before, and that were captured for the first time for this experiment.

The banded birds are individually identifiable from the radio transmitters' unique frequency. The transmitters used (www.kiwitrack.co.nz) have a data logger that is used to collect information about the kiwi's movements from a distance. Signals from the transmitter provides information about the wearer's activity the night before, the night before last, and an the average time active for the last four nights. It also provides a time when the wearer started activity the night before, and whether the bird is incubating, has deserted the nest or has died.

We used a certified kiwi dog to locate the additional kiwi that had never had any direct contact with humans. All kiwi were captured and handled by certified kiwi practitioners during the day time at their roosting burrows and were released back into the burrow after manipulations adhering to best practice.

When a bird is captured by a predator (in this case, a researcher), it responds by struggling in an attempt to escape. Physiological changes that accompany such struggle will include a higher heart rate and higher breathing rate as the animal prepares to run away from the predator and are reflective of a stress response (Cyr et al., 2009; Carere and Van Oers, 2004). We assumed that there would be differences in behaviour and physiology between birds as a response to handling due to

individual biology (sex, personality, behavioural plasticity) and circumstances (season, habitat, weather). We hypothesised that these differences could also be related to habituation (a form of learning) with birds handled over several years responding less than those handled for the first time.

To compare behavioural and physiological response between birds and test the hypotheses, we developed a quick assessment test (lasting approximately 2 minutes per bird) that subjected every bird to the same human manipulation for the same period. We applied this test to birds carrying transmitters (*i.e.* with known handling history) and birds captured for the first time.

Right after capturing the bird, we videoed the four steps of the "reactions to capture" (see Figure 5.10)

1. We laid the bird on its back while holding its feet. We then placed two fingers at the point where the ribs join the abdomen to feel the heart beat. We measured the number of heart beats for 15 seconds, then recorded the beats/min;

2. With the bird still on its back, we moved the stomach feathers aside until we could see a clear rising and falling of the chest. We measured the breathing rate by counting the number of breaths for 15 seconds, then recorded the breaths/min;

3. We lifted the bird until it was in front of us, looking into its face while supporting its back, we recorded the proportion of time spent struggling, as well as the number of snaps (possible sign of aggressiveness), any growling (sign of aggressiveness) or blowing from the nose (possible sign of fear), as well as whether the bird looked at us or looked away;

4. We held the bird upside down by its feet, we recorded the proportion of time spent struggling, as well as the number of snaps (possible sign of aggressiveness), any growling (sign of aggressiveness) or blowing from the nose (possible sign of fear).

The video recordings of phases 3 and 4 of the experiment were then analysed to extract our measurements of "struggle time" and snapping rate: for each of the two phases, a timer was set to measure the total time spent in either the "look in the eyes" position or the "upside-down" position; another timer was used to measure the total time that the kiwi spent exhibiting any sort of struggle behaviour, such as trying to escape the holder's grasp; we also counted the number of snaps the

Figure 5.10: The four stages of the "reaction to capture" experiment From left to right: measuring heart rate, measuring breathing rate, "look into the eyes", "upside-down".

kiwi made with their beak. These measurements were then used to calculate the "proportion of struggle time" and the "snapping rate" for phases 3 and 4.

In the next few sections, we present a summary and visual analysis of the data collected, followed by statistical analysis using generalised linear models to explore the effects of sex, body condition, and level of human habituation on our measured responses.

5.3.2 Summary statistics

We captured and collected data for 62 kiwi: 43 birds with radio transmitters, as well as 19 new birds. Table 5.4 shows the average values and range of the birds' reactions to human handling post-capture, as well as measurements of the weight/tarsus length ratio (a measure of weight in relation to overall bird size), and the number of years since first capture, for "banded" birds only. All measurements of the six responses measured (heart rate H_m, breathing rate B_m, struggle time props and snapping rates for the "look in the eyes" and "upside-down" treatments) are summarised in Figure 5.11. In the thesis Appendix we also present the results of a Principal Component Analysis used to reveal any patterns and clusters in our observations.

5.3.3 Effects of treatment and sex

In this section we fitted some generalised linear models (GLM) to the available data to explore the effects of the different covariates on the four measured responses (Table 5.4).

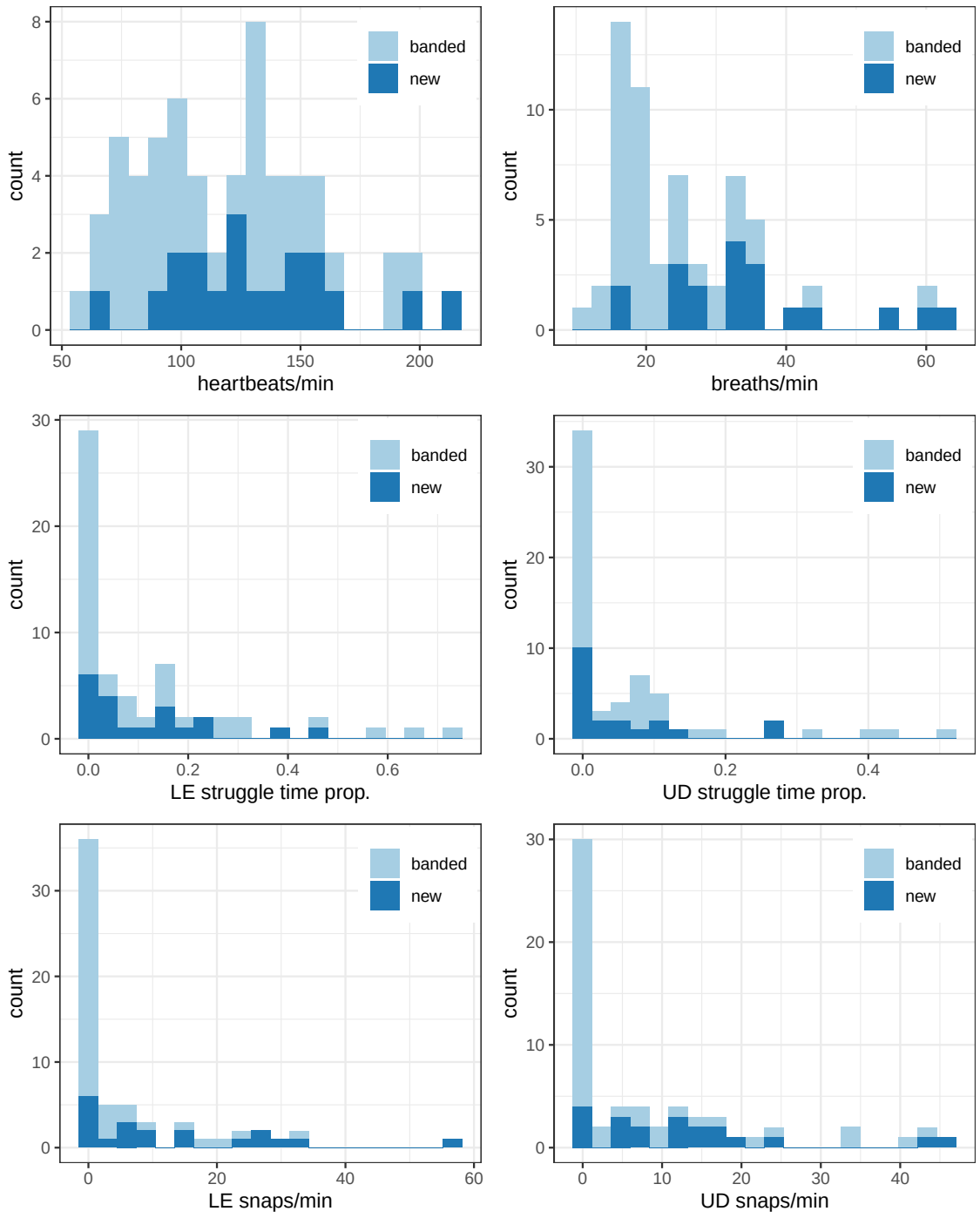

Figure 5.11: Stacked histograms of the response variables collected for the "kiwi response to capture" experiment, colour-coded by the banded/new status of the bird.

Table 5.4: Summary statistics on captured kiwi birds for the "response to capture" experiment. "LE" stands for "Look in the Eyes", "UD" stands for "Upside-Down".

Parameter	**Symbol**	**"Banded" birds** mean range	**"New" birds** mean range	**All birds** mean range
Sex	sex	F: 21 M: 22	F: 10 M: 9	F: 31 M: 31
Years since first capture	Y_{first}	10.3 1 - 16		
Weight/tarsus length ratio	wt	19.93 14.28 - 29.02		
		Behavioural responses to capture		
Heart rate (min^{-1})	H_m	112.3 60 - 200	131.8 66 - 216	119.5 60 - 216
Breathing rate (min^{-1})	B_m	22.72 12 - 60	34.79 16 - 64	26.38 12 - 64
LE struggle time prop	ST_{le}	0.1 0 - 0.67	0.12 0 - 0.48	0.11 0 - 0.73
LE snapping rate (min^{-1})	SN_{le}	3.25 0 - 31.43	13.65 0 - 56.67	6.54 0 - 56.67
UD struggle time prop	ST_{ud}	0.07 0 - 0.51	0.06 0 - 0.28	0.07 0 - 0.51
UD snapping rate (min^{-1})	SN_{ud}	6.4 0 - 43.2	13.92 0 - 45.88	8.72 0 - 45.88
UD struggle score	S_{ud}	1.8 1 - 4	2.05 1 - 4	1.877 1 - 4
LE struggle score	S_{le}	1.8 1 - 4	2.33 1 - 4	1.969 1 - 4

We fitted GLMs to two nested datasets:

1. the subset of measurements that were taken for all birds, banded and new. The only covariates we included are the birds' sex and their banded/new status. This model was run to indicate whether birds that never had any interaction with humans behave differently from those that have been captured in the past.

2. the subset of banded birds only, for which three additional measurements were taken: weight/tarsus length ratio, activity in the last four days, and years since first capture. This model was run to indicate whether these additional covariates affected the responses. In particular, to tease out whether birds change their response the more "habituated" they are to capture.

