Foraging for a foothold:
Causes and consequences of dietary variation in a threatened avian pollinator

Caitlin Elizabeth Andrews

King's College
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This thesis is submitted to the University of Cambridge
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DECLARATION

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as specified in the text. It is not substantially the same as any that I have submitted, or, is being concurrently submitted for a degree or diploma or other qualification at the University of Cambridge or any other University or similar institution. I further state that no substantial part of my thesis has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution. The thesis does not exceed the Biology Degree Committee’s prescribed word limit of 60,000 words.

Thesis Title: Foraging for a foothold: Causes and consequences of dietary variation in a threatened avian pollinator

Name: Caitlin Elizabeth Andrews

Thesis Summary:

Foraging is a central theme in ecology and underlies some of the most fundamental interactions among species. While diet has long been treated as uniform within species, a paradigm shift is now taking place as ecologists recognize that individuals vary. However, questions remain about why this intraspecific variation exists and what consequences it may have for individuals, populations, and ecosystems. This information may be particularly important for species that are threatened due to food limitation, as dietary variation could be used to inform conservation efforts.

In this thesis, I used the hihi (*Notiomystis cincta*), a threatened New Zealand passerine, as a case study to explore the causes and consequences of dietary variation and possible implications for conservation. Because observing threatened species is often difficult in the wild, I first developed methodology to obtain more reliable dietary estimates from limited foraging observations. Using these improved metrics, I found that individual hihi specialize within the broader species diet. Generalists survived better than specialists, suggesting that dietary specialization may have consequences for fitness.

I next explored whether an array of intrinsic and extrinsic factors could explain dietary variation. Results suggested a weak correlation between diet and sociality, so I then conducted an experiment to test how directly altering the social environment affects diet. Using two scheduled conservation translocations, I found that individual hihi shifted towards more generalist diets when they were moved from a highly competitive source site to a less competitive release site. This suggests hihi share the same inherent dietary preferences but must specialize to avoid competition in dense populations. Furthermore, individuals that were more generalist before the translocation were more likely to be seen five months later, but only if they remained at the source site; at translocated sites, generalists tended to be less likely to be seen than specialists. These results suggest that selectively translocating specialists may improve translocation success without jeopardizing the source population.

Finally, I investigated how foraging behavior can shape the environment. Hihi are pollinators of several threatened native plant species, so conservation of hihi could promote ecosystem recovery as well as species recovery. However, little is known about how effectively hihi translocations restore lost pollination function and whether individuals vary in their pollination abilities. Through a multi-site pollinator exclusion experiment, I found that ecosystems may be able to partially adapt to the loss of hihi. Nevertheless, hihi bring unique benefits to pollination by improving seed quality. There was also some evidence that individual hihi vary in their efficiency as pollinators.

Together, my findings demonstrate that foraging is inextricably linked to the environment: the ecosystem shapes individual variation, which, in turn, shapes ecological functions. A better understanding of dietary variation may also have important implications for threatened species and ecosystems, informing the design of conservation interventions.

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CONTENTS

Chapter 1

General introduction

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Foraging is a cornerstone of ecology: it underlies one of the most universal needs of all animals as well as some of the most consequential intra- and interspecific interactions (Stephens and Krebs 1986; Perry and Pianka 1997; Stephens et al. 2007). Thus, it is not surprising that foraging played a pivotal role in the development of behavioral ecology as a field. Early theories examined how species' diets are shaped by decisions regarding how to divide time amongst resources based on their relative profitability (MacArthur and Pianka 1966; Charnov 1976). Others uncovered how species with similar niches can coexist through resource partitioning (MacArthur 1958; Hardin 1960; R. Armstrong and McGehee 1980). Further work investigated more dynamic phenomena, such as how species' niches expand and contract in response to changes in resource availability (J. Emlen 1966; MacArthur and Pianka 1966; Pulliam 1974) and community composition (MacArthur and Wilson 1967; Roughgarden 1972). Altogether, these studies set the stage for a rapid expansion of questions about foraging behavior (Perry and Pianka 1997), which, today, pervade all aspects of behavioral ecology, from disease transmission (e.g. Hall et al. 2007), to movement ecology (e.g. Owen-Smith et al. 2010), to cognition (e.g. Kamil and Roitblat 1985; Stephens 2008).

Early foraging theories successfully explained much of the diversity seen across species, but they also recognized that diversity can exist within species. Some of the earliest adaptations of Optimal Foraging Theory acknowledged that individuals' diets could be shaped by their satiety (J. Emlen 1966), experience (Krebs et al 1978; Hughes 1979), and ability to achieve optimality (Ritchie 1988). Partridge and Green (1985) expanded beyond these intrinsic factors to show how diets may also depend on extrinsic factors related to the social environment and ecosystem. This recognition of individual-level behavioral variation was forward-thinking, because ecologists historically tended to treat individuals as uniform within species. However, in recent years, individual differences have risen to the forefront of behavioral ecology (Bolnick et al. 2003; Dall et al. 2012; Wolf and Weissing 2012). It is now widely established that individual variation is not a mere artifact of statistical noise; moreover, it can have consequences not only for individuals' fitness but for population dynamics and ecosystem functioning (Bolnick et al. 2011; Benton 2012; Barabás and D'Andrea 2016; Costa-Pereira et al. 2019). This has given rise to new avenues of research into behavioral syndromes and personality (Gosling 2001; Dall et al. 2004; Sih et al. 2004; Brommer and Class 2017), but more traditional topics, such as foraging, are also being reexamined.

Individual variation in foraging encompasses a wide range of behaviors, including habitat selection (e.g. Patrick and Weimerskirch 2014; Baylis et al. 2015; Rossman et al. 2015), search strategies (e.g. Kurvers et al. 2010; Patrick et al. 2014; Keynan et al. 2015), foraging skill (Sih et al. 2019), and innovativeness (e.g. Overington et al. 2011; Serrano-Davies et al. 2017). A direct result of this variation is that individuals often differ both in their access to resources and in their selection of available foods. This can lead them to consume different diets, such that a species' niche is actually comprised of many distinct individual niches. When these dietary differences are consistent over time and cannot be attributed to age, sex, or morphology, they are referred to as 'individual specializations' (Bolnick et al. 2003). Today, specializations have been identified in a range of taxa, including reptiles (e.g. Pajuelo et al. 2016), amphibians (e.g. Araújo et al. 2009; Costa et al. 2015), birds (e.g. Woo et al. 2008; Pagani-Núñez et al. 2016; Phillips et al. 2017), and mammals (e.g. Estes et al. 2003; Lowrey et al. 2016). Among these are many species that were long considered generalist due to their broad diets but have since been found to be composed of a mix of 'specialists' (who consume only a narrow portion of the species' niche) and 'generalists' (who consume most or all of the species' niche: Bolnick et al. 2002; Bolnick et al. 2003; Araújo et al. 2011). Thus, our view of a species' niche can be reshaped significantly through the quantification of individual variation.

As more cases of dietary specialization have emerged, behavioral ecologists have begun delving into the causes of this variation. Individuals' diets have been found to be shaped by a range of factors, from learning (e.g. Estes et al. 2003) and personality (e.g. Serrano-Davies et al. 2017) to dominance (e.g. Holbrook and Schmitt 1992) and competition (e.g. Sheppard et al. 2018). At the same time, there has been growing interest in investigating the consequences of dietary variation across different ecological levels. At the individual level, diet has been found to influence survival and reproduction. For example, in pheasants (*Phasianus colchicus*), individuals reared on complex diets survive better as adults than those reared on specialist diets (Whiteside et al. 2015), while in brown skuas (*Catharacta antarctica lonnbergi*), dietary specialization predicts the timing of breeding, a known indicator of reproductive success (O.

Anderson et al. 2009). The consequences of dietary variation can also scale up to affect populations, as those containing a greater diversity of specializations are thought to be more resilient to environmental change than those with less diverse members (Bolnick et al. 2011). When individuals vary in their diets, populations may also interact with a wider range of species, increasing their potential impact on complex ecological interactions, such as mutualisms, predation, and competition (Bolnick et al. 2011). Some dietary specializations may make individuals even more effective at performing these roles. For instance, common carp (*Cyprinus carpio*) have been found to vary in their propensity to ingest and digest seeds, potentially making some individuals better seed dispersers than others (Pollux 2017).

Despite the advances made in recent years, behavioral ecologists are still only beginning to understand the full complexity of intraspecific dietary variation, leaving several key gaps in our knowledge. First, although some studies link diet to personality (see Toscano et al. 2016 for a review), further investigation into diet's role in behavioral syndromes (Sih et al. 2004) could provide insight into the mechanisms underlying dietary variation and its broader consequences. Additionally, while the literature on dietary specialization (Bolnick et al. 2003) and behavioral variation in general (Dall et al. 2004; Sih et al. 2004; A. Bell et al. 2009) strongly emphasizes cases of variation that are repeatable across time and contexts, less is known about the extent to which even transient individual differences can have lasting consequences. This is especially important to consider given that some known determinants of diet, such as the social environment (Galef and Giraldeau 2001; Araújo et al. 2011), are dynamic. Furthermore, while behavioral ecologists have started exploring the consequences of individual variation for higher ecological levels, more work needs to be done to turn theory into evidence. Alongside this, it should also be considered how the effects of dietary specialization on the ecosystem could, in turn, influence how individuals forage, closing this feedback loop.

A final and as-yet largely unexplored direction for dietary specialization research concerns its potential relevance to conservation. Given the escalating threats to biodiversity worldwide, it is increasingly important that behavioral ecologists seek out opportunities to meld their research with conservation priorities (Curio 1996; Caro 2007; Caro 2016). As populations shrink, more attention is being given to the behavioral tendencies of the remaining individuals and how interventions can promote desired behaviors and outcomes most effectively (Watters et al. 2003; Watters and Meehan 2007; B. Bell 2016; Merrick and Koprowski 2017). However, dietary specialization has been overlooked as a potential tool for conservation, despite the fact that resource limitation driven by habitat loss (Didham 2010) and climate change (Renner and Zohner 2018; Damien and Tougeron 2019) presents a major challenge for many threatened species. If individuals vary in their diets, it could be important to account for this when designing conservation interventions, particularly if remaining individuals do not represent their species' full niche. Understanding the consequences of dietary variation for individuals could also be informative, as interventions could be used to promote specializations that are most favorable under current and projected future conditions. If diet's consequences extend to higher ecosystem levels, interventions at the individual level could also be used to achieve broader restoration goals.

In this thesis, I investigate some of the key remaining questions surrounding the causes and consequences of dietary variation in a species where this knowledge could have conservation implications: the hihi (*Notiomystis cincta*). In the next section, I give a brief introduction to hihi, their foraging behaviors, and current strategies for species recovery. I then provide a preview of the central questions and methodology of each thesis chapter. Finally, I present an overview of the objectives and structure of the thesis.

1.1 STUDY SYSTEM: THE HIHI *(NOTIOMYSTIS CINCTA)*

The hihi (Figure 1.1a–b) is a passerine endemic to the North Island of New Zealand and is currently classified as 'vulnerable' by the IUCN Red List (Birdlife International 2017) and 'nationally vulnerable' by New Zealand's Department of Conservation (H. Robertson et al. 2016). While they were long thought to be part of the honeyeater (Meliphagidae) family, genetic analyses now place hihi as the sole extant member of Notiomystidae (Driskell et al. 2007). This family was nearly lost altogether when habitat loss, predation by introduced mammals, and disease drove hihi to mainland extinction around 1890. However, they persisted in a single remnant population (~3,100 individuals: Toy et al. 2018) on Te Hauturu ō Toi (Little Barrier Island Nature Reserve) and, over the past three decades, have been reintroduced successfully to seven additional sites (Ewen et al. 2013; Figure 1.1c). Nevertheless, habitat suitability has proven an ongoing barrier to achieving self-sustaining populations. All reintroduced populations (~40–250 individuals each) require habitat that is free of introduced mammalian predators and must be provisioned with sugar water to varying degrees throughout the year (Chauvenet et al. 2012; Thorogood et al. 2013; Doerr et al. 2017). Food limitation is a major challenge for species recovery, making foraging an important direction for research.

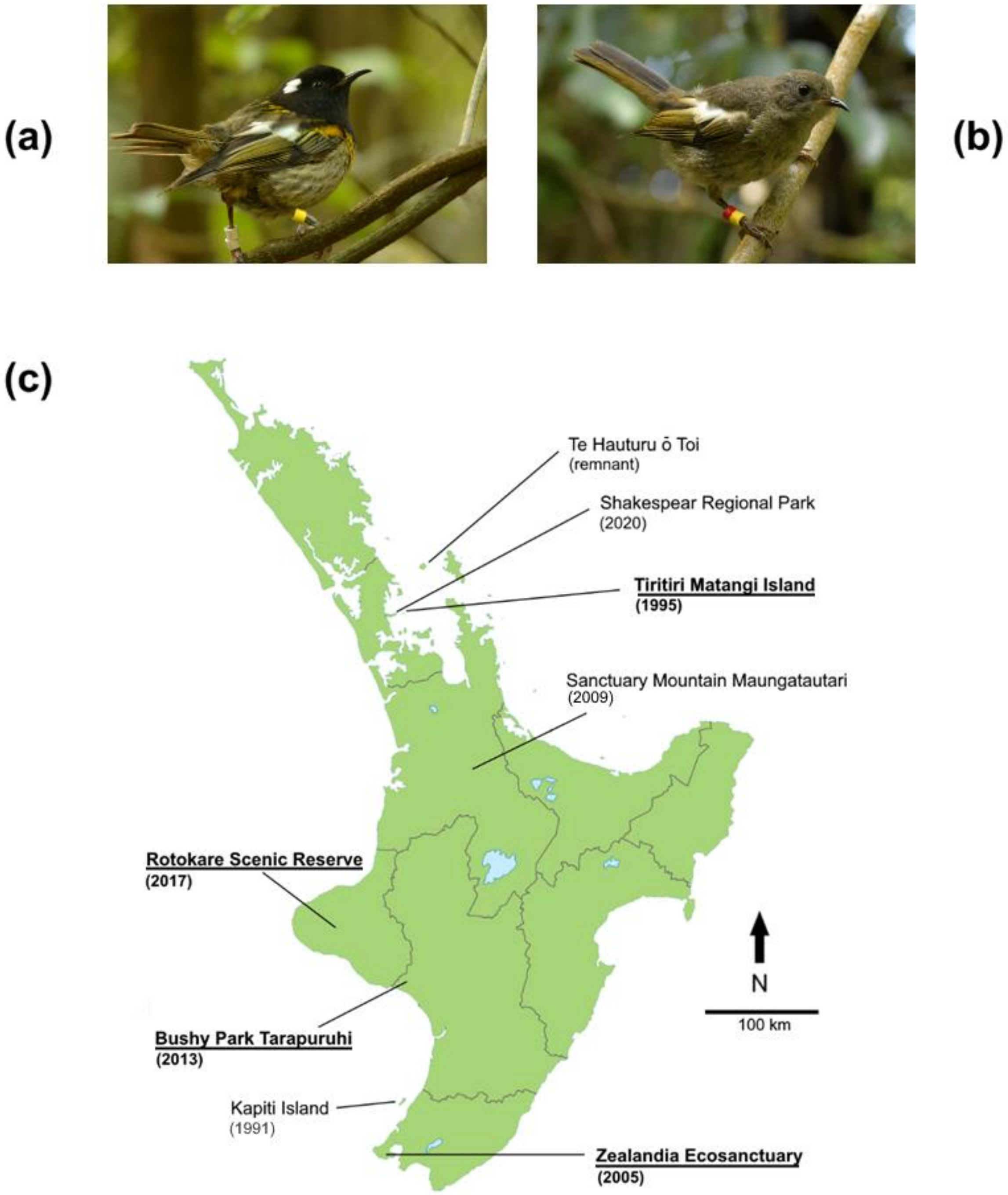

Figure 1.1. Adult (a) male and (b) female hihi. Most individuals in reintroduced populations (and all individuals in my main study population on Tiritiri Matangi Island) are color banded as nestlings to facilitate individual identification after fledging. (c) Map of the North Island of New Zealand showing the locations of all current hihi populations. Dates indicate year of establishment via translocation, except for the sole remnant population (Te Hauturu ō Toi). Study sites included in this thesis are underlined. Adapted from Thorogood et al. (2013). Photo credit: Christopher Stephens.

Most knowledge of hihi foraging comes from observations conducted on Te Hauturu ō Toi in the 1970s and 1980s. These studies revealed that the hihi diet consists of fruit, nectar, and invertebrates, with nectar use peaking at 56–75% of the diet in spring and dropping to 6% in autumn (Gravatt 1971; Angehr 1984; Rasch and Craig 1988). While less is known about the invertebrates consumed by hihi, they feed on numerous plant species exhibiting a wide range of fruit and flower forms (Castro and Robertson 1997; Perrott and Armstrong 2000). In addition to carbohydrates, these plants provide many vitamins and antioxidants known to improve hihi quality (Thorogood et al. 2013, Walker et al. 2014); therefore, although provisioned sugar water may act as a substitute energy source during times of resource scarcity (Chauvenet et al. 2012; Thorogood et al. 2013; Doerr et al. 2017), it does not replace the full suite of nutrients provided by natural foods. Preliminary results from my own fieldwork on Tiritiri Matangi Island confirm seasonal dietary trends. In autumn (my main study season), the species diet consists of 77% fruit (from 13 species), 11% nectar (from 10 species), and 12% invertebrates (Figure 1.2). In contrast, during the spring breeding season, the diet consists of 3% fruit, 70% nectar, and 27% invertebrates and is less diverse, with nectar from a single plant species (*Geniostoma ligustrifolium*) accounting for 65% of all observations (Figure 1.2). Thus, particularly during autumn, hihi consume a diverse array of foods: an important prerequisite for individual variation to arise.

In addition to their broad species diet, hihi exhibit several other traits expected to drive dietary specialization. First, they are sexually dimorphic, with males larger and more brightly colored than females (Low et al. 2006), so intrinsic dietary differences could exist between the sexes; previously, males have been found to seek out more carotenoid-rich foods than females during the molting period, which may be necessary to produce their yellow plumage (Walker et al. 2014). Other intrinsic differences may occur between age classes. Recently, juveniles and adults have been found to differ in their learning ability and foraging strategies (Franks and Thorogood 2018), which could affect their diets. Aspects of the social environment and ecosystem could also drive dietary differences. Hihi are highly territorial during the breeding season (Ewen et al. 2004), so, in heterogeneous environments, food availability may differ across territories. Dominance effects could also be particularly salient in hihi, as they exhibit intra- and interspecific dominance hierarchies, with the korimako (*Anthornis melanura*) and tūī (*Prosthemadera novaeseelandiae*) being their closest (and more dominant) competitors (Craig et al. 1981; Rasch and Craig 1988). While early researchers theorized that dominance could drive intraspecific dietary variation in all three species (Craig et al. 1981), and social behavior is an ongoing theme for hihi research (Richardson and Ewen 2016; Franks et al. 2019, 2020), the link between diet and sociality remains unexplored.