5.3.3.1 All birds

We fitted three different models for our four measured responses: heartbeats/min H_m, breaths/min B_m, proportion of time spent struggling ST and snapping rate SN. The last two phases of the experiment, "look in the eyes" and "upside-down" were included as a "treatment" covariate for the ST and SN responses.

The heartbeats and breaths per minute were log transformed (the "zero problem" was ignored as we cannot have non-positive heart and breathing rates) and fitted with two linear models:

$$\log(\hat{H}_m) = \beta_0 + \beta_1 \text{bandednew}_i + \beta_2 \text{sex}_i \tag{5.4}$$

$$\log(\hat{B}_m) = \beta_0 + \beta_1 \text{bandednew}_i + \beta_2 \text{sex}_i \tag{5.5}$$

with $i = 1, ..., 65$ being the observed kiwi. The residuals of the log-transformed data were assumed to be normally distributed.

The proportions of time spent struggling were fitted with a zero-altered (hurdle) Beta distribution with a logit-link function

$$\begin{aligned}
&\text{has.struggled}_i \sim \text{Bernoulli}(\pi_i) \\
&\text{logit}(\pi_i) = \beta_0 \\
&\text{ST}_i|(\text{has.struggled}_i = 1) \sim \text{Beta}(\mu_i, \phi) \\
&\text{logit}(\mu_i) = \log\left(\frac{\mu_i}{1-\mu_i}\right) = \beta_1 + \beta_2 \text{bandednew}_i + \beta_3 \text{sex}_i + \beta_4 \text{treatment}
\end{aligned} \tag{5.6}$$

where $i = 1, ..., 65$ is the observed kiwi and ϕ is the dispersion parameter of the Beta distribution, assumed constant.

The snapping rates were fitted with a zero-altered Gamma distribution with a logit-link function:

$$\begin{aligned}
&\text{has.snapped}_i \sim \text{Bernoulli}(\pi_i) \\
&\text{logit}(\pi_i) = \beta_0 \\
&\text{SN}_i|(\text{has.snapped}_i = 1) \sim \text{Gamma}(\mu_i, \phi) \\
&\text{logit}(\mu_i) = \log\left(\frac{\mu_i}{1-\mu_i}\right) = \beta_1 + \beta_2 \text{bandednew}_i + \beta_3 \text{sex}_i + \beta_4 \text{treatment}_i
\end{aligned} \tag{5.7}$$

Preliminary analysis of our data showed no suggestion of an effect of the covariates on either the probability of struggling versus not struggling, or the probability of snapping versus not snapping, we therefore only analyse their effect on the average times μ_i.

Table 5.5 shows a comparison by AIC of different nested models with sex, banded/new status, and treatment ("look in the eyes" or "upside-down") as covariates.

Summaries of the estimated regression parameters resulting from our model fittings can be found in Tables 5.6 and 5.7.

The AIC comparison (Table 5.5) showed substantial support of the completed model for the heart and breathing rate responses, presented in Equation 5.4. We therefore

Table 5.5: Comparison of model AIC and number of parameters for nested models fitted to the four responses measured in the "response to capture" experiment.

	$\boldsymbol{H_m}$		$\boldsymbol{B_m}$		$\boldsymbol{ST}$		$\boldsymbol{SN}$	
Model	ΔAIC	*n.p.*	ΔAIC	*n.p.*	ΔAIC	*n.p.*	ΔAIC	*n.p.*
NULL	1.6	2	15.5	2	0.7	3	1.1	3
SEX	2.7	3	17	3	1.7	4	**0**	**4**
BANDEDNEW	**0**	**3**	**0**	**3**	0.6	4	2.2	4
TREATMENT					**0**	**4**	3.1	4
SEX + BANDEDNEW	0.8	4	1.7	4	2	5	0.5	5
SEX + BANDEDNEW + TREATMENT					0.5	6	2.2	6

Table 5.6: Log-transformed estimates of heart rate (H_m) and breathing rate (B_m), standard errors, 95% confidence intervals and p-values for the linear regression models presented in Equation 5.4.

		Heart rate $\boldsymbol{H_m}$				**Breathing rate $\boldsymbol{B_m}$**			
Coeff.	*Predictors*	*Est.*	*SE*	*95% CI*	*p*	*Est.*	*SE*	*95% CI*	*p*
β_0	intercept	4.64	0.06	4.51 – 4.76		3.08	0.07	2.93 – 3.22	
β_1	banded/new (new)	0.17	0.08	-0.00 – 0.33	0.055	0.43	0.1	0.23 – 0.62	**<0.001**
β_2	sex (M)	0.08	0.08	-0.07 – 0.24	0.284	-0.1	0.09	-0.23 – 0.13	0.613
Observations		61				62			
R^2 / R^2 adjusted		0.077 / 0.045				0.249 / 0.224			

Table 5.7: Logit-transformed estimated parameters, standard errors, 95% confidence intervals and p-values for the zero-altered Beta regression model presented in Equation 5.6, fitted to the proportion of struggle time ST, and for the zero-altered Gamma regression model presented in Equation 5.7, fitted to the snapping rate SN, for the subset of data obtained from all birds (both banded and new).

		Struggle time prop $\boldsymbol{ST}$				**Snapping rate $\boldsymbol{SN}$**			
Coeff.	*Predictors*	*Est.*	*SE*	*95% CI*	*p*	*Est.*	*SE*	*95% CI*	*p*
β_1	intercept	-1.11	0.19	-1.49 – -0.73		2.82	0.16	2.51 – 3.13	
β_2	banded/new (new)	-0.33	0.22	-0.77 – 0.11	0.145	0.25	0.2	-0.14 – 0.63	0.215
β_3	sex (M)	-0.21	0.22	-0.65 – 0.22	0.342	-0.4	0.2	-0.79 – 0	**0.047**
β_4	treatment (UD)	-0.41	0.22	-0.84 – 0.02	0.059				
	Zero-Altered Model								
β_0	intercept	-0.03	0.18	-0.38 – 0.32	0.857	0.1	0.18	-0.26 – 0.45	0.59
Observations		62				62			

used the estimated parameters for this model to test all our hypothesis (Table 5.6).

The results highlight a significant effect of the banded/new status on the kiwi's breathing rates, but not on the heart rate, and no significant effect of sex on either response. In particular, kiwi that were captured for the first time in this experiment (new) are expected to have a breathing rate 53.7% higher than that of kiwi that had been captured at least once before (banded), holding constant all other variables.

The AIC comparison in Table 5.5 showed substantial support of the complete model for the proportion of struggle time, presented in Equation 5.6. We therefore reported the estimated parameters for this model to test all our hypothesis (Table 5.7). We also report the estimated regression parameters for the SEX + BANDEDNEW model for the snapping rate, which was equivalent to the best fit model.

The results in Table 5.7 highlight a significant effect of sex on the snapping rate, with male kiwi's snapping rate 33% lower that of female kiwi, holding constant all other variables. We did not find any significant effect of the banded/new status nor of treatment on either the proportion of struggle time or the snapping rate.

The underlying model assumptions of independence, normality, homoscedasticity, and outliers were verified using the standard model diagnostics for all models presented in this section. The diagnostic plots can be found in Figure 7.2 in the Appendix of this thesis.

In the next section we will analyse the subset of kiwi that had been captured in previous years (banded), for which we collected additional data that can be used as model covariates.

5.3.3.2 Banded birds only

Next, we tested the effects of our covariates on the responses obtained for the banded birds only. For these birds, we have two additional covariates to test: the number of years since first capture Y_{first} and the weight/tarsus length ratio wt.

The heartbeats and breaths per minute were log transformed and fitted with two linear models:

$$\log(\hat{H}_m) = \beta_0 + \beta_1 \mathrm{Y}_{\mathrm{first}\,i} + \beta_2 \mathrm{sex}_i + \beta_3 \mathrm{wt}_i \tag{5.8}$$

$$\log(\hat{B}_m) = \beta_0 + \beta_1 Y_{\mathrm{first}\,i} + \beta_2 \mathrm{sex}_i + \beta_3 \mathrm{wt}_i \tag{5.9}$$

with $i = 1, ..., 41$ being the observed kiwi.

The proportions of time spent struggling were fitted with a zero-altered (hurdle) Beta distribution with a logit-link function

$$\begin{aligned}
&\text{has.struggled}_i \sim \text{Bernoulli}(\pi_i) \\
&\text{logit}(\pi_i) = \beta_0 \\
&\text{ST}_i|(\text{has.struggled}_i = 1) \sim \text{Beta}(\mu_i, \phi) \\
&\text{logit}(\mu_i) = \log\left(\frac{\mu_i}{1-\mu_i}\right) = \beta_1 + \beta_2 \text{Y}_{\text{first}i} + \beta_3 \text{sex}_i + \beta_4 \text{wt}_i + \beta_5 \text{treatment}
\end{aligned} \tag{5.10}$$

where $i = 1, ..., 65$ is the observed kiwi and ϕ is the dispersion parameter of the Beta distribution, assumed constant.

The snapping rates were fitted with a zero-altered Gamma distribution with a logit-link function:

$$\begin{aligned}
&\text{has.snapped}_i \sim \text{Bernoulli}(\pi_i) \\
&\text{logit}(\pi_i) = \beta_0 \\
&\text{SN}_i|(\text{has.snapped}_i = 1) \sim \text{Gamma}(\mu_i, \phi) \\
&\text{logit}(\mu_i) = \log\left(\frac{\mu_i}{1-\mu_i}\right) = \beta_1 + \beta_2 \text{Y}_{\text{first}i} + \beta_3 \text{sex}_i + \beta_4 \text{wt}_i + \beta_5 \text{treatment}
\end{aligned} \tag{5.11}$$

An AIC comparison showed substantial support of the model with only the weight/tarsus length ratio wt and the years since first capture Y_{first} as model covariates for the heart and breathing rate responses. The complete model described in Equation 5.10 was the best fit for the proportion of struggle time, and the model with only wt, sex, and Y_{first} was the best fit for the snapping rate.