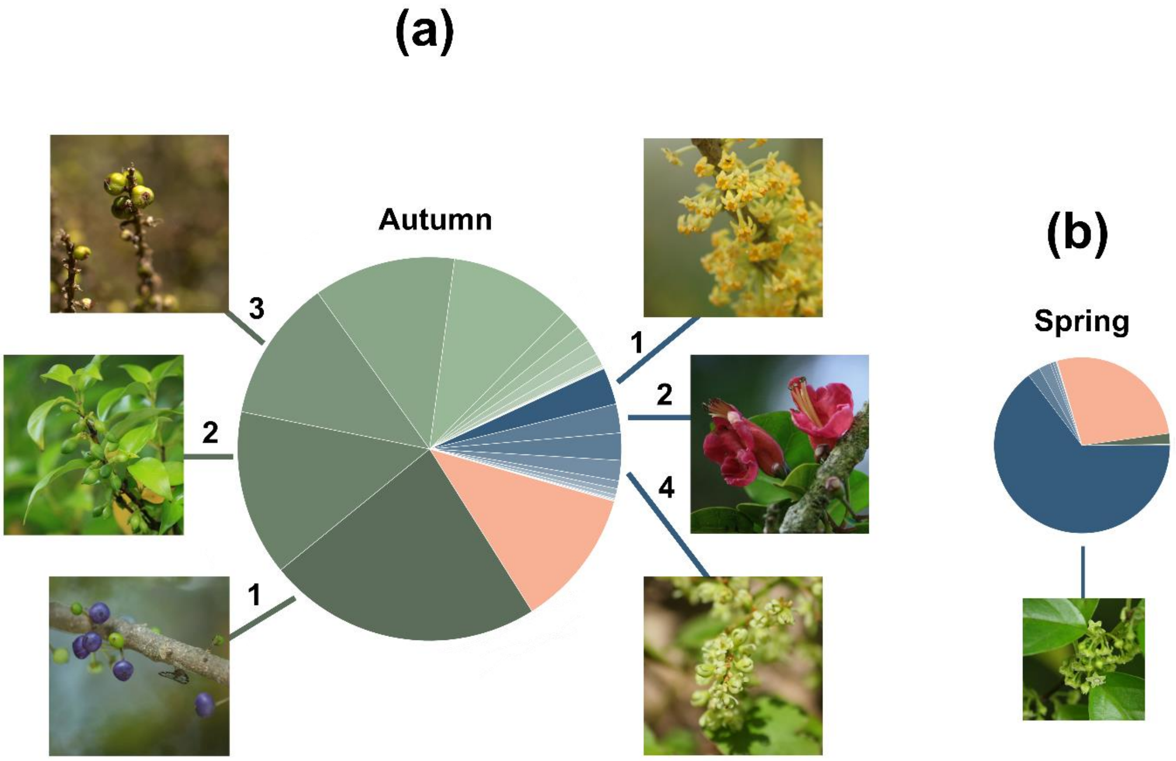

Figure 1.2. Seasonal composition of the hihi diet (from foraging observations described in Chapter 2 and repeated in Spring 2017). Pie charts show the relative proportional composition of fruit (green), nectar (blue), and invertebrates (peach), in (a) autumn and (b) spring. For fruit and nectar, each shaded section indicates one plant species; invertebrates were not classified to the species level. Photos show three of the top fruit (1: *Melicytus ramiflorus*, 2: *Geniostoma ligustrifolium*, 3: *Cordyline australis*) and nectar (1: *Melicytus ramiflorus*, 2: *Vitex lucens*, 4: *Muehlenbeckia australis*) sources in autumn; and the top nectar source (*Geniostoma ligustrifolium*) in spring. Photo credit: Ang Wickham.

A better understanding of hihi foraging at the individual level could benefit conservation efforts. Translocations are the main method of species recovery for hihi (Thorogood et al. 2013), and conservation biologists continuously seek ways to improve the viability of reintroduced populations. If individuals exhibit dietary specializations and these predict their fitness, translocations could selectively match individuals to release sites based on their dietary type, with the aim of improving survival and reducing dependence on supplementary feeding. This would require insight into the causes of dietary variation and whether moving to a new environment will change how individuals forage. Studies of dietary variation could also help conservation biologists expand the benefits of translocations beyond hihi. Alongside the decline of native avifauna, New Zealand plants have also declined precipitously in recent decades (Kelly et al. 2010). As their diet includes nectar from several threatened native plants, hihi are thought to be one of the most important endemic pollinators (Craig et al. 1981; S. Anderson 2003; Kelly et al. 2006; S. Anderson et al. 2011). Therefore, assessing their effectiveness as pollinators and whether individuals vary in their pollination ability could help to inform the design of translocations that promote broader ecosystem recovery goals.

In this thesis, I first adapt existing methodology for quantifying dietary variation to gain more reliable estimates from small sets of foraging observations. I then test whether dietary variation has any measurable consequences for hihi survival. Next, I explore the potential causes of dietary variation, focusing on social factors, both through a correlative study and by using translocations as experimental tests of changing social conditions. Finally, I use a pollinator exclusion experiment to evaluate the role of hihi in pollination, both at the species level and individual level. Most of this work was conducted within one hihi population on Tiritiri Matangi Island. This is an ideal study site, because all hihi nest in nest boxes, providing an opportunity to uniquely color band every chick so individuals can be identified after fledging. This population also serves as the main source population for translocations, and I was fortunate that my fieldwork coincided with three translocations: one to establish a new population at Rotokare Scenic Reserve in 2017, and two others to reinforce the Rotokare and Bushy Park Tarapuruhi populations in 2018. These provided unique opportunities to track changes in birds' foraging behaviors as they moved between sites.

1.2 HOW CAN WE IMPROVE EXISTING DIETARY METRICS?

Before exploring the causes and consequences of dietary variation, a critical step is ensuring that our dietary metrics are as reliable as possible. Despite the fact that dietary specialization has been measured in a range of taxa (Bolnick et al. 2003; Araújo et al. 2011), current methods are not amenable to all study systems. Stomach content (e.g. Bolnick and Paull 2009; Pires et al. 2011) and stable isotope analyses (Woo et al. 2008; Sheppard et al. 2018) can provide robust dietary estimates but may not be ethically or logistically feasible, particularly in threatened species. Observational data may be more practical but often yield small sample sizes when species are difficult to sight in the field. The challenge then lies in inferring dietary specializations from snapshots of individuals' foraging behaviors, which can lead to biased estimates when individuals vary in the duration of their foraging bouts, the number of times they were resighted, or the timing and location of their observations (Bolnick et al. 2002; Araújo et al. 2011). Common strategies for reducing these biases include counting only the first food eaten in each foraging bout (Araújo et al. 2011), excluding individuals if they fall below an arbitrary sample size cutoff (e.g. De León et al. 2012; Szigeti et al. 2018), or restricting analyses to individuals with similar ranging patterns (e.g. Tinker et al. 2008). However, all of these options for correcting bias reduce datasets that may already be limited, raising the question of whether alternative solutions can enhance the reliability of metrics while allowing more data to be retained.

In Chapter 2, I explore how the most common dietary specialization metric, the proportional similarity index (PS_i: Bolnick et al. 2002) can be made more amenable to small observational datasets using hihi as a case study. PS_i is a relative measure that ranks individuals along a specialist-generalist spectrum by comparing their diets to the average population member. However, it is vulnerable to overestimating specialization, particularly for individuals with few repeated observations (Bolnick et al. 2002; Araújo et al. 2011). Using foraging data I collected over two field seasons on Tiritiri Matangi Island, I first explore how the validity, reliability, and utility of PS_i can be improved by applying a Bayesian adjustment (adapted from Coblentz et al. 2017), accounting for the spatiotemporal availability of resources, and quantifying uncertainty. Then, finding evidence of dietary variation in hihi, I use this improved metric to test for a relationship between diet and survival.

1.3 HOW DOES DIET LINK TO SOCIAL FACTORS?

Among the many factors proposed to shape individuals' diets (Araújo et al. 2011; Phillips et al. 2017), social factors are some of the most complex to evaluate in natural settings, because they arise from a confluence of intrinsic and extrinsic elements. On the one hand, diet can be shaped by an individual's dominance and inherent sociality: dominants typically outcompete subordinates for preferred resources (Cody 1974; Whitten 1983; Gustafsson 1988; Holbrook and Schmitt 1992; Sol et al. 2005), and gregarious individuals tend to experience greater competition (Sheppard et al. 2018) but also more opportunities to pool information and foraging skills than solitary individuals (Morand-Ferron et al. 2016; Ashton et al. 2019). On the other hand, extrinsic social pressures imposed on all members of a population can also affect their foraging; for instance, while they may be free to act on their inherent resource preferences when unconstrained by competition, individuals often need to adjust their diets in dense populations or times of resource scarcity (Svanbäck and Bolnick 2005; Araújo et al. 2011; Tinker et al. 2012). Social influences on diet can also be challenging to evaluate in the field because diet can instead shape sociality (e.g. Beck et al. 2012) or be linked through a mediating factor (e.g. Aplin et al. 2014; Serrano-Davies et al. 2017) as part of a behavioral syndrome (Toscano et al. 2016). Experiments are needed to determine causality, but opportunities to observe dramatic social changes or directly manipulate social conditions are rare.

Hihi are an excellent system for exploring the potential links between diet and sociality. Not only do they forage socially on natural foods, where direct competitive interactions are relatively infrequent, but they also visit crowded supplementary feeding stations, where they encounter conspecific and heterospecific competitors. Thus, in Chapter 3, I use these two unique foraging contexts to examine whether individuals vary in their sociality while foraging and test whether this relates to the dietary specializations measured in Chapter 2. Given some evidence for a correlation, I then set out to experimentally test the causality between diet and social factors in Chapter 4. Conservation translocations provide a unique opportunity to test this in a natural setting, because individuals are typically moved from an established population to a less populated area, either to found a new population or reinforce an existing one (Ewen et al. 2012; IUCN/SSC 2013). By tracking changes in the diets of hihi as they either remain at their natal site or move to a much less competitive site, I measure the effects of competitive release on diet at the population, cohort, and individual levels.

1.4 HOW DOES FORAGING INFLUENCE THE ECOSYSTEM?

While much of the interest in behavioral variation surrounds its consequences for individuals, there is increasing recognition that individual variation can scale up to shape broader ecological dynamics (Bolnick et al. 2011; Raffard et al. 2017). Foraging behavior seems an ideal candidate, as it underlies many important interspecific interactions, including predation, competition, and mutualisms (Stephens and Krebs 1986; Perry and Pianka 1997; Stephens et al. 2007). Thus, if individuals vary in their diets and foraging patterns, they may also differ in their contributions to these ecological functions. For instance, in seed dispersing species, individuals can vary in their consumption, dispersal, and digestion of seeds, with implications for plant recruitment (Zwolak 2018; Snell et al. 2019). Such links between individual variation and ecosystem health are particularly crucial to explore today, given that some of the most devastating species declines are those that disrupt ecological functions (Eklöf and Ebenman 2006; Tylianakis et al. 2008; Brodie et al. 2014). Translocations have historically been aimed at species recovery but are increasingly used to achieve broader restoration goals, such as when species are reintroduced to ‘rewild’ a landscape, or non-native species are introduced as ‘ecological replacements’ for extinct species (Lunt et al. 2013; Seddon et al. 2014; Pettorelli et al. 2019; Seddon and Armstrong 2019). On a most basic level, understanding the effectiveness of a species at performing its ecological role is essential to ensure these efforts achieve their restoration goals. But if individuals also vary in their effectiveness, this could provide greater control over the success of these efforts, as individuals could be translocated selectively, based on their functional efficiency.

As known pollinators of several native plants (Craig et al. 1981; S. Anderson 2003; Kelly et al. 2006; S. Anderson et al. 2011), hihi are often translocated with ecosystem recovery in mind (Smuts-Kennedy 2009; Frost 2012; Collins et al. 2015), but translocation planning and monitoring typically focus on species recovery goals. In Chapter 5, I use a pollinator exclusion experiment to quantify differences in pollination outcomes across hihi territories at my main study site of Tiritiri Matangi Island and test whether these differences are explained by the territory holders’ performance in a novel foraging task. In Chapter 6, I broaden out to the species level and compare pollination outcomes across sites with and without hihi. Combined, these studies aim to challenge our implicit assumptions that all hihi are equally effective pollinators and that adding hihi to a system achieves its intended ecosystem restoration goals.

1.5 THESIS OVERVIEW

Apart from the General Introduction and Discussion, each chapter in this thesis has been prepared as a manuscript so is written in first person plural perspective, with some methodology repeated. Appendix 1 contains all supplementary materials referred to in the text, as well as details of permits. Chapter 2 has been published in *Ecosphere* in 2020 (Andrews et al. 2020).

Each chapter focuses on one of the questions outlined above, but, together, they combine to explore diet's role in a broader ecological feedback loop, as illustrated in Figure 1.3. If social factors shape individuals' diets and foraging behaviors (Chapters 3 and 4), and these, in turn, shape the ecosystem (Chapters 5 and 6), the question then arises of whether the ecosystem influences social conditions. While not explicitly explored here, this final link is well-established: the abundance and distribution of resources are known to influence competition and social interactions (Crook and Gartlan 1966; S. Emlen and Oring 1977; Terborgh and Janson 1986). Thus, in the General Discussion, I will reflect on the two links tested in this thesis to evaluate diet's role in the feedback loop, while also considering how this information can be applied to conservation.

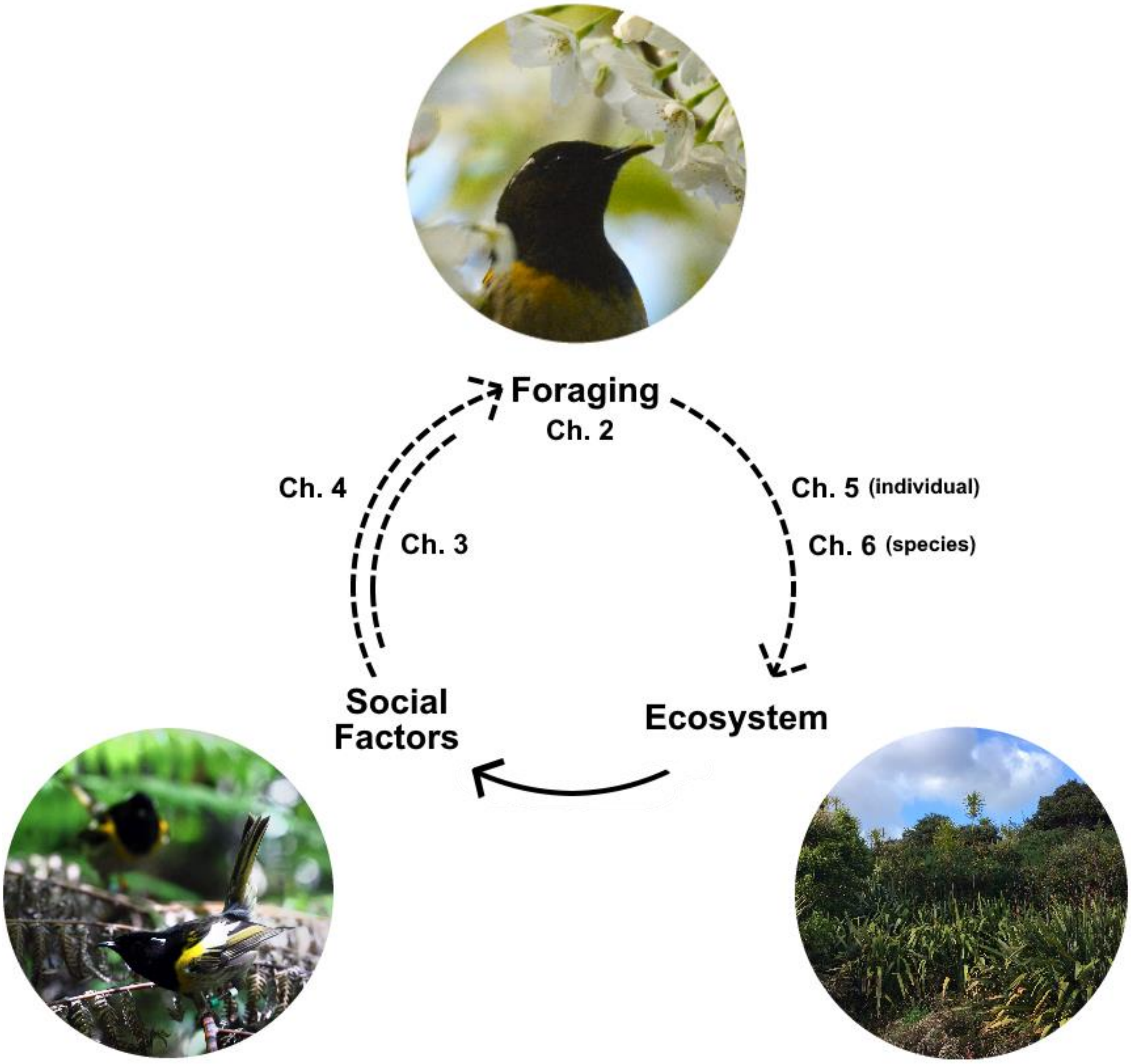

Figure 1.3. Overview of thesis chapters and objectives. Chapter 2 aims to enhance existing dietary specialization metrics. Chapters 3 and 4 then use these improved metrics to explore links between social factors and dietary variation, with Chapter 4 explicitly testing social effects on diet. I then explore the impacts of foraging—first, at the individual level (Chapter 5), and then at the species level (Chapter 6)—on the ecosystem. The link between the social environment and ecosystem is well-established in the behavioral ecology literature and not explicitly tested here. Photo credits: Christopher Stephens (top), Stuart Attwood (bottom left), CA (bottom right).

Chapter 2

Enhancing dietary specialization metrics in observational studies of wild animal populations

Caitlin E. Andrews, John G. Ewen, & Rose Thorogood (2020) *Ecosphere* 11(9):e03255

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Studies of intraspecific dietary variation can greatly enrich our view of a species' niche and role in the ecosystem, particularly when species with broad diets are found to be composed of generalist and specialist individuals. However, the current framework for quantifying dietary specialization leaves certain standards unformalized and is susceptible to overestimating specialization when there are few repeated observations per individual, as is often the case in observational studies of wild populations. Here, we use the hihi (*Notiomystis cincta*), a threatened New Zealand passerine, as a case study for demonstrating how existing statistical tools can be applied to strengthen the dietary specialization framework. First, we assess whether the reliability of common dietary measures can be improved through Bayesian adjustments and by using rarefaction to compare uncertainty levels of metrics calculated from different sample sizes. As diet links closely to environmental factors, we also demonstrate how adding phenological data and habitat assessments to standard protocols can help validate our dietary measures as evidence for resource selection rather than random foraging. Finally, in light of our finding that diet predicts survival in hihi, we discuss the utility of dietary specialization for elucidating broader behavioral syndromes.

2.1 INTRODUCTION

Among behavioral ecologists, there is a growing interest in measuring behavioral variation within species (Sih et al. 2004; Dall et al. 2012; Brommer and Class 2017). Diet is one trait that has been found to vary individually in many taxa, enhancing our view of species' niches and roles in the ecosystem (Bolnick et al. 2003; Araújo et al. 2011; Troxell-Smith and Mella 2017). Most studies quantify dietary variation using the proportional similarity index (PS_i: Bolnick et al. 2002), which measures individuals' dietary similarity to the population as a whole. Specialists on a single food receive a PS_i equal to that food's proportional representation in the population diet; meanwhile, extreme generalists consume all foods in the same proportions as the population as a whole and receive a PS_i of 1. However, even within this widely applied framework, certain standards remain unformalized: namely, (1) how many observations per individual are needed to achieve reliable measures of diet; (2) how to ensure the validity of these metrics as evidence for dietary preferences; and (3) how to account for measurement uncertainty when evaluating diet's utility as an ecologically informative trait. Addressing these limitations will help to ensure that our shared dietary framework yields comparable measures across studies.

Advocates of PS_i caution that it can overestimate specialization in individuals with few repeated observations (Bolnick et al. 2002; Araújo et al. 2011). But without a formal criterion, sample sizes vary widely throughout the literature. Often, the largest datasets come from studies conducted in captivity or using advanced technologies such as stable isotope analysis or remote tracking. For example, Tinker et al. (2012) used radio telemetry to track southern sea otters (*Enhydra lutris nereis*) over six years, recording more than 60,000 feeding dives across 74 individuals. However, these methods are not suitable for all species. Direct observation remains a valuable method for collecting detailed foraging records but often yields small sample sizes in species that are challenging to observe in the field. Nevertheless, measuring specialization could be important even when these data are difficult to collect, as dietary variation can be used to predict a population's viability (Bolnick et al. 2003; Colles et al. 2009; Clavel et al. 2011) and model its effects on ecosystem health (Bolnick et al. 2011; Raffard et al. 2017).

These benefits make it worth asking whether we can quantify or even correct for uncertainty in dietary estimates derived from small sample sizes. Currently, some studies exclude individuals falling below an arbitrary sample size cutoff (e.g. 6 in De León et al. 2012; 8 in Szigeti et al. 2018), but this can significantly reduce statistical power, particularly in field studies where sample sizes may already be limited (Garamszegi 2016). Existing statistical tools may enable us to retain more individuals. Coblentz et al. (2017) propose a Bayesian hierarchical method that shifts individuals' PS_is toward the population mean by an amount inversely proportional to their sample size; this helps to account for the uncertainty in inferring 'true' diets from a small number of observations. To measure the reliability of these 'Bayesian PS_is,' they suggest recalculating the PS_is of the most frequently observed individuals across a range of simulated sample sizes. Using this rarefaction procedure, Coblentz et al. demonstrate that the Bayesian method estimates diet reliably even at their lowest simulated sample size of five foods, while 'unadjusted' PS_is consistently overestimate specialization below 50 foods. However, this reliability test was used only on simulated data. Applying it to real-world data is an important next step toward integrating Bayesian methods into the dietary specialization framework.

Once we are confident in the reliability of our behavioral measure, we still need to ensure that it truly captures our trait of interest (i.e. is 'valid': Martin and Bateson 1993). This is especially key for traits like diet that are closely linked to extrinsic factors. PS_is are often interpreted as reflecting individuals' intrinsic preferences when dietary variation could also arise from unequal access to resources (Bolnick et al. 2003; Araújo et al. 2011). In heterogeneous environments, individuals may be exposed to different resources through their ranging patterns (Buskirk and Millspaugh 2006; Coblentz 2020; Cunningham et al. 2018). This effect can be compounded by phenological changes. For example, Szigeti et al. (2018) found that pairs of Apollo butterflies (*Parnassius mnemosyne*) had more similar diets the closer in time they were observed to one another, suggesting that phenology at the time of observation can significantly influence diet scores. Yet, studies of dietary variation rarely include detailed habitat or phenology assessments. In a review of 87 resource selection studies, only 26% measured resource availability at the individual level (Thomas and Taylor 2006). These data could be important for validating our dietary metrics, allowing us to determine whether individuals have dietary preferences or are merely sampling foods randomly in proportion to their availability.

Finally, a crucial step in placing dietary variation in a wider context is evaluating its utility as an ecologically informative trait. This could be particularly beneficial for species of conservation concern. Many threats are so urgent that even traits predicting fitness in the short-term could help conservation biologists tailor their management interventions to individuals' needs (see Arcese 2003 for an opposing view). Because diet underlies some of the most fundamental ecological interactions, variation can also scale up to affect other species through competition, predation, and mutualisms (Bolnick et al. 2011; Dupont et al. 2011; Dall et al. 2012; Phillips et al. 2017; Raffard et al. 2017); thus, diet studies could also inform strategies for ecosystem restoration. However, just as studies quantifying dietary variation should account for uncertainty, so, too, should studies examining the potential consequences of diet. This could be especially important in survival analyses, as factors driving uncertainty in dietary metrics may be confounded with individual health. For example, diseased individuals may be easier or more difficult to observe depending on how their illness affects their mobility or conspicuousness. As small sample sizes can lead to overestimates of specialization (Bolnick et al. 2002; Araújo et al. 2011), this could lead to a false correlation between diet and survival if uncertainty is not accounted for.

In this study, we use the hihi (*Notiomystis cincta*), a threatened passerine endemic to New Zealand, as a case study to demonstrate how some of the current limitations to the dietary specialization framework can be addressed using existing analytical tools. Hihi have a broad species-level diet including fruit, nectar, and invertebrates (Rasch and Craig 1988), but early researchers hypothesized that individual diets may vary (Craig 1985), and there is some evidence that the sexes exhibit seasonal differences in resource use (Walker et al. 2014). Hihi also meet many criteria predicted to drive specialization (Bolnick et al. 2003; Araújo et al. 2011): their physiological needs change with age, they exhibit inter- and intraspecific dominance hierarchies, and their territories vary in quality (Thorogood et al. 2013). Because of their conservation status, hihi are closely monitored, making it possible to study individual behavioral differences and track long-term survival. Here, we begin by showing that individuals vary in their diets. We then go on to test (1) what dietary metrics and sample sizes yield reliable estimates; (2) whether dietary differences reflect individual preferences; and (3) whether diet predicts survival.

2.2 METHODS

Study site and population

Tiritiri Matangi Island (36°36'00.7"S 174°53'21.7"E) is a 220-hectare nature reserve located 3.5 km off the coast of New Zealand’s North Island. After being cleared for pastureland and farmed for over a century, the island was extensively replanted in the 1980s. Today, the vegetation consists of regenerating native bush with small patches of remnant mature forest. The island has been free of introduced mammalian predators since 1993, and hihi were reintroduced from Te Hauturu ō Toi (Little Barrier Island Nature Reserve) two years later. During our study, the population numbered ~170 adults. Every breeding individual nests in an intensively monitored nest box, so all chicks are of known age. Individuals are classed as juveniles after fledging in summer until they become adults in the following spring breeding season. At 21-days old, each nestling is given a unique combination of colored leg bands to facilitate individual identification after fledging, and sex is determined based on early signs of sexually dimorphic plumage (C. Smith et al. 2015). While the population's productivity is enhanced by the provision of sugar water (D. Armstrong and Ewen 2001), hihi preferentially select natural foods when they are sufficiently available. Therefore, we chose to focus on natural foraging behaviors for the purposes of this study.

Foraging observations

Foraging observations were conducted by a single observer (CA) from 24th January–18th March 2017 (215 hours) and 4th February–21st March 2018 (230 hours), coinciding with the end of the hihi breeding season. The observer walked transects which were evenly distributed across the island (Figure 2.1a) and included areas of high hihi presence (14 km; walked three times weekly) and low hihi presence (6 km; walked once weekly), as determined from regular population monitoring. Morning (c. 8:00–12:30) and afternoon (c. 12:30–16:30) sessions were balanced for each transect.

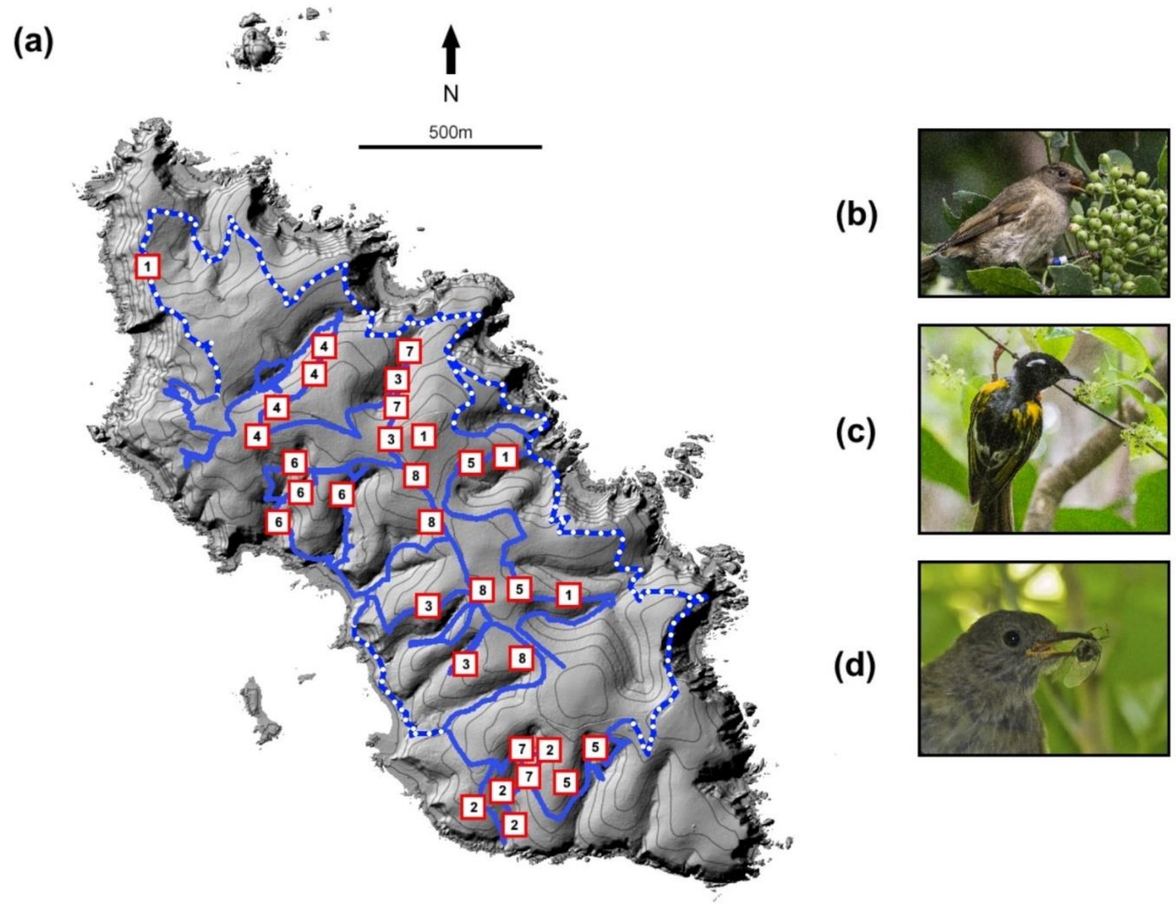

Figure 2.1. (a) Contour map of Tiritiri Matangi Island (from data obtained and modified from Land Information New Zealand Data Service on 1 July 2019) with foraging transects marked with blue lines (solid = high hihi presence; dotted = low hihi presence). Boxes indicate the locations of habitat assessment plots, with numbers corresponding to the habitat types in Supplementary Table 2.1. Hihi photos show examples of (b) a female foraging on houpara (*Pseudopanax lessonii*) fruit (photo by Martin Sanders), (c) a male foraging on hangehange (*Geniostoma ligustrifolium*) nectar (photo by Martin Sanders), and (d) a juvenile eating a cicada (Hemiptera: Cicadidae; photo by Steve Attwood).

During each session, the observer walked at a constant rate until a hihi was seen or heard within 10 meters of the transect. If the bird could be located within 10 minutes, the observer noted the individual's band combination, recorded the local habitat type (from eight predefined, visually-distinct categories; Supplementary Table 2.1), and began a focal follow of the individual. Feeding events were recorded *ad libitum*, with each food classified as a fruit, nectar, or invertebrate (Figure 2.1b–d); while plant foods were identified to species level, invertebrates could not be classified more precisely because of their small size and the distance between the observer and focal birds. When multiple birds were in view, the group was scanned to capture as many foods eaten as possible. Focal individuals were abandoned if they moved too quickly to follow through the dense understory, or if they became inactive (preening or resting) or moved out of sight for five minutes.

Habitat assessments and phenology

To assess the abundance of each known hihi food plant expected to have fruits or flowers available during the study period (determined from Perrott and Armstrong 2000 and personal communications with site managers; Supplementary Table 2.2), we conducted habitat assessments and phenological surveys. For each of the eight habitat types, we selected four representative plots distributed as evenly across the island as possible (Figure 2.1a). In each plot, we designated five 25 m sampling lines radiating evenly from a central point. Every 5 m along each line, we counted and identified (to species level) all plants of reproductive size within a 1 m radius. This resulted in 25 sampling points per plot, or 100 per habitat type. The counts for each species were then summed across these 100 sampling points to arrive at a measure of abundance for each food plant within each habitat type. Next, 15 specimens (or fewer if unavailable) were selected for each food plant species and as evenly distributed along the foraging transects as possible. Once every two weeks, we estimated the numbers of fruits and flowers on each plant (following the methods of Perrott and Armstrong 2000) and averaged these values across all monitored specimens of that species. We multiplied this number by our species counts within each habitat type to calculate an absolute abundance for each food item in each habitat type for a given two-week period. We converted this to a relative abundance by dividing by the total number of food items of all types available in that habitat type and time period.

Population surveys

Ongoing management of the Tiritiri Matangi hihi population includes biannual, constant-effort (about 40 hours in five days) surveys in September and February, in which an experienced observer attempts to sight as many individuals as possible. For the purposes of this study, two additional surveys of about 40 hours each were completed in April and May.

Data analysis

All analyses were conducted in R (version 3.5.1; R Core Team 2018) unless noted otherwise. When means are reported, they are accompanied by their standard errors.

Foraging Variation

Within each season, we tallied foods eaten by type and calculated two dietary specialization metrics for each bird we observed. First, we used the R package RInSp (version 1.2.3; Zaccarelli et al. 2013) to calculate a proportional similarity index (‘unadjusted PS_i’) for each individual (Bolnick et al. 2002). When calculating the population diet, we avoided giving greater weight to birds that were observed eating more foods by using the averaging method proposed by Zaccarelli et al. (2013). This method first calculates each individual’s proportional use of the various food types, then averages these proportions across all individuals to arrive at the population diet. Each individual’s diet is then compared to the population diet to assign the individual a PS_i, calculated as:

$$1 - 0.5 \sum_j \left| p_{ij} - q_j \right|,$$

where p_{ij} is the proportional use of food type *j* by individual *i* and q_j is the proportional use of food type *j* by the average population member (Bolnick et al. 2002). We also calculated an adjusted ‘Bayesian PS_i’ for each individual following the methods of Coblentz et al. (2017). We modified this method to match the population diet averaging technique described above, as the original version was less suited to populations with highly variable sample sizes per individual (Zaccarelli et al. 2013).

To assess the degree of variation in the population, we calculated the means and standard errors for unadjusted and Bayesian PS_i scores in each year. The RInSp package tests the significance of specialization by comparing these means to 10,000 means calculated through a Monte Carlo resampling procedure in which all foods eaten by the population are randomly redistributed across individuals. We also compared PS_i distributions between years and methods using Student's *t*-tests where distributions were normal and variances were equal, and Welch's *t*-tests where distributions were normal but variances unequal.

Because our classification of invertebrates as a single food type could affect the accuracy of our dietary estimates, we recalculated Bayesian PS_is using only plant foods for individuals that ate some (but not only) invertebrates. These were highly correlated ($r = 0.94$, $P < 0.001$) to the PS_is including invertebrates. Combined with the fact that invertebrates comprised only a small portion of foods eaten in each year (about 12%; result not presented), this suggested that retaining individuals with invertebrates in their diets would not affect further analyses. However, because we could not check this correlation for individuals that only ate invertebrates, we excluded these individuals ($n_{2017} = 11$, $n_{2018} = 19$) from all remaining analyses.

Reliability

To determine how many foods are needed to achieve reliable measures of diet, we carried out a rarefaction procedure (similarly to Coblentz et al. 2017) with the 47 birds from our 2018 dataset that had been observed eating at least 20 food items (we did not use 2017 data, as only one bird met this criterion). For every $\boldsymbol{x} \leq 20$, we randomly resampled $\boldsymbol{x}$ foods from each bird's observed diet and used these simulated diets to recalculate their unadjusted PS_is. We chose not to update the population diet in these recalculations, because we made the simplifying assumption that our observed population diet was an accurate representation of the true population diet. We repeated the resampling procedure 100 times, then conducted a paired *t*-test comparing each individual's mean simulated PS_i with their original PS_i. We repeated the entire rarefaction procedure using the Bayesian PS_i method.

We assessed the reliability of our dietary measures using two criteria. For Criterion 1, we examined the *P*-values from the paired *t*-tests and accepted sample sizes yielding simulated PS_is that, on average, did not differ significantly ($P \geq 0.05$) from the original PS_is. However, an average difference of zero says nothing about the magnitude of these differences. Therefore, for Criterion 2, we quantified the magnitude percent difference between each individual's simulated PS_i and original PS_i, calculated as:

$$\left|\frac{simulated\ PS_i - \ original\ PS_i}{original\ PS_i}\right| \times 100$$

and calculated the mean across individuals for each simulated sample size. To reduce the likelihood that individuals' original sample sizes would significantly impact their PS_i rank relative to other individuals, we *a priori* designated a maximum acceptable threshold of 18.15%, which represented half of the average between-individual difference in original PS_i scores (36.30%;

result not presented). Thus, all simulated sample sizes with a mean magnitude percent difference no greater than 18.15% were considered to have satisfied Criterion 2. After applying both reliability criteria, we repeated our assessment of population-level specialization in each year as before and compared our new mean PS_i estimates to our previous estimates using *t*-tests.

Validity

We investigated whether the observed dietary variation was a reflection of individual preferences or random sampling of available foods. In other words, birds could vary in their visitation rates to different habitat types but indiscriminately eat the foods they encounter in them. If so, we would expect birds' diets to match the resource availability that they uniquely experience based on their use of different habitats and the phenology at the time they visit.

Because phenology data were only available for fruits and flowers, we excluded invertebrates from these analyses. From the remaining observations, we noted the habitat type that each feeding event occurred in. For each bird that met our reliability cutoff (five foods eaten; see Results), we tallied their use of each habitat type within each two-week period. We multiplied these values by the proportional availability of each food in each habitat type during that period (from our phenology data) and summed across all periods to arrive at an experienced abundance of each food item for each bird. This represented their expected diets if they were randomly eating foods in proportion to their availability. Note, any food types that were not detected in phenology assessments during a two-week period were given an arbitrarily low proportional availability (10^{-6}) to avoid calculation errors due to values of 0.

In the adehabitatHS package (version 0.3.14; Calenge 2006), the compana function uses a Wilks' lambda to assess whether a population exhibits habitat selection. Here, we adapted it for resource selection by comparing individuals' observed diets to their expected diets if they were foraging randomly. As our dataset follows the structure of a Design III resource selection model (i.e. resource use and availability measured at the individual level; Manly et al. 1993), we also used the widesIII function as an additional, χ^2-based measure of population-wide resource selection and a test for resource selection at the individual level.

Utility

We tested whether dietary specialization could be used to predict survival in hihi. As dominance of different age-sex classes may influence the effects of dietary specialization on survival (Whitten 1983; Langen and Rabenold 1994; Dennehy 2001), we conducted a preliminary

analysis (using Akaike information criterion model selection: Symonds and Moussalli 2011; Mazerolle 2017) to assess whether PS_i varied by age or sex. As we found only weak evidence (a model containing an interaction between age and sex was within 2 AIC_c units of the null model; Supplementary Table 2.3), we did not consider age or sex in any further analyses.
For each bird that met our reliability cutoff ($n_{2017} = 25$; $n_{2018} = 82$) and that remained in the population following conservation translocations to other populations (21 birds observed were removed in 2017, 33 in 2018; Franks et al. 2019), we used our population survey data to construct an encounter history. We analyzed the two years separately, with any birds seen in both years appearing as two separate entries: one associated with their 2017 PS_i and one associated with their 2018 PS_i. Birds were noted present in February of the year they were observed and either present (1) or absent (0) in the following April, May, September, and February surveys.