Tables 5.8 and 5.9 show the model fit summaries.

The linear models fitted to the heart and breathing rate have a very low R^2, meaning that our covariates are not explaining much of the variation of our responses. The underlying model assumptions of independence, normality, homoscedasticity, and outliers were tested using the standard model diagnostics for all models presented in this section (Figure 7.3 in the thesis' Appendix). The model diagnostics suggest that the variance of the residuals might not be uniform across covariates, which could indicate a missing higher order term in our predictors. However, as we only use these

Table 5.8: Log-transformed estimated parameters, standard errors, 95% confidence intervals and p-values for the linear regression models presented in Equation 5.8, for the subset of data obtained from banded birds.

		Heart rate H_m				**Breathing rate B_m**			
Coeff.	*Predictors*	*Est.*	*SE*	*95% CI*	*p*	*Est.*	*SE*	*95% CI*	*p*
β_0	intercept	4.42	0.37	3.68 – 5.16		2.58	0.38	1.82 – 3.35	
β_1	w/tl	0.01	0.02	-0.02 – 0.05	0.446	0.03	0.02	-0.00 – 0.07	0.083
β_3	Y_{first}	0	0.01	-0.02 – 0.02	0.998	-0.01	0.01	-0.04 – 0.01	0.225
Observations		41				42			
R^2 / R^2 adjusted		0.016 / -0.036				0.124 / 0.079			

Table 5.9: Logit-transformed estimated parameters, standard errors, 95% confidence intervals and p-values for the zero-altered Beta regression model presented in Equation 5.10, fitted to the proportion of struggle time ST, and for the zero-altered Gamma regression model presented in Equation 5.11, fitted to the snapping rate SN, for the subset of data obtained from the banded birds only.

		Struggle time prop. ST				**Snapping rate SN**			
Coeff.	*Predictors*	*Est.*	*SE*	*95% CI*	*p*	*Est.*	*SE*	*95% CI*	*p*
β_1	intercept	-2.04	1.1	-4.20 – 0.12	0.064	-1.24	1.09	-3.38 – 0.91	0.257
β_2	w/tl	0.02	0.05	-0.08 – 0.11	0.738	0.17	0.05	0.08 – 0.26	**<0.001**
β_3	sex (M)	-0.19	0.3	-0.78 – 0.41	0.541	0.29	0.34	-0.37 – 0.96	0.39
β_4	Y_{first}	0.07	0.03	0.01 – 0.13	**0.024**	0.02	0.03	-0.04 – 0.07	0.612
	treatment (UD)					-0.56	0.29	-1.12 – 0.01	0.052
	Zero-Altered Model								
β_0	intercept	0.25	0.22	-0.19 – 0.68	0.271	0.71	0.23	0.25 – 1.17	**0.002**
Observations		41				41			

models to verify our hypothesis on the correlation between predictor variables and responses, rather than to get exact estimates of these effects, we consider the models presented above as acceptable.

Table 5.9 highlights a significant effect of the number years since the first capture on the proportion of struggle time, with a 7.3% average increase for every year passed since their first capture, when holding all other variables constant. In other words, it seems that the more encounters these kiwi have with humans, the more they struggle when we handle them. Table 5.9 also highlights a significant effect of the weight/tarsus length ratio wt on the snapping rate, with an 18.5% average increase for every unit increase in wt. This means that kiwi in better body condition snap more, when holding all other variables constant.

5.3.4 Discussion

The analysis presented in this section helped shed a better light on the effects of human manipulation on kiwi's behavioural responses. The responses of brown kiwi to manipulations show that the birds seem to habituate to human handling, with birds that have been manipulated more times having slower breathing rate. Our results also suggest that behaviour alone cannot be used as a measure of "stress": larger birds (and females) struggle more regardless of manipulation history. However, when the set of previously handled birds is examined on its own, birds with longer manipulation history struggled more but had a lower breathing rate, suggesting that behaviour and physiology might not be correlated in kiwi's response to human manipulations. To test this suggestion, future research could focus on running a multivariate analysis looking both at correlations among the physiological and behavioural responses, and the effect of human manipulation history on these responses.

Human handling of these birds is an important step in most of our monitoring and conservation programs, it is therefore important to gain a better understanding of how our interference may impact their behaviour. Future research could be devoted to better understanding the mechanisms surrounding the emergence and plasticity of brown kiwi behaviour, as well as to the exploration of differences and similarities in the behaviour of kiwi of different species.

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In these last two sections we extracted information on the behaviour of North Island brown kiwi by analysing two empirical datasets with different structures: the Y-maze

dataset had a nested structure, with multiple repetitions for each bird. This structure allowed the use of mixed effect modelling to partition the observed variation into within- and between-individual variation; the "response to capture" dataset, on the other hand, contained only one measurement for each bird, which could only be used to analyse the effects that sex, body condition and human manipulation history have on physiological and behavioural responses to human capture.

During the 2020 field experiments described in this chapter, we realised that to design experiments that are capable of testing hypotheses on animal personalities it is useful to know how much and what kind of data will be needed. In particular, it would be useful to perform a power analysis to estimate the smallest sample size needed to partition the between-individual and within-individual variations in behaviour.
A possible strategy to obtain this information would be to extract different sized random samples of a chosen, measurable behaviour from a range of simulated populations (each characterised by different levels of between-individual and within-individual variation in that behaviour). A measure of behavioural repeatability could then be calculated from each of these simulated samples, in the way described earlier in this chapter, compared to the known underlying heterogeneity level, and used to calculate the probability of correctly detecting heterogeneity as a function of sample size.
A simplified version of this method is described in the Appendix of this thesis.

CHAPTER 6

Conclusion

6.1 Overall summary

The research presented in this thesis helped answer some understudied research questions surrounding wild animal personalities. Throughout this work, we have argued that animal personalities can have a strong effect on population dynamics, and they should therefore be taken into consideration when making decisions on wildlife management strategies. In particular, our numerical models and the analysis of our field data confirmed the importance of correctly quantifying animal personalities, and demonstrated the non-negligible effects that animal personalities can have on the outcome of mammalian pest eradication.

Our findings allowed us to answer this thesis' main research questions:

1. What modelling strategies allow us to quantify the effects of animal personalities on pest eradication and threatened-species management? The meta-analysis and systematic review on the detectability of New Zealand's invasive mammal pests presented in Chapter 2 highlighted the differences in these species' home-range sizes and detectability, measured using different detection methods, in different seasons, and different habitats. This systematic review identified a number of knowledge gaps around the detectability of some less studied, but just as destructive, small mammal pest species. Very few studies were found around the detectability of some of these invasive species, and around pest detectability following mast years. This review is an important contribution to the pest eradication

efforts in New Zealand, as it provides an up-to-date and complete collection of spatial detectability parameters that pest managers and modellers can refer to when making predictions on their pest population of interest.

We then used results from our meta-analysis to calibrate the numerical simulations of Chapters 3 and 4, which allowed us to explore and quantify the effect of different distributions of a personality trait, trap-shyness, on the success and duration of pest eradication programmes. In Chapter 3, we also proposed a framework to detect trap-shyness heterogeneity from capture data in wild populations of known density. This work contributes to the existing knowledge around pest management strategies, and can be used as a guide for pest managers designing an eradication programme. For example, our model could be applied during an eradication programme to identify at what time a more intensive, targeted eradication method should be introduced to target any remaining, trap-shy survivors. Through our proposed method to detect heterogeneity in trap-shyness, we recommended quantifying behavioural heterogeneity early on in the eradication process, so that it can usefully inform adaptive management decision-making.

The work presented in in Chapter 5 called attention to both the existence of different personalities in kiwi, and the limitations of different experimental approaches in correctly estimating their personalities. The mixed-effects models presented in this chapter allowed us to distinguish between within-individual and between-individual variation in the observed kiwi behaviour. We argued that making this distinction is a crucial step in the detection of animal personalities, and that mixed-effects models are a useful tool to tease apart the different factors contributing to observed variation in behaviour.

2. What impact does individual heterogeneity in behaviour have for pest eadication and for the management of the threatened species at the focus of New Zealand's current conservation efforts? The simulation results presented in Chapters 3 and 4 highlighted the non-negligible effect that individual differences in trap-shyness, the distribution of this trait in a population, and the possible transmission of this trait across generations can have on the outcome of a pest trapping programme. We have found that heterogeneous populations pose a much greater eradication challenge than homogeneous ones. This is because the existence of even a few very trap-shy individuals can considerably lengthen eradication times, or make it very difficult to achieve. We also argued that a flawed or badly informed trapping regime might lead to populations of "super-pests" (populations mostly consisting of very trap-shy individuals), which would constitute an ecological

disaster in ecosystems such as those of New Zealand where numerous native species are threatened by these pests.

Chapter 5.1 highlighted the high behavioural plasticity in brown kiwi compared to their behavioural specialisation. In other words, most kiwi in our experiment displayed high within-individual variability in their behaviour relative to the between-individual variability. This result gives hope that these kiwi populations may be able to cope when faced with future change and challenges, and may reflect the diverse genetic heritage of Ponui Island's kiwi. Chapter 5.2 helped shed better light on the effects of human manipulation on kiwi's behavioural responses. We found that manipulation history doesn't have a significant effect on kiwi stress responses, but sex and body condition do. Human handling of these birds is an important step in most of our monitoring and conservation programmes, it is therefore important to gain a better understanding of how our interference may impact their behaviour.

3. How much and what kind of field data is needed for a robust and accurate prediction of personality distributions in wild animal populations? Throughout this thesis we argue that one of the biggest challenges associated with measuring animal personalities and incorporating them in models of wild population dynamics is the robust and precise measurement of these personalities. Some behavioural traits, such as trap-shyness, and their distribution in the population, are particularly hard to measure because of their very nature: to measure a behaviour one must first detect the individual displaying it, which in the case of animals with high levels of trap-shyness can be quite challenging. In Chapter 3 we proposed a method to use capture data to make predictions about the distribution of trap-shyness in a population, without having to detect the most trap-shy individuals. However, as we showed in that study, the accuracy of these estimates strongly depends on previous knowledge of population size.