Using a live-recaptures model (Cormack-Jolly Seber, CJS) in Program MARK (version 6.2; White and Burnham 1999), we tested the dietary and time dependence of monthly survival probability (ϕ) (for each inter-survey interval) and resighting probability (ρ) (for each sampling occasion). Our global model explaining individuals' encounter histories was $\phi(PS_i * \text{time})\rho(PS_i * \text{time})$, which we compared to successively reduced models using Akaike information criterion (AIC_c) values. AIC_cs for the 2017 model selection were corrected for a small degree of overdispersion ($\hat{c} = 1.10$) using quasi-likelihood AIC_cs ($QAIC_c$s). Goodness-of-fit testing indicated underdispersion ($\hat{c} < 1$) for the 2018 model selection, so we did not apply any corrections, following common practice for Program MARK. When two or more models emerged as equally well-supported ($\triangle(Q)AIC_c < 2$), we used model averaging to examine the relationship between PS_i and monthly survival during the first three inter-survey intervals; otherwise, we extracted estimates from the single top model. Using these monthly estimates, we calculated seven-month (February–September) survival estimates for each study year. 95% confidence intervals (restricted between 0 and 1) were derived in R by applying the delta method (Powell 2007) to the confidence intervals of the monthly estimates using the msm package (Jackson 2011, version 1.6.2).

To account for the uncertainty inherent to the Bayesian PS_i method, we repeated our survival analyses using modified PS_i scores. Each PS_i was randomly increased or decreased by a percentage within the 95% confidence interval of the mean magnitude percent difference for the individual's sample size of foods eaten (see Results). For individuals with sample sizes greater than 20 (the maximum tested in our rarefaction procedure), the 95% confidence interval for a sample size of 20 was used. This procedure represents a more conservative estimate of the relationship between survival and PS_i.

2.3 RESULTS

Foraging variation

In 2017, 127 individuals (45 females, 82 males; 75 juveniles, 52 adults) were observed eating 538 food items of 15 types (Supplementary Table 2.2) over 364 discrete encounters (totaling 22 hours). In 2018, 164 hihi (69 females, 95 males; 84 juveniles, 80 adults) were observed eating 2,362 food items of 23 types (Supplementary Table 2.2) over 838 discrete encounters (totaling 66 hours). The number of foods eaten per individual varied widely in each year (1–30 in 2017, 1–88 in 2018), with most falling toward the lower ends of these distributions ($\bar{x}_{2017}$ = 4.24 ± 0.41; $\bar{x}_{2018}$ = 14.40 ± 1.11; Figure 2.2). The number of discrete encounters per bird was also highly variable, ranging from 1–14 in 2017 ($\bar{x}$ = 2.87 ± 0.20) and 1–17 in 2018 ($\bar{x}$ = 5.11 ± 0.32).

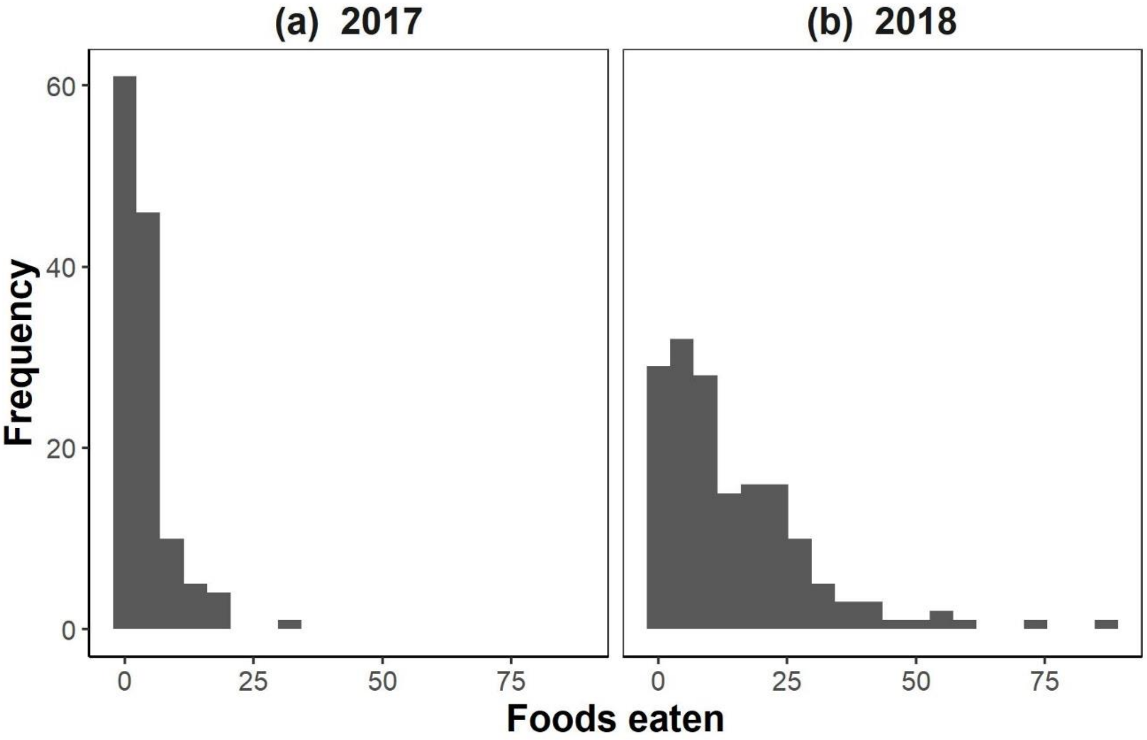

Figure 2.2. Distribution of the number of foods eaten per individual in (a) 2017 and (b) 2018.

In both years, dietary variation differed significantly from what would be expected by chance (Monte Carlo $P < 0.001$), regardless of the method used to calculate PS_i. Individuals were somewhat specialized ($PS_i < 0.5$) on average, with a mean unadjusted PS_i of 0.22 ± 0.01 in 2017 and 0.30 ± 0.01 in 2018, and mean Bayesian PS_i of 0.45 ± 0.01 in 2017 and 0.42 ± 0.09 in 2018 (Figure 2.3). The population was significantly more specialized in 2017 than in 2018 whether unadjusted PS_is (Student's *t*-test: $t = -4.64$, df = 289, $P < 0.001$) or Bayesian PS_is (Welch's *t*-test: $t = 3.17$, df = 255.49, $P = 0.002$) were used. The Bayesian method consistently yielded less specialized estimates (higher PS_is) than the unadjusted method in both 2017 (Welch's *t*-test: $t = 17.22$, df = 168.76, $P < 0.001$) and 2018 (Welch's *t*-test: $t = 8.02$, df = 301.38, $P < 0.001$).

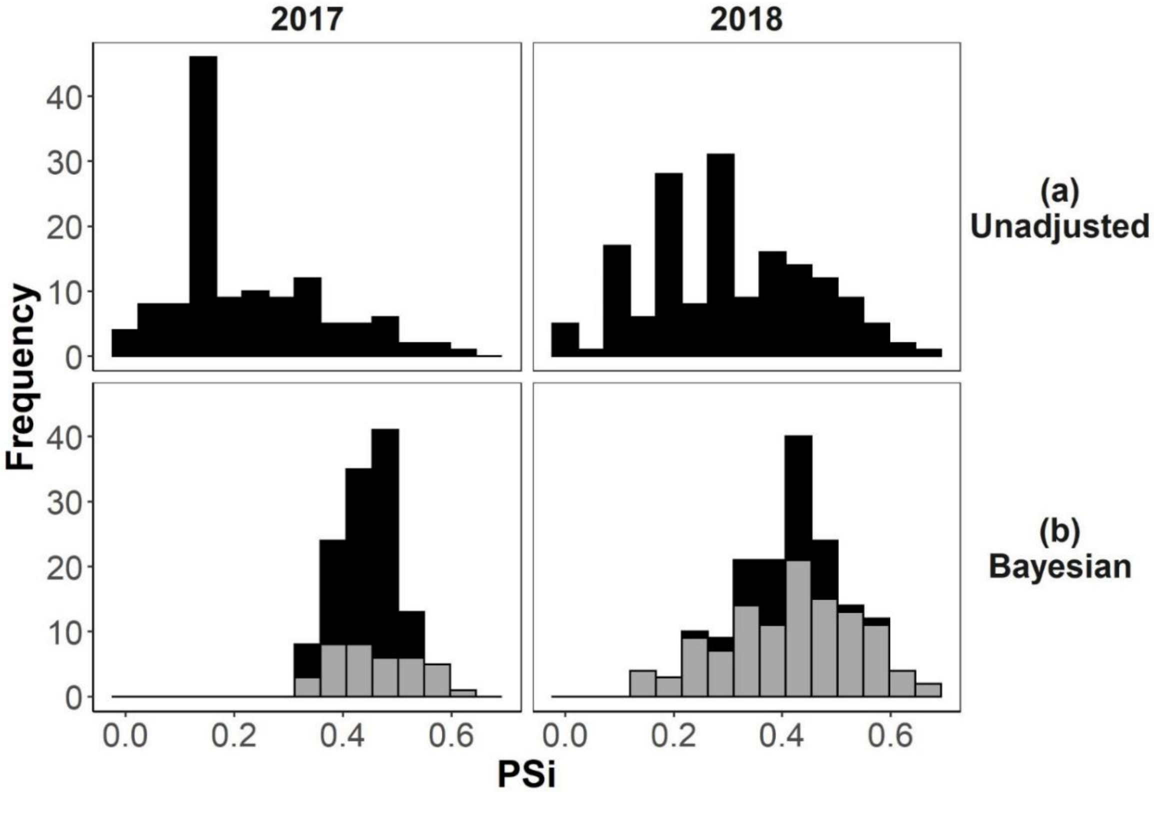

Figure 2.3. Distribution of dietary specialization scores in 2017 and 2018 calculated as (a) unadjusted PS_is and (b) Bayesian PS_is. In (b), distributions show PS_is before (black bars) and after (gray bars) the reliable sample size cutoff of five foods eaten was applied.

Reliability

The unadjusted PS_i method consistently overestimated specialization (underestimated PS_i) at all simulated sample sizes ($\bar{x}_{\text{simulated}} < \bar{x}_{\text{original}}$, $P < 0.05$ for all paired t-tests; Figure 2.4a). In contrast, while the Bayesian method underestimated the range of PS_is in the population at low sample sizes, it satisfied Criterion 1 at all sample sizes by accurately estimating the population mean ($P > 0.05$ for all paired t-tests; Figure 2.4b). For both methods, sample sizes of five or more foods satisfied Criterion 2 by yielding PS_i scores that were on average less than 18.15% different from their corresponding original PS_is (Figure 2.5). However, as only the Bayesian method met Criterion 1, we applied a cutoff of five foods eaten and used only Bayesian PS_is in further analyses. Thirty-seven individuals met the reliability cutoff in 2017 and 114 individuals in 2018. Applying this cutoff did not change the mean Bayesian PS_i significantly in 2017 (Welch's t-test: $t = -0.78$, df = 47.72, $P = 0.44$) or 2018 (Student's t-test: $t = 0.04$, df = 276, $P = 0.97$; Figure 2.3b), but it raised the mean number of discrete encounters per bird to 4.78 ± 0.46 in 2017 and 6.13 ± 0.34 in 2018.

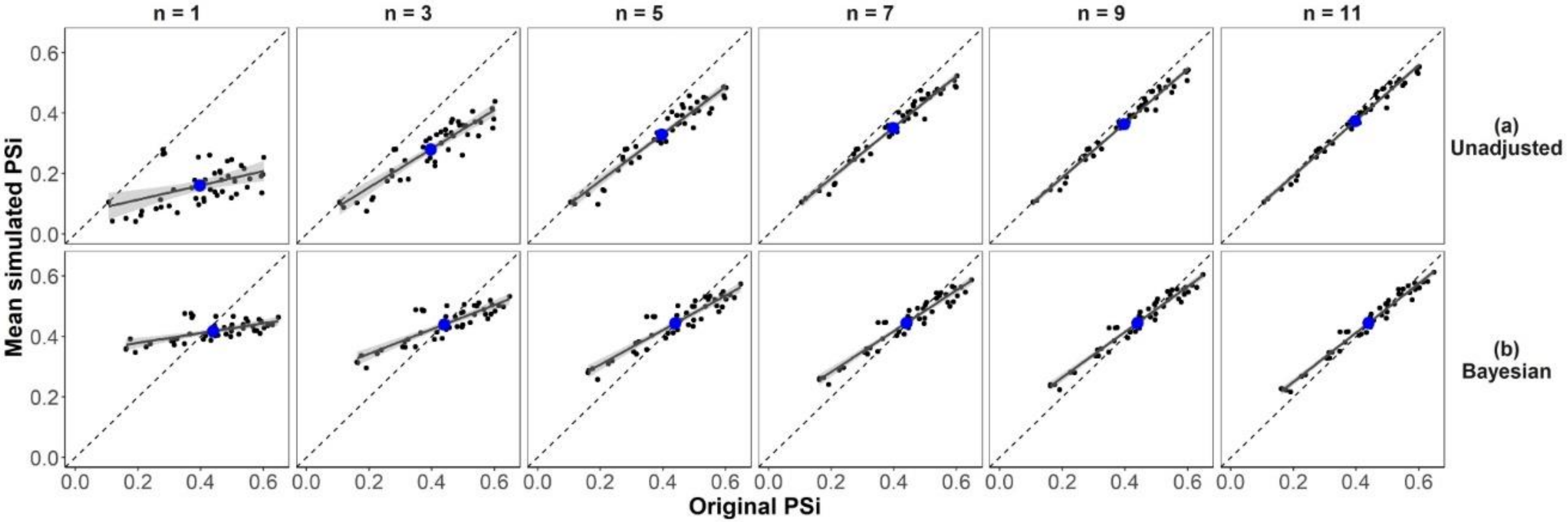

Figure 2.4. Relationship between the original PS$_i$s (calculated from the full dataset) and mean simulated PS$_i$s (calculated from simulated diets of *n* foods eaten) using (a) the unadjusted PS$_i$ method and (b) the Bayesian PS$_i$ method. Dotted lines indicate equality between the original PS$_i$ and simulated PS$_i$ values. Solid lines are regression lines with 95% confidence intervals shaded in gray. Blue dots represent population means.

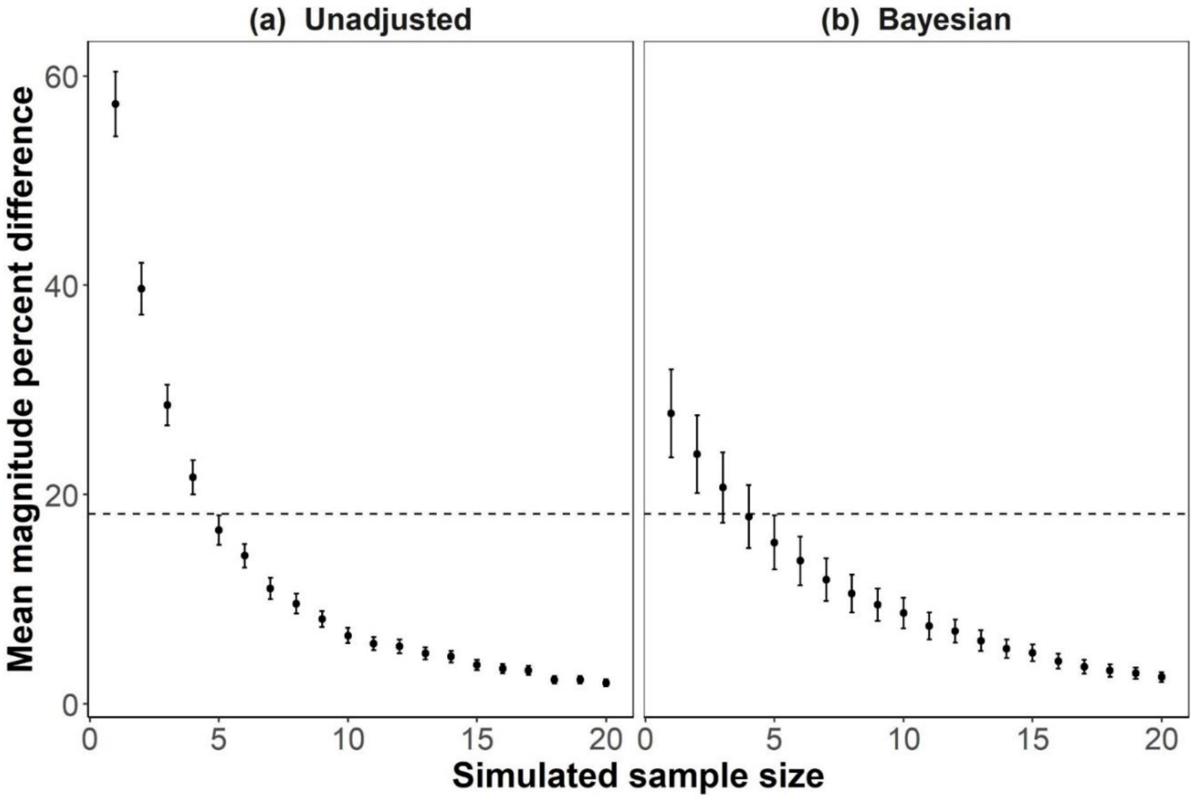

Figure 2.5. Mean magnitude percent difference between original PSis and (a) unadjusted PS_is or (b) Bayesian PS_is at each simulated sample size (foods eaten per individual). Dotted horizontal line represents our designated acceptable difference of 18.15%.

Validity

Both methods for quantifying resource selection found evidence for significant resource selection in 2017 (Wilks' $\lambda = 0.0056$, $P = 0.002$; $\chi^2 = 1082$, df = 73, $P < 0.001$) and 2018 (Wilks' $\lambda = 0.0025$, $P = 0.002$; $\chi^2 = 5810$, df = 173, $P < 0.001$). Resource selection was evident in 95% of individuals in 2017 (35/37) and 96% in 2018 (110/114), while the remaining individuals appeared to be randomly eating foods in proportion to their availability.

Utility

In both study years, the survival analyses indicated a possible relationship between diet and monthly survival (ϕ). In 2017, this relationship was weak. Our initial model selection did not find PS_i to be a significant predictor of survival (Supplementary Table 2.4a), and all individuals were predicted to have a 71% (95% CI = 55%–86%) chance of survival over a seven-month period, regardless of diet (Figure 2.6a). However, when rerun with uncertainty-corrected PS_is, a model containing PS_i appeared in the top model set alongside four others (Supplementary Table 2.4b). After averaging these models, seven-month survival ranged from 69% (95% CI = 25%–100%) for the most specialist individuals ($PS_i = 0.28$) to 79% (95% CI = 57%–100%) for the most generalist individuals ($PS_i = 0.65$), but uncertainty was high (Figure 2.6a).

In 2018, a larger dataset enabled us to estimate survival with more certainty and for a wider range of PS_is. A strong relationship between PS_i and survival emerged, as the two top models both included PS_i in the survival term (Supplementary Table 2.5a). Seven-month survival ranged from 48% (95% CI = 14%–83%) in the most specialist individuals ($PS_i = 0.13$) to 98% (95% CI = 93%–100%) in the most generalist individuals ($PS_i = 0.67$) and began to plateau as PS_i approached 0.70 (Figure 2.6b). A second model selection using uncertainty-corrected PS_is identified the same two top models (Supplementary Table 2.5b) and found a similar range in seven-month survival probabilities, from 49% (95% CI = 13%–85%) in the most specialist individuals ($PS_i = 0.11$) to 98% (95% CI = 93%–100%) in the most generalist individuals ($PS_i = 0.68$; Figure 2.6b).

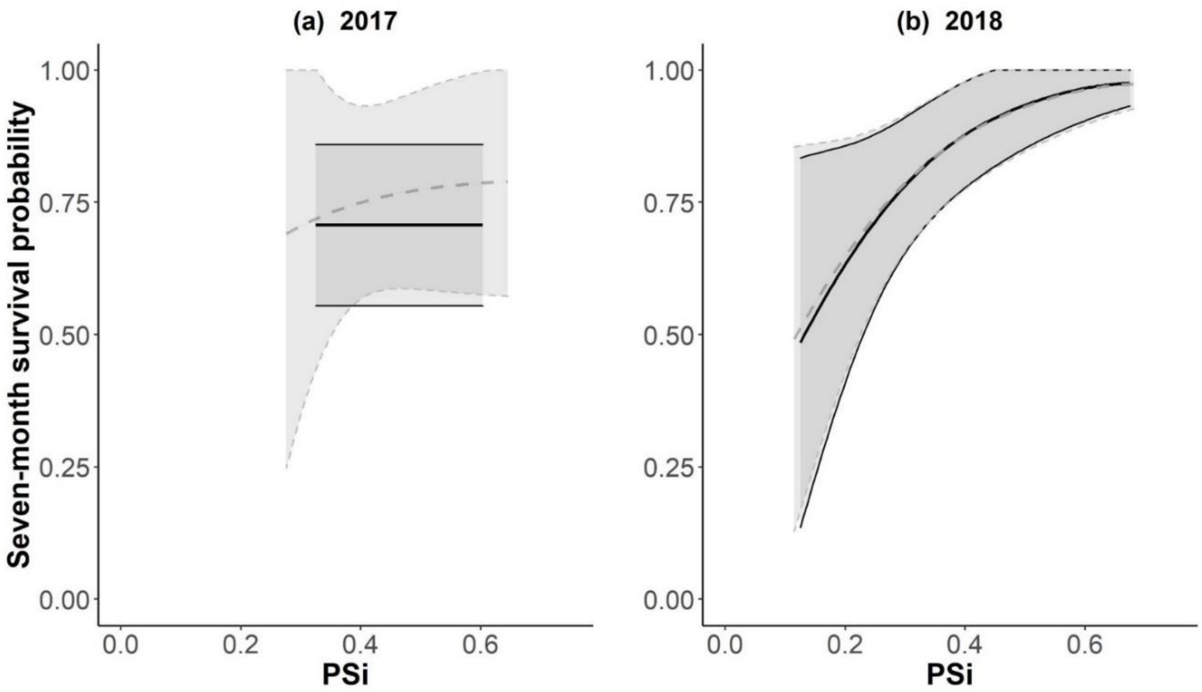

Figure 2.6. Estimates of seven-month (February–September) survival probability as a function of dietary specialization (PS_i) in (a) 2017 and (b) 2018. Solid black curves are estimates derived from our Bayesian PS_is. Dashed gray curves are more conservative estimates derived from Bayesian PS_is that were randomly corrected to account for the uncertainty inherent to each individual's sample size of foods eaten. 95% confidence intervals (restricted between 0 and 1) are shaded in gray.

2.4 DISCUSSION

While diet has historically been treated as uniform within species, many populations have now been found to contain a diverse array of specialists and generalists (Bolnick et al. 2003; Araújo et al. 2011). In our study, we demonstrated how the current dietary specialization framework could be enhanced and made more amenable to a range of sample sizes using the hihi, a threatened New Zealand passerine, as a case study. We first demonstrated that individual hihi vary in their use of foods within the broad species diet. Next, by applying a Bayesian adjustment (adapted from Coblentz et al. 2017) to the proportional similarity index (PS_i), we improved the reliability of our dietary estimates, particularly for individuals with the fewest repeated observations. We also showed that dietary variation did not arise from individuals randomly selecting foods in proportion to their availability, ensuring the validity of PS_i as a measure of individual preferences. Finally, a rarefaction procedure helped us decide which individuals to exclude from further analyses while providing a measure of uncertainty for the PS_is we retained. Even after accounting for this uncertainty, we found that diet predicted survival in at least one of our study years, highlighting the utility of diet as an ecologically informative trait.

Having a common dietary metric is crucial if we are to compare results across studies. Over the past two decades, PS_i has become the most widely used metric, but it may be vulnerable to overestimating specialization when sample sizes are small (Araújo et al. 2011). Our rarefaction procedure supported these concerns. However, a Bayesian adjustment enabled us to correct this error and expand upon the findings of Coblentz et al. (2017) by showing that this method can estimate a population's mean PS_i reliably even below sample sizes of five foods. While judging reliability is still somewhat subjective, there are two ways that this method improves upon the current practice of using an arbitrary sample size cutoff (or none at all). First, to maximize objectivity, an uncertainty threshold can be set *a priori*, informed by the variability in one's PS_i data. Second, the procedure enables uncertainty to be quantified and considered in further work, as we did in our survival analyses. Thus, future studies could benefit from using Bayesian PS_is, but they will need to exercise caution when comparing results to previous studies. In our case, comparing our mean Bayesian PS_is (0.42–0.45) to the mean of 0.47 reported in a review of 142 studies (Araújo et al. 2011) may have led us to conclude that hihi are similarly specialized to other taxa. However, if the Bayesian adjustment were applied consistently, the PS_is in these past studies could shift higher and hihi could lie at the specialist end of the spectrum.

Despite the benefits of the Bayesian method, it does have limitations which may be important to consider depending on the aims of a study. Studies vary widely in their reasons for exploring dietary variation. Some calculate individual-level specialization but focus their discussion on population or species means; for example, Araújo et al. (2007) compared mean PS_i values across four Brazilian frog species, finding that individuals are more specialized in species with broader diets. Other studies use dietary differences among individuals to explain variation in other traits; for example, in the spectacled salamander (*Salamandrina perspicillata*), Costa et al. (2015) showed that specialists exhibit better body condition than generalists. In our analyses, the Bayesian method always estimated the population's mean PS_i accurately but tended to underestimate the range of PS_is in the population at low sample sizes. Therefore, while Bayesian PS_is may be well-suited to questions relating to higher ecological levels (e.g. populations or species), studies attempting to explain individual differences may need to consider that these differences could be underestimated. Nevertheless, the accuracy with which the Bayesian method calculates population means still makes it the most useful method currently available.

Regardless of the ecological level they examine, many studies interpret PS_is as indicators of intrinsic dietary preferences without controlling for extrinsic factors such as environmental heterogeneity (Bolnick et al. 2003; Coblentz 2020). Some circumvent the need for this control by limiting their analyses to certain individuals. For example, Lowrey et al. (2016) focused their analysis of cougar (*Puma concolor*) diets on seven individuals with significantly overlapping home ranges so that resource availability could be assumed to be equal for all. Similarly, in a comparison of two sea otter (*Enhydra lutris nereis*) populations, Tinker et al. (2008) selected focal individuals so that each group had approximately equal spatial concurrence; this helped to ensure that an equal amount of dietary variation could be attributed to environmental variability in each population. In both examples, the number of individuals had to be limited to control for environmental heterogeneity. While phenology and habitat assessments can be time-consuming, adding these data (when feasible) could provide greater control over environmental effects and allow more individuals to be examined. In our study, we were able to demonstrate that very few hihi foraged randomly, and instead, most seemed to select foods based on individual preferences. Because our method provides a measure of the relative strengths of these preferences, it could enable us to explore the factors driving individual selectivity in future work.

Linking behavioral variation to fitness can provide key insights into ecological and evolutionary dynamics (Dingemanse and Réale 2005; B. Smith and Blumstein 2008). In at least one study year, we found that generalists survived significantly better than specialists over a seven-month period including winter, a resource-limited time for hihi (D. Armstrong and Ewen 2001) and many other animals. These results align with a broader trend at the species level, where generalist species tend to survive better than specialists in the face of climate change (Clavel et al. 2011; but see Colles et al. 2009). Generalization in other traits, such as habitat use, has also been shown to give species an advantage in anthropogenically-disturbed landscapes (Börschig et al. 2013; Devictor et al. 2008). The most common explanation for this ‘generalist advantage’ is that generalists are better equipped than specialists to respond flexibly to changing resource availabilities (Beever et al. 2017). However, it is difficult to determine the direction of causality between diet and survival based on an observational study like ours. In the case of hihi, a generalist diet could increase one’s chance of survival, or individuals could shift toward more specialist diets when they are old or diseased, as they may be less able to forage efficiently or compete successfully for preferred resources. Similarly, in the wandering albatross (*Diomedea exulans*), foraging behavior is considered a key indicator of senescence; after a foraging trip, older males exhibit increased corticosterone, likely reflective of decreased foraging efficiency (Lecomte et al. 2010).

Alternatively, diet and survival may not be related causally but could be linked as part of a broader behavioral syndrome (Réale et al. 2007; Sih et al. 2012; Raffard et al. 2017). Dietary specialization could have wide-reaching effects by shaping an individual’s developmental trajectory (Dall et al. 2012), predation risk (Toscano et al. 2016), or mate choice (Merrick and Koprowski 2017). Réale et al. (2007) also suggest that foraging behavior may be one of several component traits within a broader syndrome of boldness; instead of directly impacting fitness itself, foraging could act as an indicator of an individual’s boldness, which influences fitness via effects on dominance, dispersal, or antipredator behaviors (see Figure 2 in Réale et al. 2007). In fact, Richardson et al. (2019) recently found that bold hihi are more likely to survive to adulthood than shy hihi, suggesting that boldness may confer an advantage when individuals compete to establish territories or exploit risky food sources. To better understand the mechanisms linking diet to fitness, future work should examine possible correlations between diet and other traits, such as boldness, and examine whether generalists survive better in all environments.

To conclude, by applying statistical enhancements to the existing dietary specialization framework, we have outlined a path forward that could enable more taxa and methodologies to be assessed with greater accuracy. We have also identified a new case of dietary variation within a generalist species—adding to the growing literature on this phenomenon—and found evidence that dietary specialization can be used to predict survival. This highlights the value of dietary specialization as an ecologically meaningful trait that is worthy of greater consideration in the broader literature on behavioral variation.

Chapter 3

Foraging with friends and foes: Individual dietary variation predicts sociality in a threatened passerine

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Individuals within species often vary in their diets along a specialist-generalist spectrum, raising questions about why they pursue different diets and what consequences these specializations have for them. While many studies have related diet to intrinsic factors or the spatiotemporal availability of resources, linking diet to variation in other behavioral traits could provide further insight into its causes and consequences. Here, we tested for possible links between diet and sociality in the hihi (*Notiomystis cincta*), a threatened New Zealand passerine in which individuals have previously been found to vary in their diets and social tendencies. We found that small-bodied and presumably subordinate individuals were more likely to forage socially if they were generalists rather than specialists, with no significant relationship in larger (likely dominant) birds. Given past evidence that generalist hihi survive better than specialists, this result could suggest that foraging in a group helps subordinates obtain higher-quality diets than they could obtain alone, or that subordinates with better diets are more capable of enduring the competitive costs of group living. However, the relationship between diet and sociality was absent in a more competitive foraging context, with no evidence that diet predicts an individual’s gregariousness or the strength of its social bonds at crowded supplementary feeding stations. Thus, the relationship between diet and sociality appears to be mediated by dominance, but its context-dependence warrants further investigation to determine whether it constitutes a behavioral syndrome with broader consequences for the individual.

3.1 INTRODUCTION

In recent years, intraspecific dietary variation has gained recognition as a crucial factor underpinning species' niches and ecological interactions (Bolnick et al. 2011; Dall et al. 2012; Raffard et al. 2017). The refinement of methods for quantifying dietary specialization (Bolnick et al. 2002; Coblentz et al. 2017; Chapter 2) has led to the discovery that many species contain both specialist and generalist foragers (Bolnick et al. 2003; Araújo et al. 2011). However, as more cases of dietary specialization emerge, questions arise about whether this variation reflects statistical noise or ecologically-based differences. Some studies have related individuals' diets to intrinsic factors, such as their age, sex, and morphology (e.g. Rothman et al. 2008; Garduño-Paz and Adams 2010; Nsi Akoue et al. 2017; Szigeti et al. 2020), or to aspects of the ecosystem, such as the spatiotemporal distribution of resources (e.g. Buskirk and Millspaugh 2006; Pagani-Núñez et al. 2016; Coblentz 2020). However, less attention has been given to examining whether dietary specialization links to variation in other behavioral traits (but see Dall et al. 2012; Toscano et al. 2016; Troxell-Smith and Mella 2017). If such links exist, it could provide insight into longstanding evolutionary questions about how behavioral variation is maintained within populations (Sih et al. 2004; Réale et al. 2007) and how it might shape the trajectory of an individual's life (Dall et al. 2012; Toscano et al. 2016).

Sociality is a key behavioral trait that could influence diet, as many species forage socially (Stephens and Krebs 1986; Giraldeau and Caraco 2000; Galef and Giraldeau 2001). Past studies examining social effects on diet have focused mainly on social pressures imposed on an entire population; for instance, in highly competitive environments, all individuals may need to shift toward specialist diets to avoid competing directly with one another (Svanbäck and Bolnick 2005; Araújo et al. 2011; Tinker et al. 2012). However, individuals may also experience different social pressures within the same population. Some individuals may be inherently more gregarious than others and therefore forage in larger groups, where their diets may be constrained by greater competitive pressures (e.g. Sheppard et al. 2018) but also enhanced by opportunities to share information, pool skills, and forage cooperatively (e.g. Morand-Ferron and Quinn 2011; Dumke et al. 2018; Majer et al. 2018; Ashton et al. 2019). The identities of an individual's groupmates can also alter the social conditions they experience. Individuals that forage consistently with the same groupmates may form stronger social bonds, which can facilitate greater social learning and information sharing (Lachlan et al. 1998; Schwab et al. 2008; Atton et al. 2014) than in groups with variable membership. Within social groups, dominance hierarchies can also give rise to dietary differences, as dominant individuals typically receive preferential access to the most profitable feeding sites (Cody 1974; Whitten

1983; Gustafsson 1988; Holbrook and Schmitt 1992; Sol et al. 2005). Thus, an individual's diet may arise from a confluence of social factors, including its inherent sociability, its competitive ability, and the quantity and identities of its social partners.

Although sociality may influence diet, however, it is also possible for the two to be linked through other means. In some cases, diet may shape sociality. Theory predicts that generalist species will be more central to interaction networks than specialists, because their foraging brings them into contact with a wider range of interaction partners (Martín González et al. 2010; Bolnick et al. 2011); similarly, while searching for a broad array of foods, generalist individuals may encounter a greater number of conspecifics, making them appear more social than specialists. Certain diets may also favor different social groupings. For instance, orca (*Orcinus orca*) subpopulations that hunt primarily for seals tend to forage in smaller groups than those foraging on herring, as the risk of detection by seals is greater than for other prey types (Beck et al. 2012). Finally, diet and sociality may not be related causally at all but through another mediating factor, such as personality. For example, in great tits (*Parus major*), an individual's 'pace of life' explains both its dietary composition and its sociality: fast-exploring (proactive) individuals tend to select different foods (Serrano-Davies et al. 2017) and be less gregarious at supplementary feeding stations (Aplin et al. 2014) than slow-exploring (reactive) individuals.

While it is not possible to determine causality without an experiment, testing for correlations between traits of interest in multiple contexts can help to elucidate the mechanisms connecting these behaviors. Here, we explore the potential links between dietary variation and sociality in the hihi (*Notiomystis cincta*), a threatened passerine endemic to New Zealand. Because of their conservation status, hihi are monitored closely, providing us with a unique opportunity to measure diet at the individual level and track sociality across different foraging contexts. Hihi have a broad species diet of fruit, nectar, and invertebrates, but individuals within a population on Tiritiri Matangi Island exhibit dietary variation across a specialist-generalist spectrum (Chapter 2). In this population, generalists also survive significantly better than specialists over a seven-month period including winter (Chapter 2), a food-limited time for many birds, including hihi (D. Armstrong and Ewen 2001). While this could indicate that diet affects survival, diet could instead be correlated with other traits that directly impact survival. Although males are known to consume more carotenoid-rich foods than females (Walker et al. 2014), and past work suggests that adult females may be slightly more specialist than other age-sex classes (Chapter 2), little is known about why individuals pursue different diets. Sociality could be a key factor to explore, because hihi often forage socially and are known to exhibit intra- and interspecific dominance hierarchies (Craig et al. 1981; Craig 1985; Rasch and Craig 1988).

Our study tested for a relationship between dietary specialization and sociality in three main ways. First, we examined whether individuals' diets vary with the size of their social groups while foraging on natural food sources. Second, because direct social interactions were relatively rare in this context, we also examined sociality at permanent supplementary feeding stations used only by hihi and their closest and more dominant competitor, the korimako (*Anthornis melanura*: Craig et al. 1981; Craig 1985; Rasch and Craig 1988). Both species visit the feeders frequently, allowing us to test whether individual hihi with certain diets are more likely to visit a crowded resource in the presence of conspecifics or dominant heterospecifics. Third, we constructed social networks from our feeder observations to explore whether diet predicts the strength of an individual's social bonds and whether individuals tend to associate with others sharing similar diets. Throughout these analyses, we also considered possible interactions between diet and dominance by accounting for differences based on age, sex, and body size.

3.2 METHODS

Study population

Tiritiri Matangi Island (36°36'00.7"S 174°53'21.7"E) is a 220-hectare nature reserve located 30 km northeast of Auckland, New Zealand. The island is home to a hihi population of about 220 individuals. All breeding adults nest in intensively monitored nest boxes, so all individuals are of known age and are banded with a unique combination of colored leg bands at 21-days old. At the same time, they are sexed based on early signs of sexually dimorphic plumage (C. Smith et al. 2015) and their tarsus length (tarsometatarsal notch to the base of the toes) is measured; tarsus length remains unchanged beyond banding age in hihi (Low et al. 2006) and is a common proxy for body size in passerines (Senar and Pascual 1997). Once fledged, individuals are classified as juveniles until they become adults in the following spring breeding season, and color bands enable individual behavioral differences to be tracked.

Quantifying dietary variation

To quantify dietary variation among individuals, foraging observations were conducted during the New Zealand summer of 2017 (24th January–18th March; 215 hours) and 2018 (4th February–21st March; 230 hours). A single observer walked transects through areas of high hihi presence (14 km) three times weekly and low hihi presence (6 km) once weekly (hihi presence determined from regular population monitoring). Morning (c. 8:00–12:30) and afternoon (c. 12:30–16:30) sessions were balanced for each transect. During these sessions, the observer walked at a constant rate until a hihi was seen or heard within 10 meters. If the bird could be located and identified within 10 minutes, the observer conducted a focal follow of the individual. Each food eaten was classified as an invertebrate, fruit, or nectar; plant foods were identified to species level, but invertebrates could not be classified more precisely due to their small size. When multiple birds were in view, the group was scanned to capture as many foods eaten as possible. Focal individuals or groups were abandoned if the birds moved too quickly to follow through the dense understory, or if all birds became inactive (preening or resting) or moved out of sight for five minutes.