The field work presented in Chapter 5 also highlighted the need for guidelines around how much and what kind of field data is necessary for the accurate measurement of animal personalities. The power analysis presented in Chapter 5.3 addresses this need by providing some general guidelines, but further work is needed to create a more robust set of recommendations for researchers aiming to quantify animal personalities from field experiments.

6.2 Limitations and future research

This thesis, just like most other pieces of research, comes with its own set of limitations. These limitations give an opportunity for further research and a more in-depth exploration of the research questions presented.

The literature review highlighted several knowledge gaps surrounding small mammal pest detectability in New Zealand. As pest eradication is an issue at the core of New Zealand's wildlife conservation goals, filling these knowledge gaps is an important step in supporting pest management efforts.

The models of population dynamics presented in this thesis suffered from a lack of field data on personality distributions and on behavioural plasticity around trappability in the animal species we simulated. This made it very difficult to calibrate our models and to apply them to real-case scenarios of pest eradication. While we suggested a method to estimate heterogeneity in trappability using capture data, this method relies on good knowledge of population size, which is not always easily achieved. It is important that future research investigates and quantifies heterogeneity in trappability, as well as behavioural plasticity in wild animals. Ideally, this would be done through repeated measures of both space use and trap-shyness of large numbers of individuals in a pest population. This data could then be analysed through mixed-effects modelling to first measure repeatability in trap-shyness, and to then give some indication of the possible distributions of trap-shyness levels in different pest populations. However, as trap-shy individuals are, by definition, very difficult to detect, this could prove to be a challenging and resource-intensive task. Another possible approach to estimate their numbers could be to identify a correlation between trap-shyness and another, more easily measured trait, and to use measurements of this other trait to infer trap-shyness.

The simulation models presented are also limited in their representation of real-life pest population dynamics. While they are sufficient to isolate and describe the effects of individual heterogeneity in trap-shyness and its vertical transmission on eradication outcomes, they could be complexified to include other factors affecting mortality and population size, such as resource competition and immigration. In addition, our models of New Zealand's pest population dynamics could gain accuracy from a better understanding of these species' home-range use and movement patterns, as these could impact animals' probability of trap encounter.

Our analysis of the kiwi field data presented a number of limitations. The dataset on brown kiwi's stress response to capture was produced with the goal of quantifying

differences in personalities between different birds and differences in the reaction to capture between human-habituated and non-human-habituated birds. While the analysis of the data resulted in some interesting findings around the influence of human habituation, sex and body condition on kiwi's stress responses, the experimental design including a single measurement available per bird made it impossible to partition the observed variation into within- and between-individual variation. Future research should certainly further test the repeatability of kiwi's stress responses, by identifying what proportion of behavioural variance is attributable to either of those two sources. In addition, the large amount of genetic data collected over the years on the population of brown kiwi in Ponui Island could be used in conjunction with new or existing experimental data to elucidate the role of genetics and epigenetics on kiwi's personalities and behavioural plasticity.

Our power analysis in Chapter 5.3 provides experimental guidelines to robustly estimate individual heterogeneity in behavioural traits in wild animals. Our analysis was limited to four different scenarios of data availability. This work provides a good starting point for the development of a more robust guide to measure personalities, but more research is needed to explore different modes of data collection for different species and different personality traits.

Finally, in line with previous research, this thesis as a whole calls attention to the complex nature of animal personalities, to the difficulties associated with their quantification, and to the many implications that these have on population dynamics and wildlife conservation strategies. Future research should further develop these ideas and methods to uncover the nature of animal personalities.

CHAPTER 7

Appendix

Probability distribution function of distances between trap and home-range centre

We simulate scenarios where a gird of regularly spaced traps (distance between traps d) are placed in a territory with randomly placed animal home-range centre.

The probability distribution function of the distance d between a trap and a randomly placed home-range centre can be found by calculating the PDF $f(x)$ of the distance x from a point to the centre of a dxd square:

$$f(x) = \begin{cases} \frac{2\pi x}{d^2}, & \text{if } 0 < x \leq \frac{d}{2} \\ \frac{4x}{d^2}\left(\frac{\pi}{2} - 2\arccos\left(\frac{d}{2x}\right)\right), & \text{if } \frac{d}{2} < x \leq \frac{d\sqrt{2}}{2} \\ 0, & \text{otherwise} \end{cases} \tag{7.1}$$

Parameter estimates under different modelling scenarios

N	μ_{th}	σ_{th}	$\hat{\mu}_{est}$ mean	sd	$\hat{\sigma}_{est}$ mean	sd
100	0.3	0.001	0.308	0.018	0.007	0.014
100	0.3	0.1	0.283	0.011	0.067	0.057
100	0.3	0.289	0.181	0.049	0.143	0.038
100	0.5	0.001	0.537	0.052	0.048	0.09
100	0.5	0.1	0.56	0.085	0.135	0.091
100	0.5	0.289	0.43	0.024	0.225	0.021
100	0.7	0.001	0.714	0.09	0.021	0.037
100	0.7	0.1	0.741	0.042	0.055	0.063
100	0.7	0.289	0.621	0.089	0.18	0.12
300	0.3	0.001	0.295	0.03	0.038	0.042
300	0.3	0.1	0.307	0.04	0.104	0.076
300	0.3	0.289	0.211	0.009	0.17	0.006
300	0.5	0.001	0.49	0.015	0.02	0.035
300	0.5	0.1	0.476	0.035	0.037	0.047
300	0.5	0.289	0.495	0.02	0.27	0.005
300	0.7	0.001	0.727	0.09	0.038	0.071
300	0.7	0.1	0.709	0.067	0.068	0.068
300	0.7	0.289	0.617	0.012	0.242	0.014
500	0.3	0.001	0.336	0.067	0	0
500	0.3	0.1	0.297	0.025	0.034	0.044
500	0.3	0.289	**0.073***	0.019	**0***	0
500	0.5	0.001	0.48	0.252	0	0
500	0.5	0.1	0.597	0.118	0.017	0.034
500	0.5	0.289	**0.316***	0.048	**0***	0
500	0.7	0.001	0.609	0.013	0	0
500	0.7	0.1	0.628	0.049	0.032	0.065
500	0.7	0.289	**0.523***	0.156	**0***	0

Table 7.1: Estimates of the parameter of the β-distribution used to simulate individual heterogeneity in the probability of interaction with a trap p_{int}, for different values of population size N, mean probability of interaction μ and standard deviation (measure of heterogeneity) σ. These estimates correspond to the mean of 500 simulations, run using a constant probability of encounter $p_{enc} = 0.2$ and under the assumption of known population size N.

* For high values of N and σ_{th} (giving a large number of very trap-shy individuals), our model gives inaccurate estimates of both μ and σ, consistently underestimating both parameters.

Model diagnostics for the models fitted to the kiwi data in Chapter 5

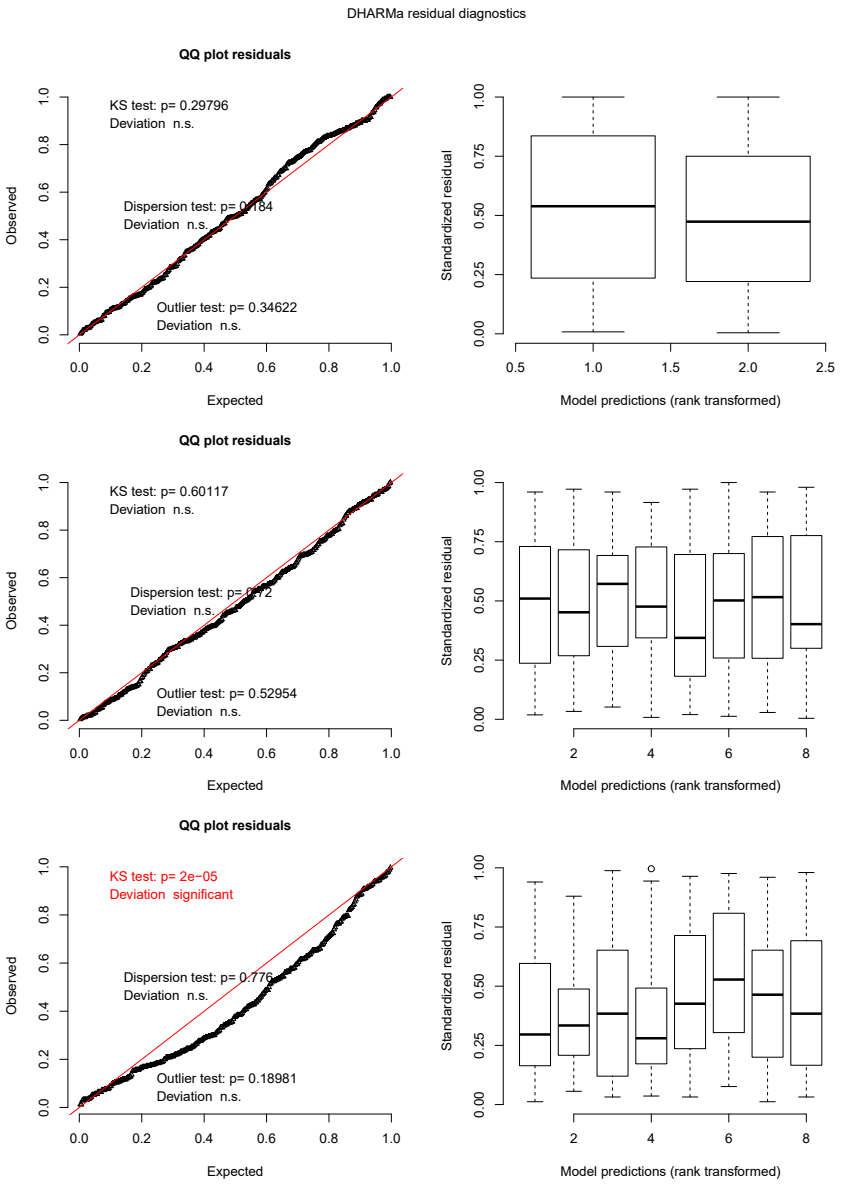

Figure 7.1: Models fitted to the Y-maze data. Model diagnostics to test independence, normality, homoscedasticity, and outliers for each of the four models presented in Section 5.2.3.3, fitted to the "Y-maze" experiment dataset. From top to bottom, diagnostics plots for models fitted to: t_0, t_{inv}, t_{tot}. Plots obtained using the R package DHARMa (Hartig, 2021).