Within each year, we calculated each bird's (n_{2017} = 127; n_{2018} = 164) proportional use of the different food types (2017: 15 types; 2018: 23 types) and the average proportional use across the entire population. Individuals varied greatly in the number of foods they were observed eating (2017: 1–30; 2018: 1–88), so we applied a Bayesian adjustment (Coblentz et al. 2017; Chapter 2) to shift each individual's dietary proportions toward the population's mean values by an amount inversely proportional to the individual's sample size. These adjusted values were then used to calculate a Bayesian-adjusted Proportional Similarity Index (PS_i) for each individual. PS_i is calculated as:

$$1 - 0.5\ \sum_j \left|p_{ij} - q_j\right|,$$

where p_{ij} is the proportional use of food type *j* by individual *i* and q_j is the proportional use of food type *j* by the average population member (Bolnick et al. 2002); a specialist on a single food type *j* receives a PS_i of q_j, while a generalist whose diet exactly matches that of the average population member receives a PS_i of 1.

Previous work has demonstrated that Bayesian-adjusted PS_is provide reliable dietary estimates from as few as five foods eaten (Coblentz et al. 2017; Chapter 2) and that classifying invertebrates as a single food type does not affect accuracy, although this cannot be confirmed for individuals specializing exclusively on invertebrates (Chapter 2). Thus, to ensure the reliability of our dietary metrics, we excluded birds that were observed eating fewer than five foods (n_{2017} = 90, n_{2018} = 48) or only invertebrates (n_{2018} = 2) in a given year. Because adult females were underrepresented in the remaining dataset (n_{2017} = 2, n_{2018} = 11; mean PS_i = 0.34 ± 0.04 S.E.) and past work suggested that they may have slightly more specialist diets than other age-sex classes (weak evidence for an age∗sex effect on PS_i: Chapter 2), we excluded them from all further analyses. Six adult males (mean PS_i = 0.43 ± 0.03 S.E.) were excluded because their tarsus lengths (a predictor used across all further analyses) were missing from our long-term database. This resulted in a dataset of 132 birds (n_{2017} = 34, n_{2018} = 98; mean PS_i = 0.43 ± 0.01 S.E.).

Quantifying sociality

From our foraging data, the number of unique hihi seen in each focal follow was counted and assigned as the ‘group size’ for that follow. This variable was highly skewed toward group sizes of one (individuals traveling alone), so we transformed it into a binary variable indicating whether an individual was seen alone or with at least one conspecific. We then defined an individual’s ‘grouping tendency’ as the proportion of its follows in which it was observed with at least one conspecific.

All reintroduced hihi populations currently depend on supplementary feeding to varying degrees throughout the year (Chauvenet et al. 2012; Thorogood et al. 2013), and our study population is provided sugar water *ad libitum* in six feeder cages across the island. These feeders are visited not only by hihi but by korimako (Tiritiri Matangi population: ~2,000 individuals), providing an opportunity to observe intra- and interspecific social interactions. In each of the two study years, a single observer conducted 48 hours of feeder observations (less 19 minutes in 2017; two sessions were cut short due to weather) consisting of one hour per feeder per week across eight weeks, with morning and afternoon sessions balanced for each feeder. The observer noted the number of hihi and korimako inside the feeder cage at the start of each session and recorded a running commentary of every entrance and exit from the feeder during the hour-long observation; individual hihi were identified from their band combinations, while korimako were identified to the species level only. To help characterize the competitive environment at the feeder, agonistic interactions at the feeders were also noted *ad libitum* (n_{2017} = 855, n_{2018} = 2,371). In preliminary observations, most aggression occurred outside the feeder cage, so we recorded interactions inside and within a 3 m radius of the feeder cage, noting the species identity (hihi or korimako) of the aggressor and recipient involved in every ‘chase’ (Bird A pursues Bird B in flight), ‘displacement’ (Bird A approaches Bird B and Bird B moves away), and ‘snap’ (Bird A leans toward Bird B while snapping its beak).

In 2017, we recorded 3,262 entrances to the feeder by at least 208 unique hihi (the visitor could not be identified on 19% of entrances) and 17,900 by korimako. In 2018, there were 2,519 entrances by at least 172 unique hihi (visitor unidentifiable on 9% of visits) and 17,563 by korimako. From the transcribed audio recordings, we determined the number of hihi and korimako in the feeder at the time of each hihi entrance and the duration of each visit (in seconds). To assess the strength of an individual's associations with other hihi, we also created a social network from this entrance data. Using the asnipe package (Farine 2013) in R (version 4.0.0; R Core Team 2020), we used the gmmevents function to identify periods of activity across feeder entrances (Psorakis et al. 2015) and produce an association matrix with a simple ratio index ('SRI') for each pair of birds. SRI represents the probability that individual A and B are seen together across all times A or B are observed. While other association metrics can account for imperfect detection of individuals (Whitehead 2008; Farine and Whitehead 2015), SRI may be preferred when calibration data are unavailable (Hoppitt and Farine 2018); given our imperfect identification of feeder visitors, we accepted that SRI would likely estimate associations conservatively. Using our association matrix, we constructed a weighted social network (Farine 2017; visualized using a force-atlas layout with the Gephi program, version 0.9.2: Bastian et al. 2009), which was used to extract a weighted degree centrality ('network degree') value for each bird, reflecting both the strength and number of its associations. In both years, our observed network differed significantly from 1,000 randomized networks (constructed by randomly swapping individuals' feeder entrances: Croft et al. 2011; Farine and Whitehead 2015; Farine 2017) with respect to mean network degree ($P_{2017} = 0.03$, $P_{2018} = 0.007$) and the coefficient of variation ($P_{2017} < 0.001$, $P_{2018} < 0.001$), confirming that associations were non-random.

Data Analysis

All analyses were conducted in R (version 4.0.0; R Core Team 2020) using an Akaike information criterion (AIC_c) model selection approach (Symonds and Moussalli 2011; AICcmodavg package: Mazerolle 2017). Model sets were constructed based on the global models described below, with successively simplified models included to test the significance of each interaction and additive effect; because adult females were absent from our dataset (see above), interactions between age and sex were excluded. Unless noted otherwise, all models included year as a covariate (to account for interannual variation) in addition to the main effects, and models were structured either as Generalized Linear Mixed Models (GLMMs) with a bound optimization by quadratic approximation (BOBYQA) optimizer to reduce convergence errors (where necessary) or as Linear Mixed Models (LMMs) fit using a maximum likelihood approach. In some model selections, the total number of hihi (n_{total}) differed from the number of unique hihi (n_{unique}), because some individuals were observed in both years and therefore appeared twice in the dataset, once associated with their 2017 PS_i and once with their 2018 PS_i; in these cases, models included a random effect of bird identity to account for repeated individuals.

In each model set, the model with the lowest AIC_c value and any models within 2 AIC_c units were considered the top models. Effect sizes and 95% confidence intervals were obtained from the single top model or calculated via model averaging (MuMIn package: Bartoń 2009) where there were multiple top models. A parameter was considered to have a significant effect if its confidence interval did not span zero.

Is diet correlated with dominance factors?

Using our complete dataset (n_{total} = 132, n_{unique} = 123), we first checked whether dietary specialization was correlated with intrinsic factors expected to influence dominance. This was important to determine whether these variables could be included in interaction with PS_i in future model sets where dominance might be important. Because PS_is were normally distributed, models were structured as LMMs. The global model explained PS_i by a three-way interaction between age, sex, and tarsus length. Age and sex were included as proxies for dominance, because female hihi are known to be subordinate to males and juveniles to adults (Craig 1985). Tarsus length was included as a proxy for body size, an important factor determining dominance in many bird species (e.g. Koenig et al. 2011; Funghi et al. 2015). In this and all further analyses, tarsus length was scaled within sex across all individuals in our complete dataset, as, otherwise, tarsus and sex could be confounded (male hihi are larger than females: Thorogood et al. 2013).

There was no evidence that dietary specialization depended on any dominance factors. While models containing age and tarsus length appeared in the top model set, the null model was supported best (Supplementary Table 3.1), and no effects were significant after model averaging (95% CI: scaled tarsus length = −0.013 – 0.026, age = −0.019 – 0.067). This indicated that interactions between PS_i and age, sex, and tarsus could be included in further analyses.

Does diet vary with group size while foraging on natural food sources?

We used our complete dataset (n_{total} = 132, n_{unique} = 123) to investigate whether dietary specialization varied with an individual's grouping tendency (proportion of focal follows observed with at least one conspecific) while foraging on natural food sources. Because grouping tendency is a proportion, models were structured as GLMMs with a binomial family and logit link function. The model set was constructed from global models representing all possible three-way interactions between PS_i, age, sex, and tarsus length, excluding age-sex interactions (as above) and models without PS_i (our main variable of interest).

Does diet vary with sociality at a crowded artificial resource?

Before examining individuals' sociality at supplementary feeding stations, we first confirmed that our analyses would not be biased because individuals differed in their feeder use based on diet. Past work in another hihi population found a positive correlation between feeder visitation and invertebrate consumption (D. Armstrong et al. 1999), suggesting that frequent feeder visitors may fulfill their carbohydrate needs quickly, enabling them to specialize on other nutrients away from feeders. Using the same models and dataset as in the previous analysis, we tested whether diet predicted the total number of feeder watch sessions (out of 48) in which an individual was observed entering the feeder in a given year; because the response variable was a count skewed toward zero, models were structured as negative binomial models. We then used GLMMs with a Poisson family to explain an individual's total number of feeder entrances from the same set of predictors. In both cases, no effects were significant after model averaging (Supplementary Table 3.2, Supplementary Table 3.3; model averaging results not presented), indicating that individuals did not vary in their feeder use based on diet.

Next, to characterize the social dynamics at feeders (Figure 3.1a), we completed a model selection examining the relationship between feeder visitation and aggression. Each model explained the rate of korimako visitation (feeder entrances per hour) by the rate of aggression (aggressive acts per hour) observed (i) between korimako, (ii) between hihi, (iii) by korimako toward hihi, or (iv) by hihi toward korimako during each of the 96 feeder watches (48 per year). Models were structured as linear models with year as a fixed effect to account for interannual variation. Korimako visitation was best explained by korimako-korimako aggression (Supplementary Table 3.4): as rates of aggression among korimako increased, more korimako entered the feeder (estimate: 3.440 ± 0.877 S.E.; $t = 3.925$; $P < 0.001$; Figure 3.1b). We then used a linear model to test the effect of korimako-korimako aggression on hihi visitation and found an opposite trend: as aggression increased among korimako, fewer hihi entered the feeders, although this effect was marginally non-significant (estimate: −0.374 ± 0.196 S.E.; $t = -1.906$; $P = 0.0597$; Figure 3.1c). This justified our further use of the number of korimako inside the feeder as a proxy for the perceived 'riskiness' of the social environment (from the perspective of hihi), as higher numbers of korimako inside the feeder correlated with elevated aggression rates, and there was some evidence that these deterred hihi from entering.

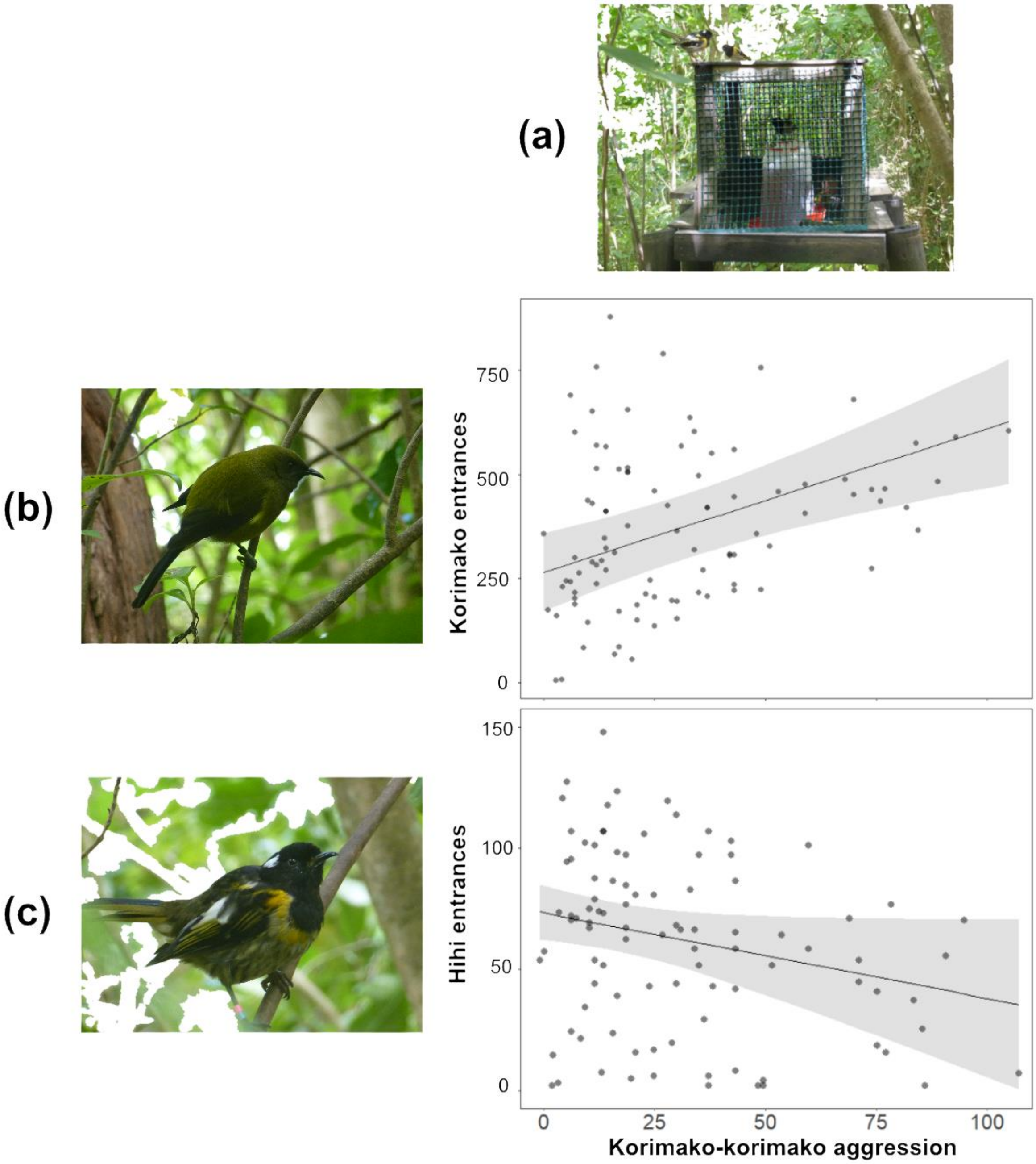


Figure 3.1. (a) A supplementary feeder on Tiritiri Matangi Island (photo by CA). (b–c) Relationship between the number of (b) korimako or (c) hihi entrances and the number of aggressive acts among korimako (inside and within a 3 m radius of the feeder cage) observed per hour in a feeder watch session. Solid lines are regression lines (95% confidence intervals shaded in gray), with a significant slope ($P < 0.001$) in (a) and a marginally non-significant slope ($P = 0.0597$) in (b). Each point (from the raw data) represents one feeder watch session. Photos (by CA) show each focal species next to the corresponding axis.

Finally, we tested whether dietary specialization varied with three social metrics measured at feeders. In each model selection, each row of data consisted of one entrance to the feeder (entrances: n = 1,006; hihi: n_{total} = 84; n_{unique} = 79). Model sets were constructed from global models representing all possible three-way interactions between PS_i, age, sex, and tarsus length, excluding age-sex interactions and models without PS_i (as above). All models included a random effect of session number to control for possible differences in sociality across sessions. In the first model selection, the response variable was binary, indicating whether the focal bird entered the feeder with (1) or without (0) a conspecific already inside, so models were structured as GLMMs with a binomial family and logit link function. The second model selection repeated this analysis but included the number of heterospecifics inside the feeder as an additive effect in all models; based on the analyses above, we predicted that a greater number of heterospecifics would increase the perceived riskiness of the feeder, making it more likely that hihi (particularly subordinates) would benefit by entering with conspecifics. The third model selection tested only the number of heterospecifics present inside the feeder. Because the response variable was a count, models were structured as GLMMs with a Poisson family.

Does diet vary with the strength of social bonds?

We considered whether dietary specialization varied with the strength of an individual’s social ties, as measured by their network degree. A preliminary examination showed that individuals’ network degrees were positively correlated with their feeder visitation rates (r = 0.608, $P <$ 0.001), suggesting that infrequent feeder visitors may not have had the opportunity to accrue social bonds in the network. Thus, we removed individuals from the dataset if they visited the feeder fewer than nine times (n = 84; mean PS_i = 0.44 ± 0.01 S.E.), which eliminated the correlation (r = 0.251, P = 0.086). Given the small resulting sample size ($n_{total} = n_{unique}$ = 48; mean PS_i = 0.43 ± 0.02 S.E.), candidate models were restricted to single two-way interactions between PS_i and age, sex, or tarsus length and additive models with up to three terms (age-sex interactions and models without PS_i excluded, as above). Because network degree was normally distributed, models were structured as linear models with a fixed effect of year; a random effect of bird identity was not needed, as there were no repeated birds in this dataset.

Lastly, we calculated an assortativity coefficient for all individuals that were observed visiting the feeder at least once and that had a qualifying PS_i score (n_{2017} = 26; n_{2018} = 58). Using the assortnet package in R (Farine 2014), we used the assortment.continuous function to calculate an assortativity coefficient from a weighted network composed of only those birds that met our qualifying criteria. This analysis tested whether individuals were more likely to associate with conspecifics with similar dietary specializations.

3.3 RESULTS

Does diet vary with group size while foraging on natural food sources?

Dietary specialization (PS_i) varied with group size while foraging on natural food sources. The model selection identified two top models (Supplementary Table 3.5). After model averaging, an individual's grouping tendency (the proportion of times it was observed with at least one conspecific) was explained by its age and a significant interaction between its PS_i and tarsus length (Table 3.1). Adults were observed in groups significantly less frequently than juveniles (95% CI: −1.352 – −0.617), averaging 55% of their observations in groups versus 76% for juveniles. While neither the PS_i (95% CI: −0.695 – 2.605) nor tarsus terms (95% CI: −0.149 – 1.383) were significant on their own, the interaction between them was significant (95% CI: −3.624 – −0.290). In other words, the relationship between diet and grouping tendency depended on an individual's body size. Individuals with smaller tarsi were more likely to forage in groups if they were generalists than if they were specialists; for individuals with a scaled tarsus length of −1 (one standard deviation below the mean for their sex), this equated to an approximately 40% higher grouping tendency for extreme generalists than extreme specialists. Meanwhile, there was little effect of dietary specialization on grouping tendency in larger individuals (Figure 3.2). This result could also be interpreted by examining how the relationship between body size and grouping tendency depended on dietary specialization: specialists tended to have similar grouping tendencies regardless of body size, while small-bodied generalists were more likely to be observed in groups than large-bodied generalists (Figure 3.2).

Table 3.1. Results of model averaging the two best supported GLMMs explaining grouping tendency (proportion of focal follows an individual was observed with at least one conspecific) while foraging on natural food sources by dietary specialization (PS_i), scaled tarsus length, and age (juvenile versus adult). In both models, year was included as a covariate to control for interannual variation. Significant *P*-values are starred.