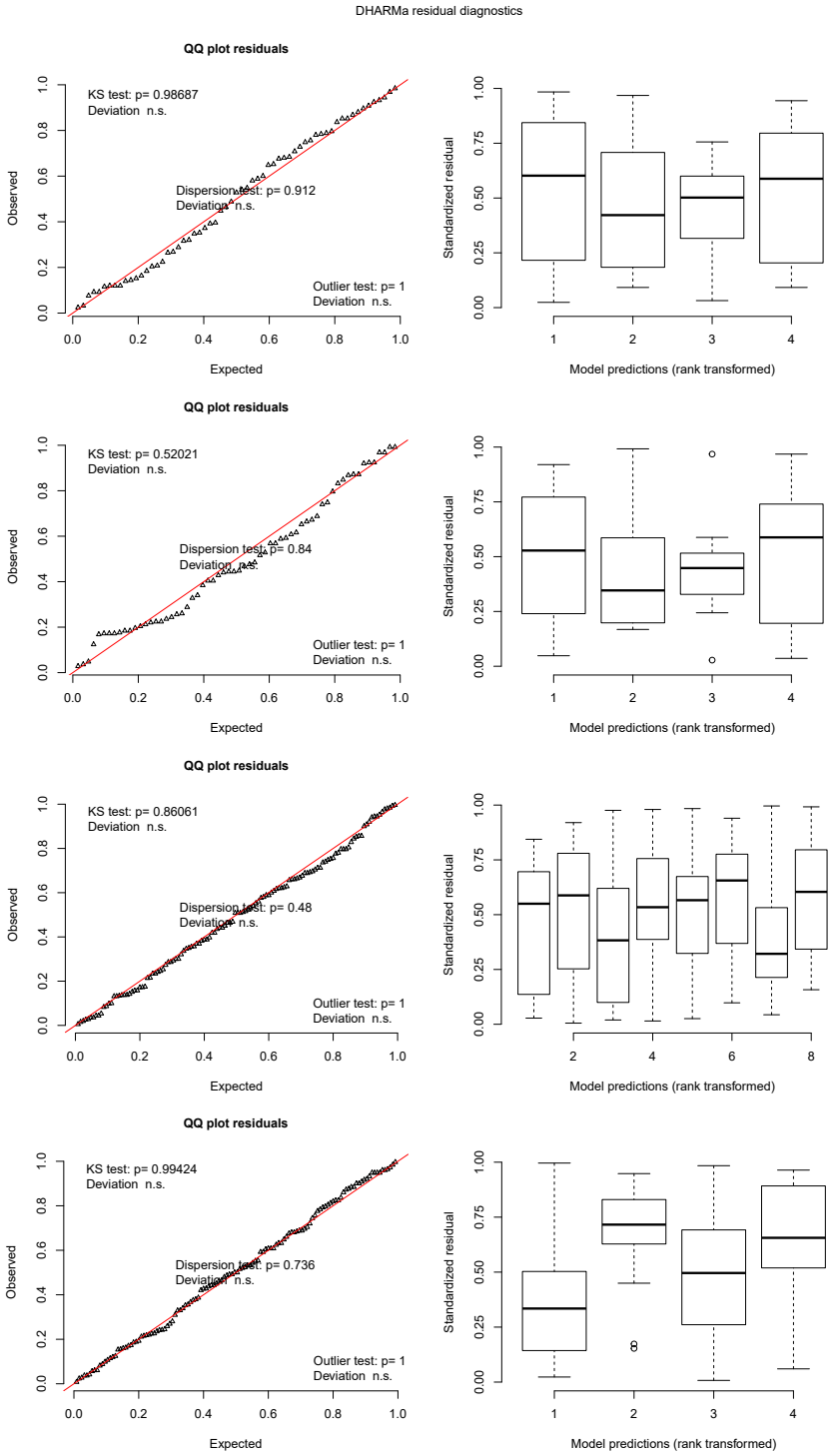

Figure 7.2: Models fitted to the "reaction to capture" complete dataset. Model diagnostics to test independence, normality, homoscedasticity, and outliers for each of the four models presented in Section 5.3.4.1, fitted to the complete kiwi dataset. From top to bottom, diagnostics plots for models fitted to: H_m, B_m, ST, SN. Plots obtained using the R package DHARMa (Hartig, 2021).

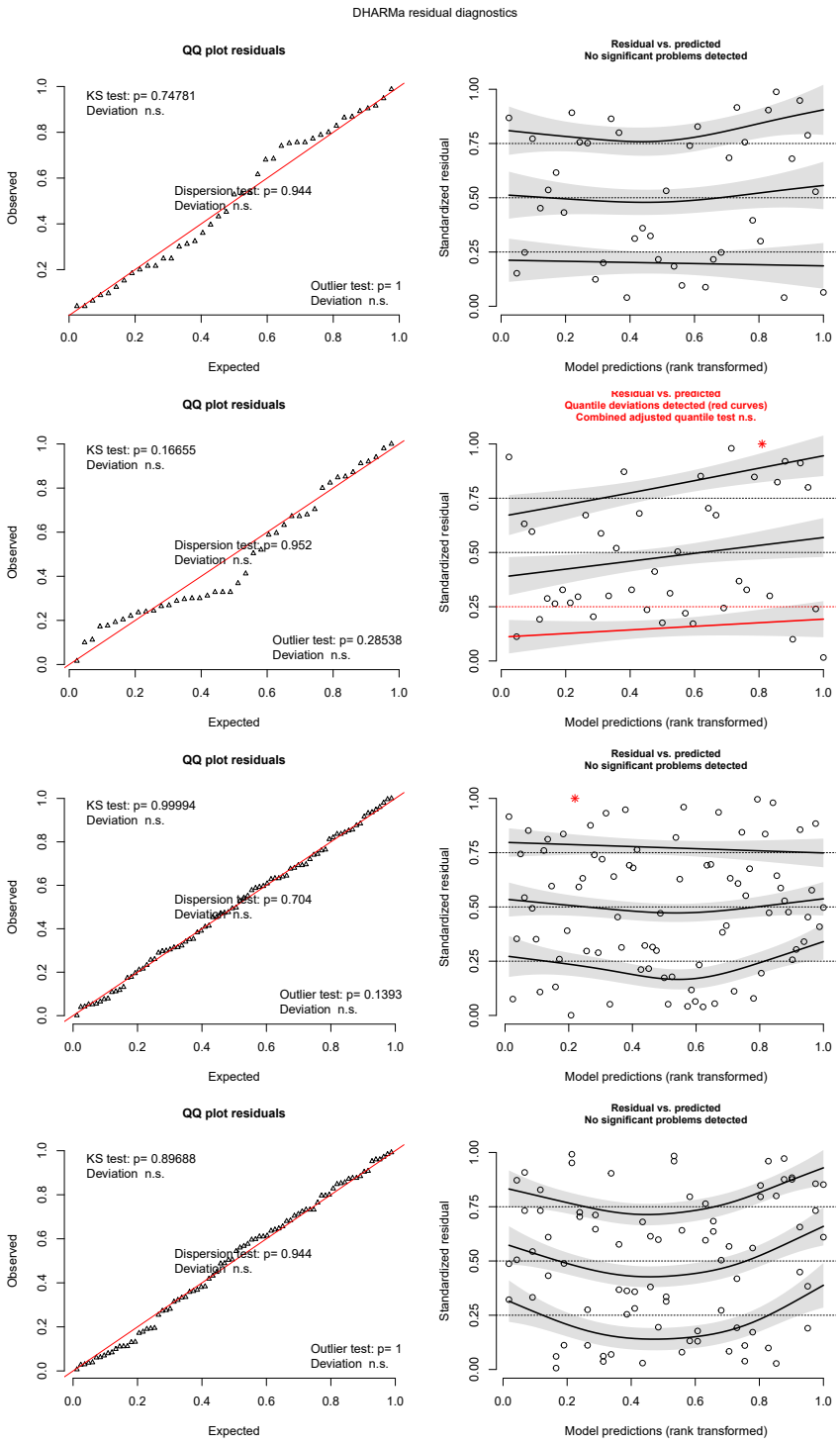

Figure 7.3: Models fitted to the "banded-only" subset of the "reaction to capture" data. Model diagnostics to test independence, normality, homoscedasticity, and outliers for each of the four models presented in Section 5.3.4.2, fitted to the subset of banded birds. From top to bottom, diagnostics plots for models fitted to: H_m, B_m, ST, SN. Plots obtained using the R package DHARMa (Hartig, 2021).

PCA analysis on the data from the "reaction to capture" experiment

Given the high number of variables that could explain the kiwi's responses to capture, we performed a Principal Component Analysis (PCA) to combine the possibly related continuous covariates into a single score. This helped reveal patterns and clusters in the population.

All birds

We started by performing a PCA on the six variables measured for all birds, new and banded (see Table 5.4). The PCA combines the original variables into principal components, all orthogonal to one another. The loading plot in Figure 7.4 shows how much weight each of the original variable has on the two principal components, and the angles between the vectors tell us how characteristics correlate with one another (0° angle - perfect positive correlation, 90° angle - no correlation, 180° - perfect negative correlation).

Figure 7.4 suggests a positive correlation between the proportions of time spent struggling and the proportion of time spent snapping in the "look in the eyes" stage of the experiment, meaning that birds that struggled more usually snap many times. It also shows that heartbeats per minute and the proportion of time spent struggling while upside-down are positively correlated with each other.

We then projected each individual bird on the two principal components (Figure 7.5). This projection maximises variation between birds, making it easier to identify patterns and groups.

Grouping birds by weather they were banded (captured in previous years) or new showed some separation between the two groups: human habituation could be a significant variable to included in our model. The individuals plot also gives an idea on which birds might be significantly different from the rest. Louise, Emily, George and Meital are examples of birds with more "extreme" behaviours, as their projections on the two PC are quite far from those of the other birds.

banded birds only

We then performed a PCA on the banded birds only, to explore the relationship between our measured responses and the three additional measurement that were taken for these birds (Table 5.4): weight/tarsus length ratio, years since first capture,

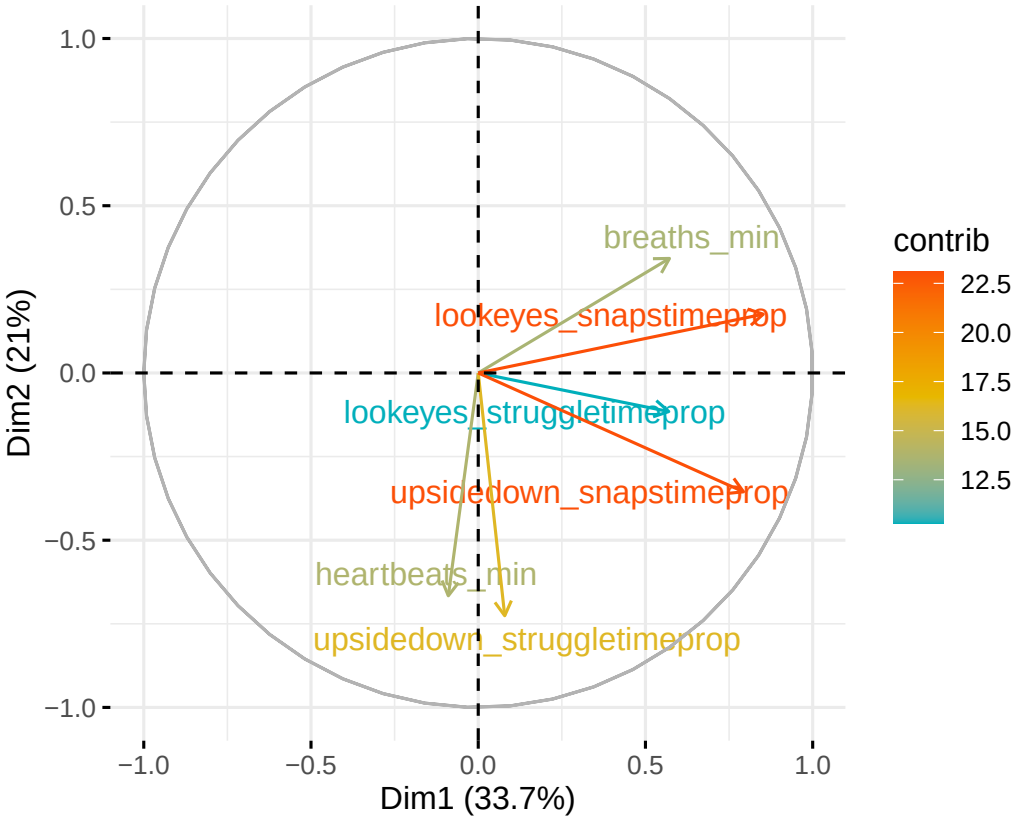

Figure 7.4: Loading plot of the variables included in the PCA.
The length and colours of the vectors are a measure of the strength of their contribution to the principal components. In other words: the longer the vector, the more variability of this variable is represented by the two displayed principal components; short vectors are thus better represented in other dimension. Also, the more parallel to a principal component axis is a vector, the more it contributes only to that PC. The angles between vectors of different variables show their correlation in this space: small angles represent high positive correlation, right angles represent lack of correlation, opposite angles represent high negative correlation.

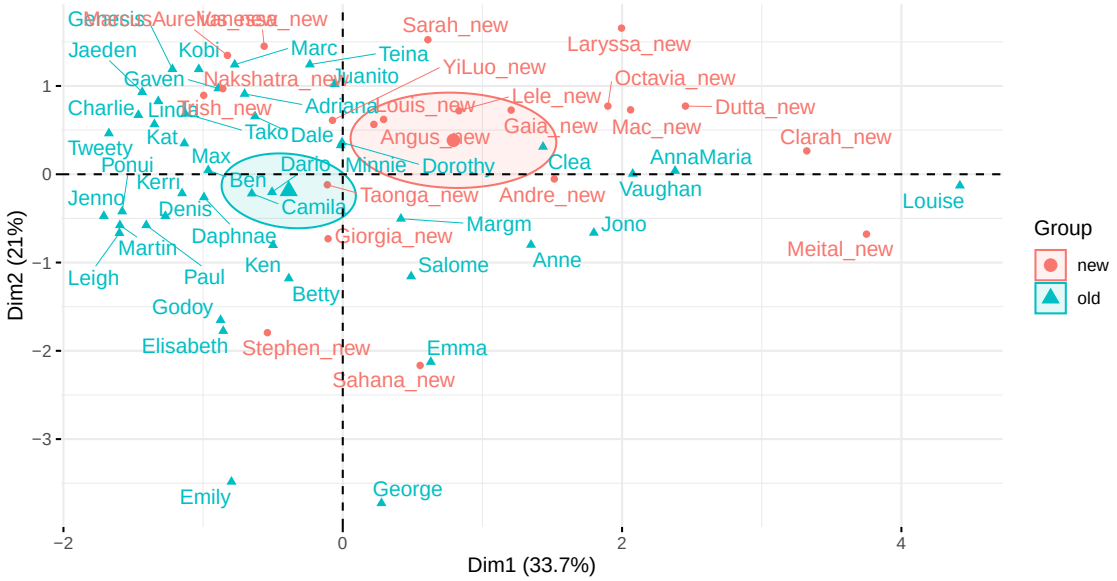

Figure 7.5: Projection of the individual birds on the two principal components. new birds are shown in red, banded birds are shown in blue. The shaded ellipses are 95% confidence ellipses, *i.e.* confidence regions of the group means (the smaller the ellipse, the more accurate the estimated mean).

activity in the last four days.

The loading plot in Figure 7.6 shows a positive correlation between the proportion of time spent struggling and the proportion of time spent snapping for both the "look in the eyes" and "upside-down" stages of the experiment, indicating that birds that struggled more usually snapped many times.

The weight/tarsus length ratio, which we use as a measure of the bird's body condition, is somewhat positively correlated to the proportion of time struggling as well as the breathing rate. This would suggest that birds with a better body condition struggle more and have a higher breathing rate than birds with a worse body condition.

To explore the possible differences between sexes, we performed two additional PCAs for each sex.

Females The females' biplot (Figure 7.7) suggests that the proportion of snaps in both stages 3 (looking in the eyes) and 4 (upside-down) and the proportion of time spent struggling during stage 3 are positively correlated with each other and negatively correlated with the proportion of time struggling in stage 4. This indicates that the female birds that snapped many times struggled for longer when looked

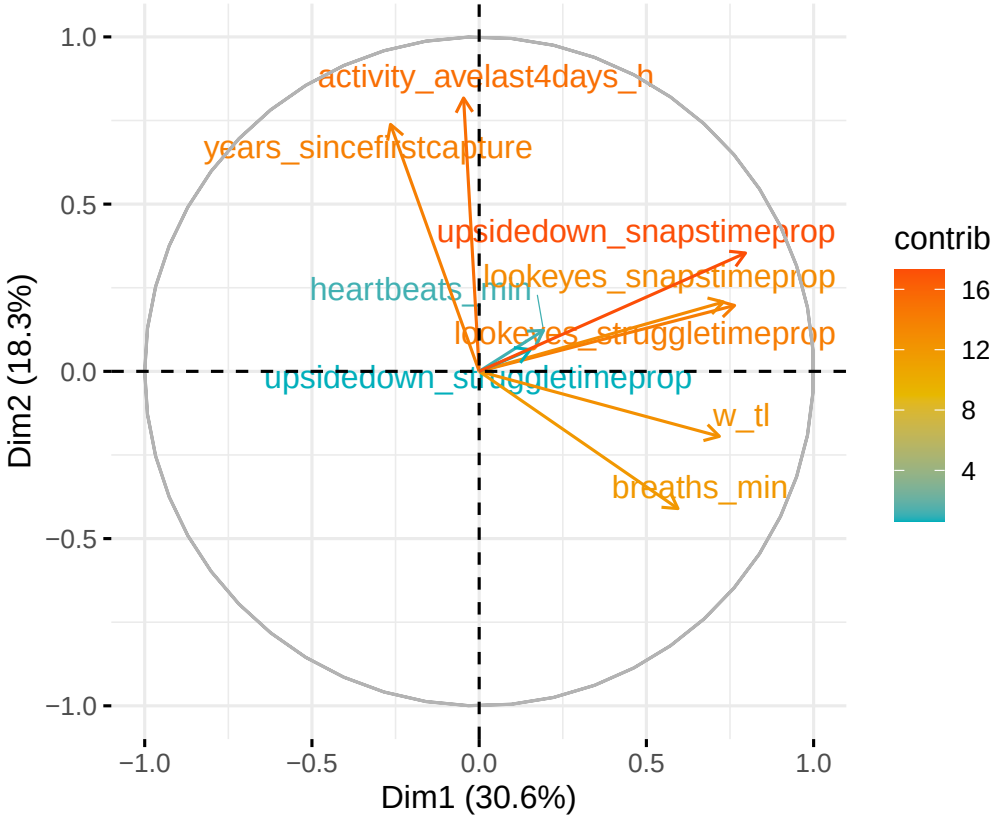

Figure 7.6: Loading plot of the variables included in the PCA with the banded birds only.

in the eyes but were calm when held upside-down. The heartbeats per minutes are negatively correlated with the number of years since first capture, suggesting that female kiwi that have been in the study for longer and have had more interactions with humans have a lower heart rate after capture. This finding supports our hypothesis that these birds may have habituated to the human handling and respond with less stress. Finally, the weight/tarsus length ratio is positively correlated with the breathing rate, which would indicate that female kiwi with better body conditions have a higher breathing rate after capture than those in worse conditions.