Predictor	**Estimate**	**S.E.**	***z***	***P*-value**	
(Intercept)	1.050	0.434	2.394	**0.017**	*
PS_i	0.955	0.834	1.134	0.257	
tarsus	0.617	0.387	1.579	0.114	
age [Adult]	−0.985	0.186	5.248	**<0.001**	***
year [2018]	−0.287	0.221	1.287	0.198	
PS_i : tarsus	−1.957	0.842	2.301	**0.021**	*
age [Adult] : tarsus	0.144	0.187	0.759	0.448	

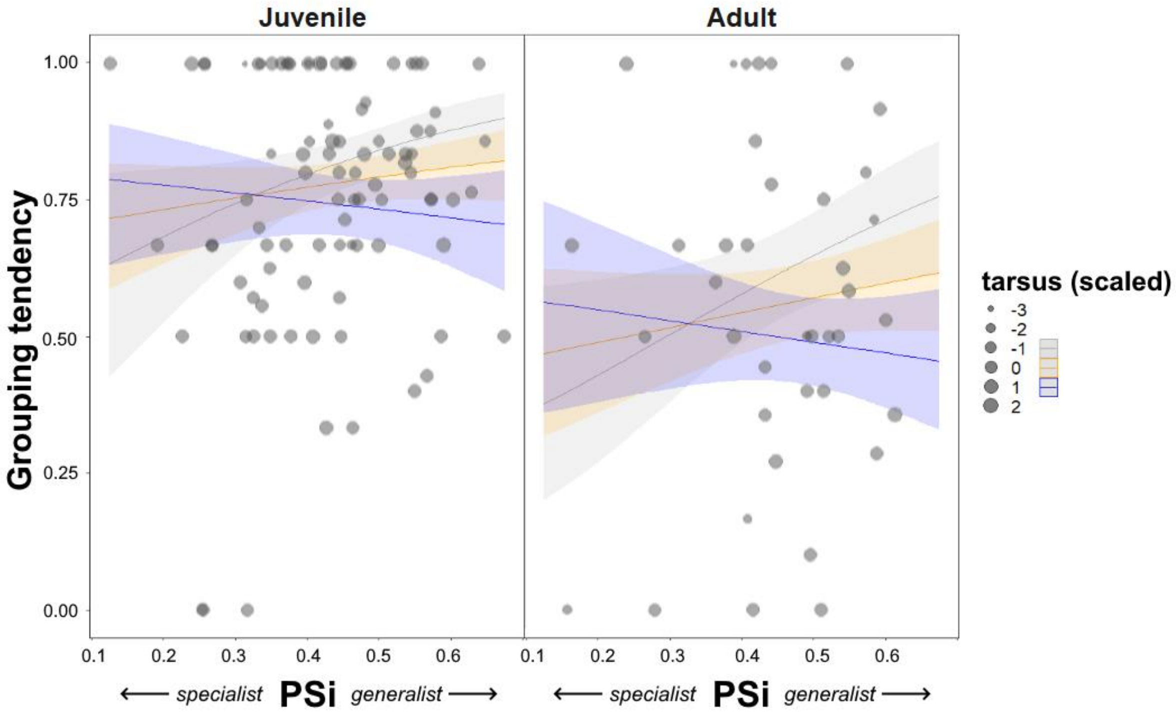


Figure 3.2. Relationship between grouping tendency (proportion of focal follows an individual was observed with at least one conspecific) while foraging on natural food sources and dietary specialization (PS_i) for juveniles (left panel) and adults (right panel). Solid curves (with shaded 95% confidence intervals) were extracted by model averaging the two top-ranked models in Supplementary Table 3.5, which explain grouping tendency by an interaction between PS_i and tarsus length (scaled within sex) and an additive effect of age. Colors represent the relationship for individuals with a scaled tarsus length of −1 (gray; tarsus length 1 S.D. below sex's mean), 0 (orange; tarsus length equal to sex's mean), or 1 (blue; tarsus length 1 S.D. above sex's mean). Each point (from the raw data) represents one individual observed in a given year, with size indicating scaled tarsus length.

Does diet vary with sociality at a crowded artificial resource?

While dietary specialization varied with sociality during natural foraging, there was no evidence for a similar relationship at a crowded artificial resource. In a model selection testing whether individuals with certain diets were more likely to enter the supplementary feeder if there was already a conspecific inside, the null model appeared in the top model set alongside nine other models including PS_i, age, sex, and scaled tarsus length as predictors (Supplementary Table 3.6). No main effects were significant after model averaging; generalists were no more likely than specialists to enter the feeder with a conspecific (95% CI: −0.602 – 3.343; Figure 3.3a), nor did PS_i have a significant effect in interaction with other variables (95% CI: PS_i:age = −3.332 – 1.519; PS_i:sex = −6.151 – 0.934; PS_i:tarsus = −1.712 – 0.716). Results were nearly identical when the number of heterospecifics in the feeder was included as an additive effect in all models (Supplementary Table 3.7; 95% CI: PS_i = −0.908 – 3.887; PS_i:age = −3.381 – 1.473; PS_i:sex = −6.360 – 0.749; PS_i:tarsus = −1.690 – 0.737). Furthermore, an individual’s diet did not predict its likelihood of entering the feeder with more heterospecifics inside (Figure 3.3b). The null model appeared in the top model set alongside four other models involving PS_i, age, and sex (Supplementary Table 3.8). After model averaging, no main effects were significant, including those involving PS_i (95% CI: PS_i: −0.685 – 0.777; PS_i:age: −1.055 – 0.731; PS_i:sex: −1.726 – 0.726).

Does diet vary with the strength of social bonds?

There was no evidence that PS_i varied with the strength of an individual’s associations within the social network (Figure 3.4). In a model selection explaining network degree by a combination of PS_i, age, sex, and scaled tarsus length, the null model was supported best (Supplementary Table 3.9). Moreover, individuals did not assort within the social network based on their dietary specializations, either in 2017 (r = 0.159, S.E. = 0.131) or in 2018 (r = −0.070, S.E. = 0.059). However, uncertainty was high in both cases, likely due to our small sample sizes.

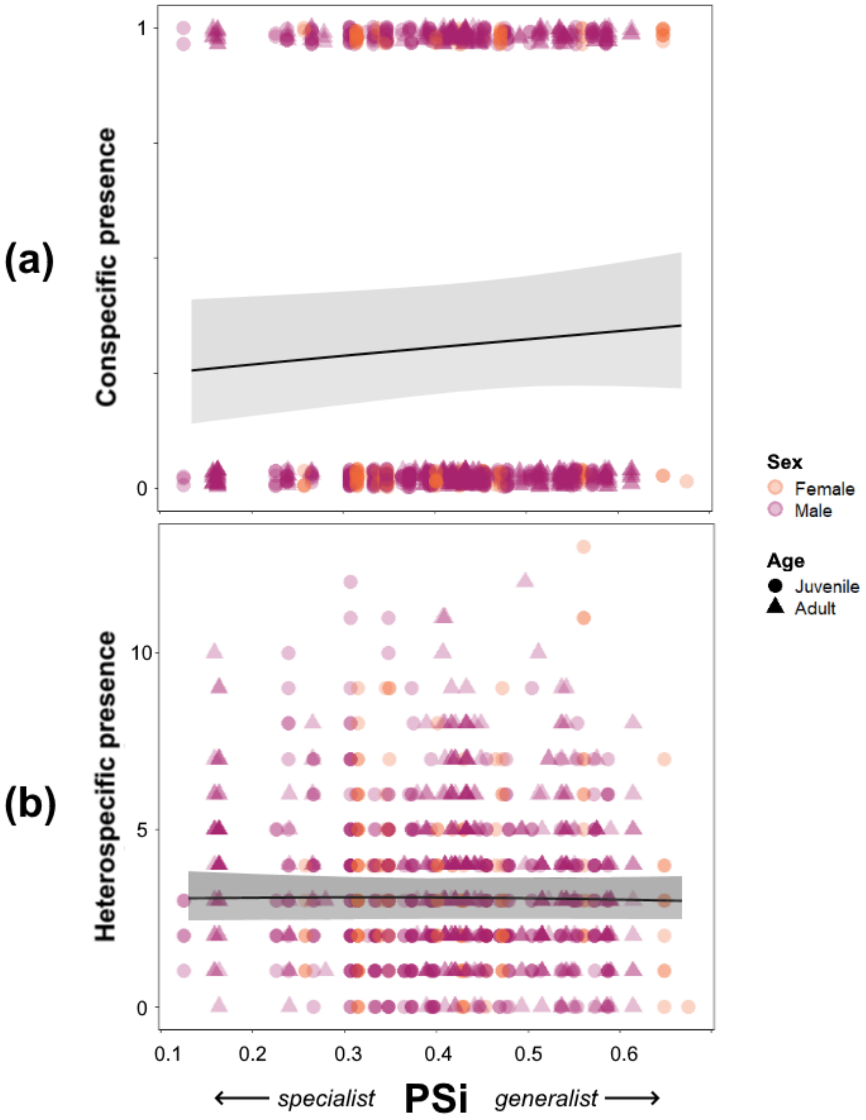
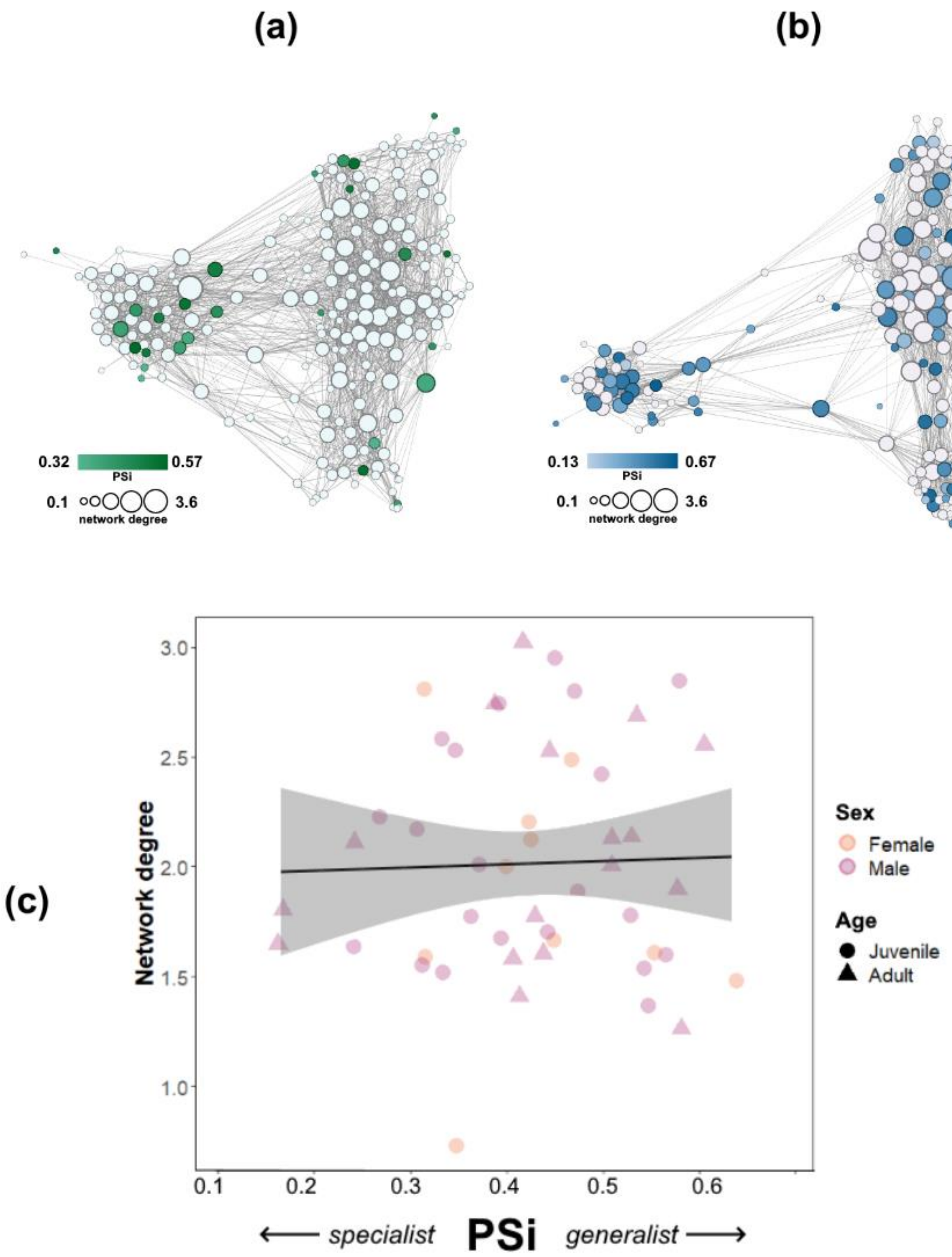


Figure 3.3. Relationship between sociality while foraging at supplementary feeding stations and dietary specialization (PS_i). Each point is from the raw data and represents one feeder entrance, with color indicating the sex of the focal individual and shape indicating age. In (a), PS_i does not explain whether a focal individual entered the feeder with (1) or without (0) a conspecific already inside. In (b), PS_i does not explain the number of heterospecifics in the feeder at the time of entry. Regression lines (with 95% confidence intervals shaded in gray) were derived by model averaging the top-ranked models identified in Supplementary Table 3.6 (top panel) and Supplementary Table 3.8 (bottom panel); no main effects were significant after model averaging.



(Figure caption on following page)

Figure 3.4. Visualization of the social network derived from entrances to the supplementary feeding stations in (a) 2017 and (b) 2018, with node color indicating the individual's dietary specialization (PS_i; white indicates PS_i unavailable) and node size indicating their network degree. In each year, individuals clustered into two groups: a smaller cluster that predominantly used the island's two southerly feeders and a larger cluster that frequented the four more northerly feeders. (c) Relationship between network degree and dietary specialization (PS_i). Each point is from the raw dataset, including only those individuals observed visiting the feeder at least nine times (to eliminate the correlation between network degree and visitation rate), with color indicating sex and shape indicating age. The regression line (with 95% confidence interval shaded in gray) was derived from a model predicting network degree from PS_i (slope not significant; $\triangle AIC_c = 2.19$ from top (null) model; Supplementary Table 3.9).

3.4 DISCUSSION

Quantifying dietary variation can enhance our understanding of a species' niche. However, determining why individuals vary is crucial for explaining how this variation might arise and what consequences it has for individuals and those around them. Nevertheless, studies often focus on relating diet to intrinsic factors or the ecosystem, overlooking potentially informative links to other behaviors (Dall et al. 2012; Toscano et al. 2016; Troxell-Smith and Mella 2017). Here, we took advantage of the close monitoring of a threatened species, the hihi, to conduct a rare investigation of the potential links between diet and sociality at the individual level. Individuals' dietary specializations (measured using the Proportional Similarity Index: Bolnick et al. 2002) varied with their tendency to travel in a group (with at least one conspecific) while foraging on natural food sources. This effect depended on body size: small-bodied individuals were more likely to forage in groups if they were generalists than if they were specialists, while there was little effect of diet on sociality for larger individuals. However, when we tested for effects of diet on social behavior at crowded supplementary feeding stations, we found no evidence that diet explained an individual's tendency to visit the feeders in the presence of conspecifics or more dominant heterospecifics. Furthermore, diet did not predict their position within a social network derived from these feeder observations. Thus, while sociality and dietary variation appear to be connected in hihi, the relationship may be context dependent.

Our study raises intriguing questions about the mechanisms linking diet to sociality. The fact that generalists were more gregarious than specialists, but only if they were small-bodied, suggests that dominance may play an important role. Body size is a proxy for dominance in many birds (e.g. Koenig et al. 2011; Funghi et al. 2015), so small hihi are likely subordinate to larger individuals. Combined with past evidence that generalist hihi survive better than specialists (Chapter 2), our results could indicate that foraging in a group helps subordinate (smaller) hihi obtain higher-quality (more generalist) diets than they could obtain alone. Indeed, despite the costs of competition (Giraldeau and Caraco 2000; Ward and Webster 2016), foraging socially can bring subordinates unique benefits, including opportunities to scrounge on dominant individuals' discoveries (Chiarati et al. 2012; Keynan et al. 2015), a reduced risk of foraging failure (Baker et al. 1981), and more optimal foraging time (Monaghan and Metcalfe 1985). Meanwhile, dominant individuals typically have priority access to preferred foods (Cody 1974; Whitten 1983; Gustafsson 1988; Sol et al. 2005), regardless of the social context, so their diets may depend less on sociality. Even if causality runs in reverse, with diet driving sociality, dominance could still explain the observed trend. Consuming a high-quality diet can improve an individual's competitive ability (Lomborg and Toft 2009; Poulos and McCormick

2015; Łukasiewicz 2020), so small-bodied generalists may be more likely to forage in groups than specialists of the same size because their diets enable them to withstand the negative effects of competition. Further work to characterize dominance at the individual level in hihi would be beneficial so that subtle differences within body size classes can be discerned.

Given that dominance appears to mediate the relationship between diet and sociality, our results could suggest that diet is nested within a broader dominance-related syndrome. Behavioral syndromes, defined as suites of correlated behaviors (Sih et al. 2004), can have potentially far-reaching consequences for individuals’ fitness and how they interact with others (Dall et al. 2012; Toscano et al. 2016; Troxell-Smith and Mella 2017). However, they require consistency across time and contexts (Sih et al. 2004), and our data did not provide the power to test the repeatability of diets across years. Moreover, we did not find any evidence for a relationship between diet and sociality in a more competitive foraging context (at supplementary feeding stations), where we might predict that a dominance-mediated syndrome would be even stronger. This could suggest that the social pressures experienced at feeders differ not only in strength but in kind from those experienced during natural foraging. Anecdotally, heterospecific interactions were very rare while hihi foraged on natural foods, so their high frequency at feeders may have introduced new dominance effects, altering the relationship between diet and sociality. Past studies have shown that aggression is highest between species (e.g. Rasch and Craig 1988) and individuals (e.g. Robinson 1985; Kitchen et al. 2005) of similar dominance status, so dominant hihi may be perceived as a greater threat to korimako than subordinates and receive more aggression; thus, the social pressures experienced by dominant and subordinate hihi could be more equal at feeders than during natural foraging. Furthermore, the social pressures at feeders may also be complicated by the fact that they represent a sort of foraging bottleneck, bringing together members of different social groups at just six small foraging patches across the island

Associating with the same individuals consistently is hypothesized to be beneficial because it can increase the reliability and transmission of social information (Lachlan et al. 1998; Schwab et al. 2008; Atton et al. 2014). However, we found no evidence that individuals’ diets predicted the strength of their social bonds. Additionally, within the social network, individuals did not associate with conspecifics sharing a similar diet, as we might expect if there were a benefit to foraging with others on the same foods or if associations arose as a byproduct of individuals with similar diets foraging in the same location. Instead, this result might suggest that individuals benefit by foraging in groups of mixed dietary specializations, either as a way to avoid competition (Giraldeau and Caraco 2000) or pool mixed knowledge and skill sets (Giraldeau 1984; Morand-Ferron and Quinn 2011). Nevertheless, like many studies on passerine birds (e.g. Aplin et al. 2014; Farine et al. 2014; Evans et al. 2018), we derived the social network from visits to supplementary feeding stations when it would have been ideal to measure social associations in the same context as individuals' diets. Future work would benefit from building more robust social networks for hihi foraging on natural food sources; this would provide a better sense of their sociality during natural foraging and would improve statistical power by ensuring that every individual has both a diet and network score.