Males The biplot of the male kiwi (Figure 7.7) shows a positive correlation between the proportion of time spent struggling, the proportion of snaps in stage 4, and the weight/tarsus length ratio, indicating that the male birds who had better body conditions also struggled more. Once again, the heart rates are negatively correlated with the number of years since first capture, suggesting that birds that are more human-habituated are less stressed than the "newer" birds.

We also tried grouping the bird by their "relationship status" ("single" birds are thought to have very changing activity patterns), and by the amount of parasites found on their bodies (scored 1-3) but no clear cluster could be identified.

The following results are consistent across the different PCA presented previously:

1. The four measures of behaviour used (proportion of time spent struggling and number of snaps/minute in stages 3 and 4 of the experiment) are usually positively correlated with each other, indicating that **birds that struggle a lot usually also snap a lot**;

2. The heart and breathing rates are usually uncorrelated with each other, and the heart rate is usually negatively correlated with the number of years since first capture (measure of human habituation), indicating that **birds that are more used to being captured have a lower heart rate than "newer" birds**. However, these measures are uncorrelated with the struggling and snapping;

3. The birds' body condition is sometimes found to be correlated with the time spent struggling and snapping, indicating that **birds in better body conditions struggle more**;

4. The average number of active hours in the last four days is usually uncorrelated with the other covariates;

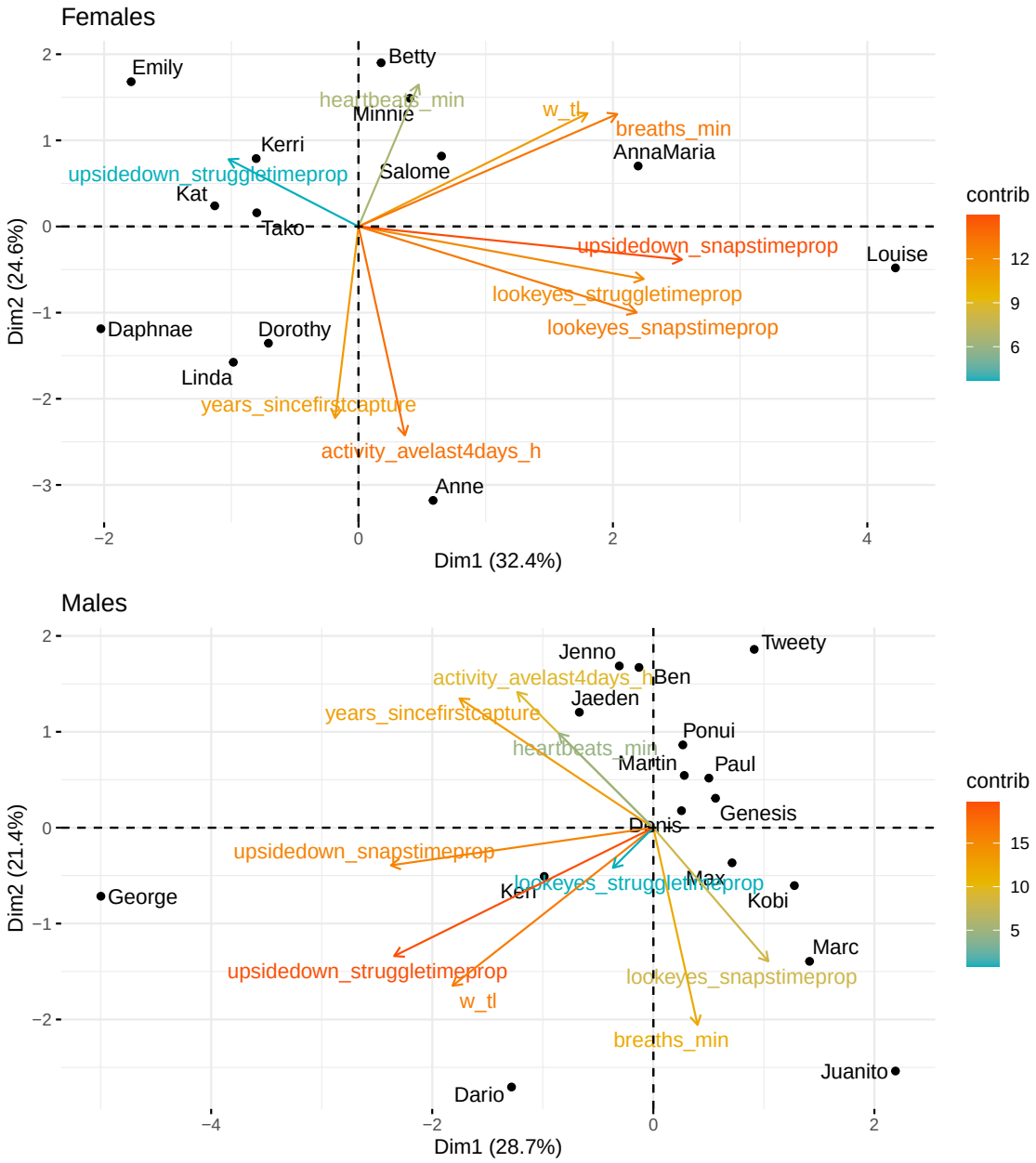

Figure 7.7: PCA biplots for female (**top**) and male (**bottom**) kiwi separately (banded birds only), showing each bird's projection on the two principal components as well as the covariates included in the PCA.
The length and colours of the vectors are a measure of the strength of their contribution to the principal components. In other words: the longer the vector, the more variability of this variable is represented by the two displayed principal components; short vectors are thus better represented in other dimension. Also, the more parallel to a principal component axis is a vector, the more it contributes only to that PC. The angles between vectors of different variables show their correlation in this space: small angles represent high positive correlation, right angles represent lack of correlation, opposite angles represent high negative correlation.

5. **Female birds struggle more than male birds**;

6. We found no evidence for an effect of "relationship status" or amount of parasites on the measured behavioural responses

Power analysis on behavioural data sample

Animal populations can exhibit different levels of heterogeneity. Knowing the exact behavioural composition of a population is difficult, if not impossible, as this would require not only being able to perfectly score and describe the personality of every member of the population, but also having a perfect knowledge of how individual behaviours vary in any given situation and across time.

During the 2020 field experiments described in the previous section, we realised that to design future experiments that are capable of testing hypotheses on animal personalities it is useful to know how much and what kind of data will be needed. This is what inspired the work presented in this section.

While we cannot directly measure the level of heterogeneity of a population, we can model and simulate different scenarios of population heterogeneity and compare the simulated data to the real one.

The main goal was to find out how much and what kind of data we would need to be able to make robust and accurate predictions on a population's behavioural profile. In particular, we are interested in how much data is needed to estimate both the within-individual and between-individual variation components.

We analysed each of the datasets to know how likely it is to detect any amount of heterogeneity in the population for any given scenario of population type and dataset size.

Methods

We simulated datasets of different size and coming from different "population types" (see below). Populations were characterised by different levels of between-individual variance (also called population heterogeneity) and within-individual variance (also called behavioural plasticity).

A flowchart of the simulation process is found in Figure 7.8. We assumed each population to have different levels of heterogeneity for one personality trait, measured as a variable between 0 and 1 to simulate a continuous range between two personality trait extremes (*e.g.* bold/shy, curious/indifferent). The population distribution of this trait was modelled using a beta distribution with constant mean $\mu = 0.5$ and variance s^2 (this corresponds to the between-individual variance). The higher s^2, the more heterogeneous the population.

Simulated individuals also have a within-individual variance, or behavioural plastic-

ity. To account for this, simulated behavioural responses were drawn from a gamma distribution. We chose a gamma distribution to match the distribution taken by our field data, presented in the previous sections. This gamma distribution's mean is given by the individual's personality (drawn from the population's beta distribution), and the distribution variance σ^2 depends on the individual's behavioural plasticity. The higher σ^2, the higher the behavioural plasticity.

Population types We define a population type as a combination of the population's level of individual heterogeneity (between-individual variation) and the level of each individual's behavioural plasticity (within-individual variation).

A population with a low level of individual heterogeneity is made of similar individuals, whereas one with a high level of individual heterogeneity is made of individuals that are different from one another. This level of individual heterogeneity is described using the variance of the population's distribution of a personality trait (e.g. curiosity level, aggressiveness, shyness), and can take values ranging from zero (a completely homogeneous population where all individuals are the same) to any chosen upper bound s^2_{max} corresponding to the most heterogeneous population.

The individual behavioural plasticity describes how much variation we can observe in the behaviour of a single individual under the same experimental conditions. In other words, does an individual always behave the same way when all external factors are kept the same, or does it change its behaviour for no apparent reason other than its own choice and personality?

As we cannot always control all external factors, especially when working in the field, this last parameter will absorb all individual variation due to uncontrolled or unconsidered factors, such as life history, weather conditions, hunger and thirst.

Detecting heterogeneity

We estimated the probability of detecting heterogeneity in a population by looking at the p-value of an ANOVA performed on the measurements for each individual. If the p-value was $< 5\%$, we assumed that the means of at least two individuals were significantly different, therefore that the population was heterogeneous. Note, however, that the ANOVA returns a significant p-value even if only one individual was found to be different from the others. It does not provide any information on the level of heterogeneity, which is why subsequent model fitting will be necessary to get that information.

We ran 1000 simulations for each combination of parameter values and calculated

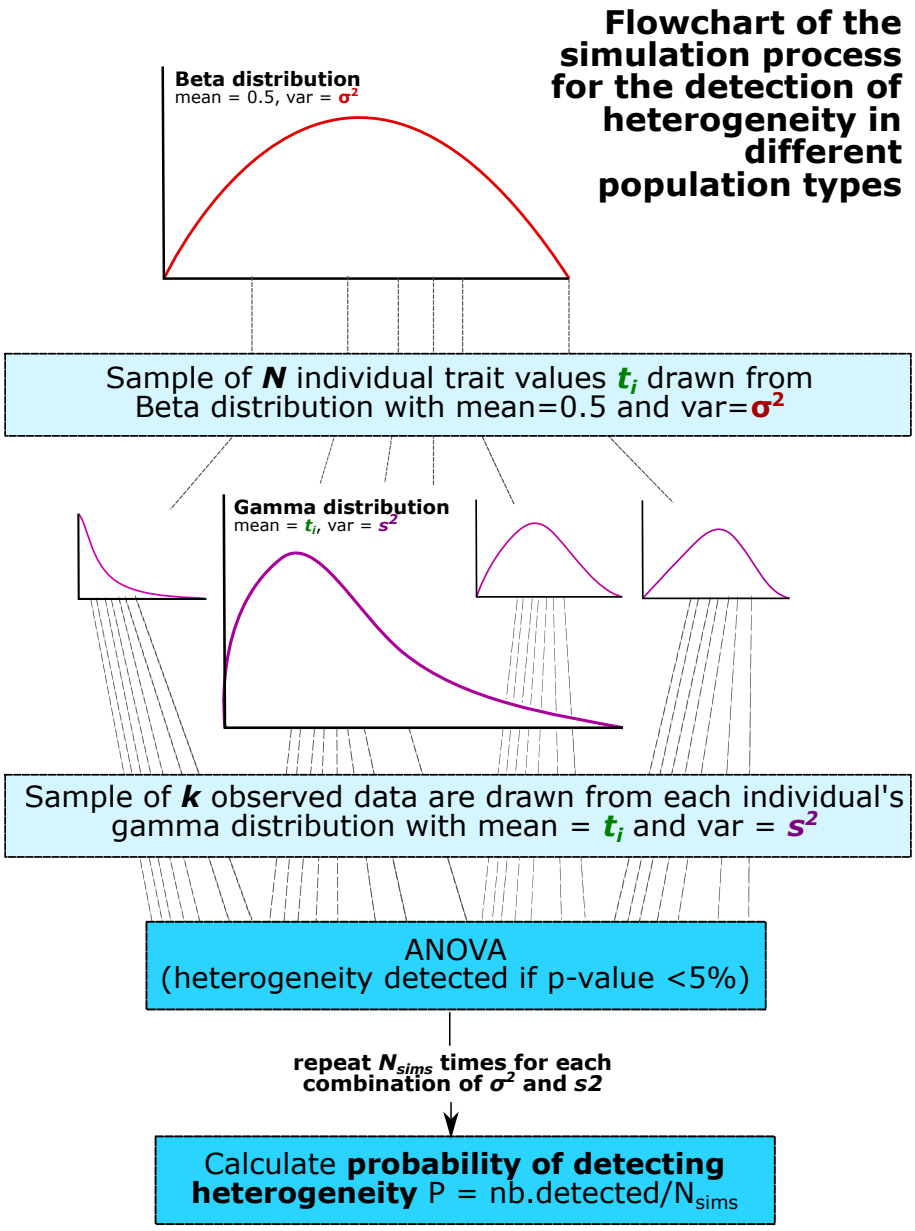
Flowchart of the simulation process for the detection of heterogeneity in different population types
Beta distribution
mean = 0.5, var = σ²
Sample of N individual trait values t_i drawn from Beta distribution with mean=0.5 and var=σ²
Gamma distribution
mean = t_i, var = s²
Sample of k observed data are drawn from each individual's gamma distribution with mean = t_i and var = s²
ANOVA
(heterogeneity detected if p-value <5%)
repeat N_sims times for each combination of σ² and s2
Calculate probability of detecting heterogeneity P = nb.detected/N_sims

Figure 7.8

the proportion of datasets that were found to come from a heterogeneous population (ANOVA's p-value $< 5\%$).

The model parameters chosen for the simulations are the following:

Parameter		**Values**
Population size	N	[10, 50]
Number of repetitions per individual	k	[5, 50]
Within-individual variance	σ^2	[1, 4, 9, 16, 25]
Between-individual variance	s^2	[0, 0.0025, 0.0225, 0.0625, 0.08]
Number of simulations	N_{sims}	1000

Table 7.2: Model parameters used for our simulations of heterogeneity detection. Results are summarised in Figure 7.9.

Results and discussion

The results of our simulations are summarised in Figure 7.9.

As we would expect, heterogeneity is most likely to be found for high levels of population variance and low levels of individual variance. This last parameter plays a very important role in the detection of heterogeneity using ANOVA. If the individual variance σ^2 is low, meaning that individuals have a consistent behaviour under the same conditions, we are more likely to detect differences between individuals. This is because the individuals' gamma distributions will be very narrow and will hardly ever overlap, even for small values of population variance s^2. Therefore, we are more likely to conclude that a population is heterogeneous (even if the population variance is low) if individuals behave consistently across many repetitions of the same experiment.

On the other hand, if the individual variance σ^2 is very high (inconsistent behaviour), it is hard to detect heterogeneity in the population, as individual distributions will be wide and will often overlap, even though their means are different. This is especially true if the number of repetitions per individual k is too low, as the mean for each individual might not be representative of their average behaviour. In other words, we are less likely to conclude that a population is heterogeneous (even if the population variance is high) if individuals behave inconsistently across many repetitions of the same experiment.

Population size also influences our predictions on population heterogeneity, to a certain extent. For similar values of k, s^2 and σ^2, we are more likely to detect heterogeneity for large population sizes. This is because a larger population size

(or larger sample of individuals from the same population) gives a better sample of values from the beta distribution. However, the effect of population size is overshadowed by that of individual and population variance: even for high values of N, it is unlikely that we detect heterogeneity if the population variance is too low or the individual variance is too high, as explained in the previous paragraphs.

ANOVA is a good first tool to use on a dataset of repeated measurements per individual to check if there are any outliers in a population. However, this method does not provide any information on how many individuals are different from the average, or on the distribution of personalities in the population. Furthermore, our simulations showed that the predictions made using ANOVA are greatly influenced by the individual's behavioural plasticity, which is usually hard to accurately measure in real life as it would require a great number of repetitions of the same experiment on each individual.

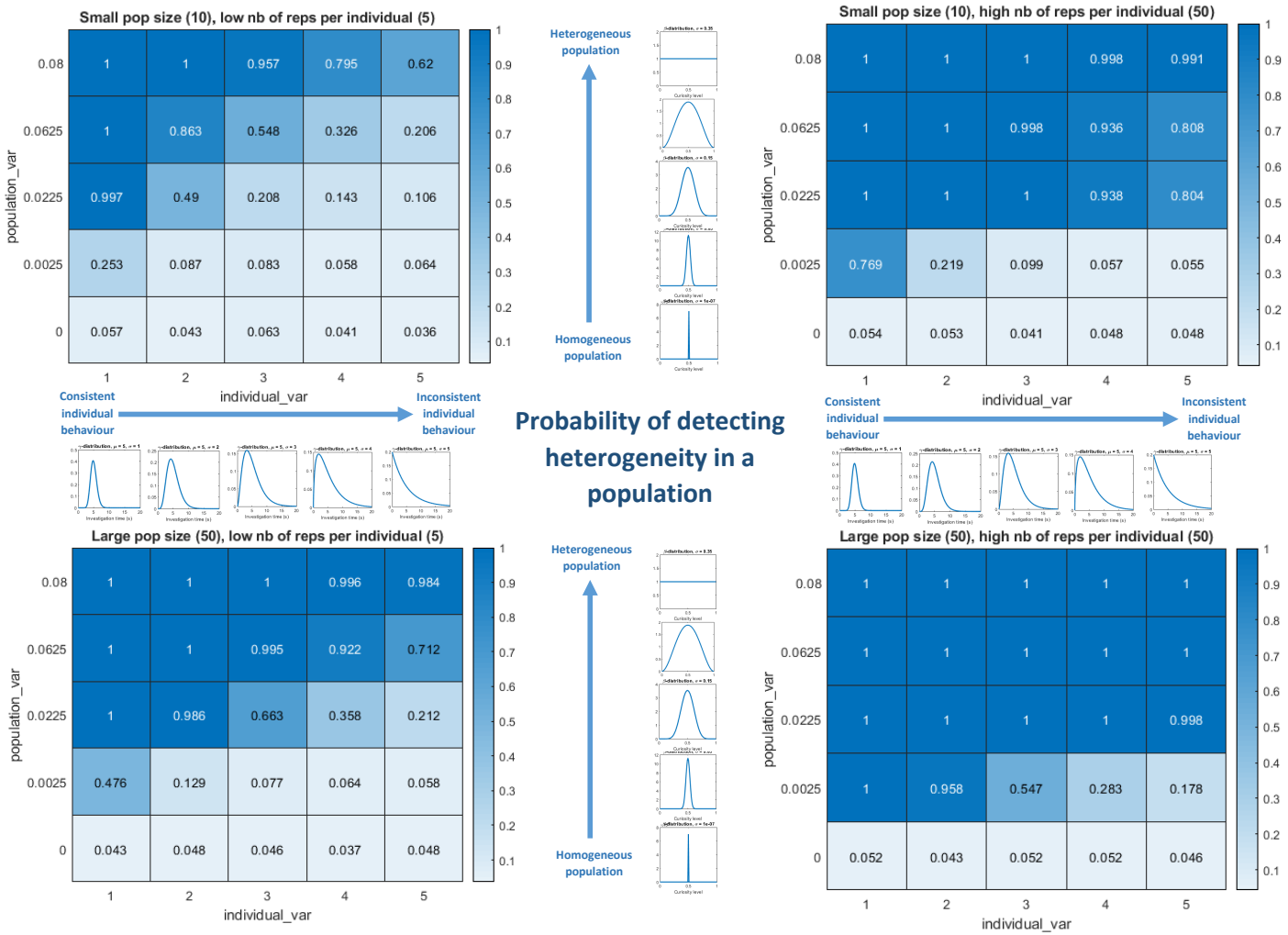

Figure 7.9: The probability of detecting heterogeneity is different for different population sizes. Summary of our simulation results where we measure the probability (colour of the heatmaps) that an ANOVA detects a significant difference between at least two individuals in the population, for different population types and different amounts of data collected (repetitions of the experiment per individual).

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