Why else might the link between diet and sociality be absent at feeders? First, our assumption that hihi perceive feeders as competitive resources might need reexamination as, despite high rates of aggression, sugar water is provided *ad libitum*; thus, hihi may actually perceive this unlimited resource to be a low-competition (albeit chaotic) social environment. Alternatively, it could be that the link between diet and sociality is actually context dependent, and hihi behave differently while foraging on natural versus artificial resources. We did not find any evidence for a relationship between an individual's natural diet and its use of the feeders, suggesting that foraging is unrelated between these contexts. More importantly, early work on food provisioning showed that plentiful and easily-accessible artificial food sources can erode natural sociality among birds by reducing the benefits of foraging socially (Szekely et al. 1989; but see: Kubota and Nakamura 2000). The unique features of artificial food sources could be important to consider in studies of sociality more broadly, because there is a widespread trend toward using social metrics derived from feeders to predict broader behavioral strategies, particularly in birds (Aplin et al. 2014; Jones et al. 2017; Evans et al. 2018). Wherever possible, we encourage others to test whether links between sociality and other traits hold whether sociality is measured at feeders or in natural foraging contexts.

Despite its apparent context-dependence, the link we found between diet and sociality could have implications for hihi conservation. As for many threatened species (Seddon et al. 2014), translocations are a key strategy for hihi recovery and are known to disrupt the social environment (Letty et al. 2007; Ewen et al. 2012; Franks et al. 2019). Recent evidence also suggests that hihi whose social networks are more greatly disrupted by translocation exhibit lower post-release survival (Franks et al. 2019). If sociality influences diet, then the social disruptions caused by translocations might also affect how individuals forage, explaining why translocated individuals struggle in an unfamiliar environment. This could underscore the importance of maintaining a consistent social environment across translocations (as much as possible) to ensure that disruptions to foraging are minimized. Meanwhile, if diet determines sociality, then this could also provide a means for improving translocation success, as social relationships favorable at the release site could be achieved by selecting individuals for translocation based on diet. Experiments to tease apart the causality between diet and sociality could be relatively easy to incorporate into translocation programs. Individuals are often provided food in temporary captivity (IUCN/SSC 2013), providing an opportunity to manipulate diets so that potential effects on sociality can be examined after release (e.g. Whiteside et al. 2015; Oudman et al. 2016). Furthermore, the social environment often differs significantly between release sites and source sites due to different food abundances and competitor densities, so social effects on diet can be assessed as individuals are moved between sites. Thus, as well as attempting to conserve species, translocations could also provide ideal experimental settings for testing the causality between diet and sociality, a possibility worth pursuing for the mutual benefit of behavioral ecologists and conservation biologists.

Chapter 4

Foraging for a foothold: Using conservation translocations to test dietary responses to competitive release

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Competition is thought to be a major force shaping dietary specialization, but its effects can depend on individuals' inherent resource preferences. Observing how individuals respond to a release from competition can elucidate competitive pressures on diet, but opportunities to experimentally test this under natural conditions are rare. Conservation translocations provide a unique opportunity to do so, as release sites typically have smaller populations than source sites. Here, we measured dietary specialization in three populations of hihi (*Notiomystis cincta*), a threatened New Zealand passerine, and found that dietary specialization was highest in the densest population. We then tracked 40 juveniles as they were translocated from the densely populated site to one of the less dense sites and found a significant shift toward generalization after release. This finding held even after controlling for seasonal effects on diet; juveniles remaining at the source site also trended toward generalization, but not significantly. Thus, the dietary changes experienced by the translocated cohort support the 'shared preferences model' of dietary variation: individuals specialize to avoid competition but converge on a generalist diet of shared, preferred foods once competition is reduced. Lastly, we assessed whether individuals' pre-translocation diets predicted their survival after release. Specialists were more likely to survive to the next breeding season than generalists, with an opposite trend among individuals remaining at the source site. Therefore, diet could potentially be used as a behavioral indicator for selecting individuals for translocation, improving the viability of translocated populations without weakening the source population.

4.1 INTRODUCTION

There is growing recognition that individuals within species often differ in their use of resources within a broader population diet (Bolnick et al. 2002, 2003; Araújo et al. 2011). Some studies explain these dietary specializations by linking them to variation in other traits as part of a behavioral syndrome (Sih et al. 2012; Toscano et al. 2016; Troxell-Smith and Mella 2017; Chapter 3). However, diet can also be influenced by the environment in which it is measured (Pagani-Núñez et al. 2016). It has long been known that the social environment, particularly competition, is a powerful force shaping diet (Roughgarden 1972; Schoener 1974; Pianka 1981; Partridge and Green 1985; Stephens and Krebs 1986). Even if individuals have intrinsic dietary preferences, they may be unable to obtain their preferred resources in highly competitive environments, particularly if they are subordinate (e.g. Cody 1974; Craig et al. 1981; Holbrook and Schmitt 1992) or unskilled (e.g. Heinrich 1976) compared to other foragers. Thus, examining how individuals forage under different levels of competition can provide a deeper understanding of a species' niche and the mechanisms driving dietary diversity.

Theory predicts two alternative outcomes for how diet will respond to a change in competition, both of which depend on individuals' inherent food preferences (Svanbäck and Bolnick 2005; Araújo et al. 2011). In the 'shared preferences' model (and its variant, the 'competitive refuge' model; Figure 4.1a), individuals prefer the same foods, but there are not enough of these foods for all individuals when competition is high. Therefore, individuals must seek out unique specializations as 'refuges.' If competition relaxes, however, they can then converge on a shared, generalist diet of their most highly preferred foods. In contrast, in the 'distinct preferences' model (Figure 4.1b), individuals inherently prefer different subsets of available resources but are prevented from acting on these preferences while competitors are present. Reducing competition should allow individuals to shift from a generalist diet to distinct specializations reflecting their true resource preferences. Some studies attempt to distinguish which of these models drives dietary diversity by comparing populations living under different competitive conditions (e.g. Tinker et al. 2012). Others track changes within a population as individuals respond to seasonal fluctuations in resource availability (e.g. Mori et al. 2019) or interannual changes in population density (e.g. Svanbäck and Persson 2004). However, these approaches may confound dietary changes with other factors, such as genetic differences between populations or seasonal changes in nutritional needs. Without experimentally manipulating competition, it can be difficult to attribute dietary changes to the environment. Nevertheless, opportunities to do so are rare outside of a laboratory setting (e.g. Bolnick 2001; Fontaine et al. 2008), so these two theories remain largely untested in natural populations.

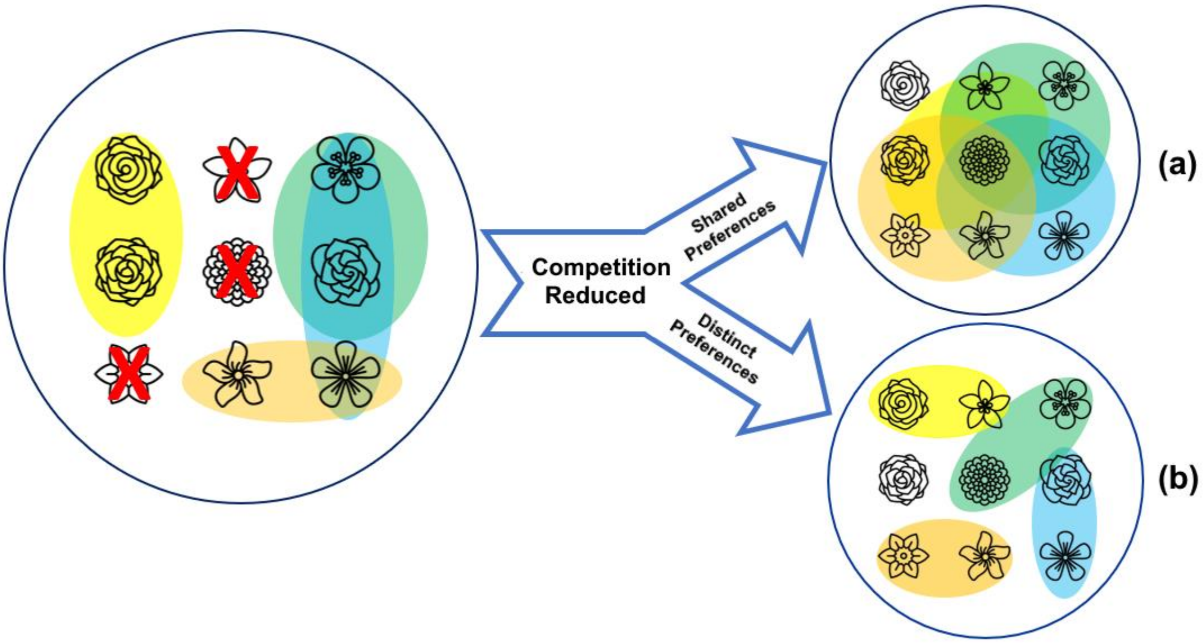

Figure 4.1. Visualization of the two preference models of dietary variation. In both cases, individuals begin in a highly competitive environment (left), where resources indicated by red Xs are monopolized by competitors, and each individual in the population (colored ovals) consumes a subset of the available resources. Once competition is reduced, individuals either (a) become more generalist as they converge on shared preferred foods (‘shared preferences model’), or (b) become more specialist as they pursue unique food preferences (‘distinct preferences model’).

Behavioral ecologists could look to the field of conservation biology for an alternative approach. Many conservation interventions intentionally or unintentionally alter the competitive landscape that individuals experience. For example, translocations have become a vital tool for species recovery and often involve moving animals between disparate social environments (Sarrazin and Barbault 1996; D. Armstrong and Seddon 2008; Ewen et al. 2012; IUCN/SSC 2013). In translocations for the purpose of species reintroductions, individuals typically experience a sharp reduction in competition as they are moved from existing populations to unpopulated areas (IUCN/SSC 2013). Thus, individuals experience a strong competitive release over a short period: exactly the environmental change needed to distinguish between the two competing models of dietary specialization. However, only rarely have these (or other) behavioral ecology theories been tested in the context of translocation. One notable exception is Tinker et al.'s (2008) study of sea otters (*Enhydra lutris*), which found support for the shared preferences model by comparing dietary specialization between individuals at a food-poor source site and a food-rich release site. However, the authors were unable to track individual responses to competitive release, because the population at the release site was established over a decade prior to the study. Therefore, the speed and consistency of dietary responses at the individual level and possible founder effects in the diets of translocated populations remain unknown.

In addition to enabling tests of foraging theory, translocations could also provide a valuable opportunity for behavioral ecologists to contribute directly to conservation. Finding food in an unfamiliar environment is a major challenge for translocated populations (Berger-Tal et al. 2020). While this can be mitigated by choosing release sites that best satisfy species' needs (D. Armstrong and Seddon 2008; IUCN/SSC 2013), for many species, our only knowledge of their diets comes from environments where their foraging may be constrained by competition, or from degraded habitats that no longer reflect their ideal conditions (Ewen and Armstrong 2007). Observing how diets change when individuals are released from competition could provide insight into their inherent resource preferences, which could be used to identify suitable release sites for future translocations. If individuals vary in their diets or dietary flexibility, and these traits predict survival, we may also be able to improve a population's chance of establishment by selectively translocating individuals with the most favorable traits.

In this study, we used two planned conservation translocations to test the competing models of dietary variation in a species that could benefit from this knowledge. The hihi (*Notiomystis cincta;* Figure 4.2a) is a threatened passerine that was once widespread across the North Island of New Zealand before being reduced to a single offshore island (Te Hauturu ō Toi/Little Barrier Island Nature Reserve) around 1890. Subsequently, seven additional populations have been established through intensive translocation efforts (Thorogood et al. 2013; Panfylova et al. 2016; Franks et al. 2019), but habitat suitability presents an ongoing barrier to achieving self-sustaining populations; for example, all reintroduced populations depend on supplementary feeding to support them through periods of food scarcity (Chauvenet et al. 2012; Thorogood et al. 2013). Previously, individual hihi were found to specialize within the broad species diet of fruit, nectar, and invertebrates, with generalists surviving better than specialists over winter on Tiritiri Matangi Island (Chapter 2), the main source site for translocations. Diet has also been linked to possible dominance effects (Chapter 3), suggesting a social basis for resource selection. Thus, we predicted that the competitive changes experienced during a translocation could strongly influence diet and related fitness outcomes in translocated individuals.

In 2018, 40 hihi were translocated from Tiritiri Matangi, a highly competitive site, to two less competitive mainland sites: Rotokare Scenic Reserve (30 birds) and Bushy Park Tarapuruhi (10 birds). Our aims were to (1) explore which of the two preference models explains dietary variation across hihi populations, while also determining (2) how dietary changes across a translocation manifest at the individual level, and (3) what impacts these changes have on survival. Under the shared preferences model, we would expect translocated birds to become more generalist as they move from a highly competitive source site to a less competitive release site. In contrast, the distinct preferences model predicts a shift toward specialization as competition is released. However, individuals may also differ in their dietary flexibility, so we predicted that some may respond more strongly and immediately to this competitive change than others, which could potentially improve their chances of survival.

4.2 METHODS

Study sites and populations

Tiritiri Matangi Island (‘Source Site’; 36°36'00.7"S 174°53'21.7"E; Figure 4.3a) is a 220-hectare nature reserve located 3.5 km off the coast of New Zealand’s North Island. The island is free of introduced mammalian predators and consists mainly of regenerating native bush, the result of extensive replanting efforts in the 1980s. A hihi population (~200 individuals) was established through a translocation of birds from Te Hauturu ō Toi in 1995 and serves as the main source population for translocations today (Thorogood et al. 2013). All individuals nest in intensively monitored nest boxes, so each chick is of known age and is uniquely color banded at 21-days old to facilitate individual identification. Once fledged, these individuals experience high levels of competition from conspecifics (~0.91 birds/ha) and their two main heterospecific competitors (~8.6 birds/ha): tūī (*Prosthemadera novaeseelandiae*: Figure 4.2b) and korimako (*Anthornis melanura*: Figure 4.2c; Figure 4.2d). This is reflected in a strong reliance on supplementary feeding compared to other sites; in April and May 2017 (one year prior to our study), sugar consumption was estimated to be 0.83 liters per hihi per month (Figure 4.3e).

Rotokare Scenic Reserve ('Release Site 1'; 39°27'15.4"S 174°24'33.0"E; Figure 4.3b) is a 230-hectare predator-free (fenced) sanctuary located in remnant mature forest on the mainland of the North Island. Hihi were extirpated from the region in the late 1800s but were reintroduced to Rotokare in 2017 with a translocation of 40 birds from Tiritiri Matangi (Franks et al. 2019). At the start of our study, the population density was ~0.17 hihi/ha, or one fifth that of the Source Site (Figure 4.2d). Heterospecific densities are also lower (~6.9 birds/ha), primarily due to a low density of korimako (Figure 4.2d). While the forest is similar in size to the Source Site, it differs significantly in structure (PERMANOVA: P = 0.003, see Supplementary Materials 4.1 for methodology), with a higher canopy and sparser understory (Figure 4.3d). This mature forest structure matches the historic habitat of hihi more closely than the regenerating forest of the Source Site and indicates a potentially greater abundance of resources. Combined with its low competitor density, Release Site 1 therefore represents a much less competitive environment than the Source Site. This is supported by the population's lower consumption of sugar water (~20% that of the Source Site; Figure 4.3e). Conditions are similar at Bushy Park Tarapuruhi ('Release Site 2'; 39°47'47.9"S 174°55'51.2"E; Figure 4.3c), a 100-hectare forest located 65 km southeast of Release Site 1. Bushy Park is home to a small hihi population (~40 adults) established in 2013 with a translocation of birds from Tiritiri Matangi. Heterospecific competitors are scarce (<0.17 birds/ha: Figure 4.2d), the forest structure differs significantly from the Source Site (PERMANOVA: P = 0.003) but not Release Site 1 (PERMANOVA: P = 0.626, see Supplementary Materials 4.1; Figure 4.3d), and sugar consumption is low (~12% that of the Source Site; Figure 4.3e).

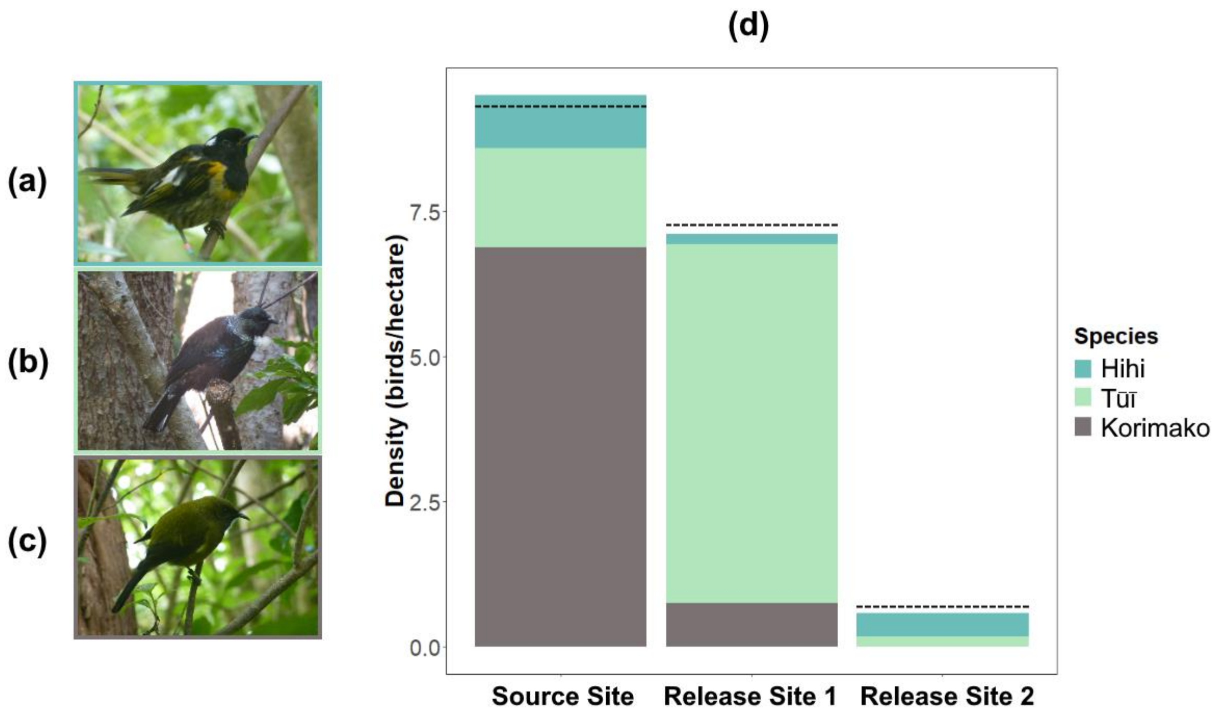

Figure 4.2. The social environments of the three study sites. Estimated densities (birds/hectare) of (a) hihi, (b) tūī, and (c) korimako are displayed for each site in (d). Dashed lines indicate total bird densities adjusted for the hihi removed from (Source Site) or added to (Release Sites) the population due to translocation during our study. All data are derived from transect surveys (Source Site: Stewart and Milton 2018; Hihi Conservation Charitable Trust, unpublished data; Release Site 1: D. P. Armstrong, unpublished data; Drummond and Armstrong 2019; Hihi Conservation Charitable Trust, unpublished data; Release Site 2: Bombaci et al. 2018; Hihi Conservation Charitable Trust, unpublished data). Photo credit: CA.

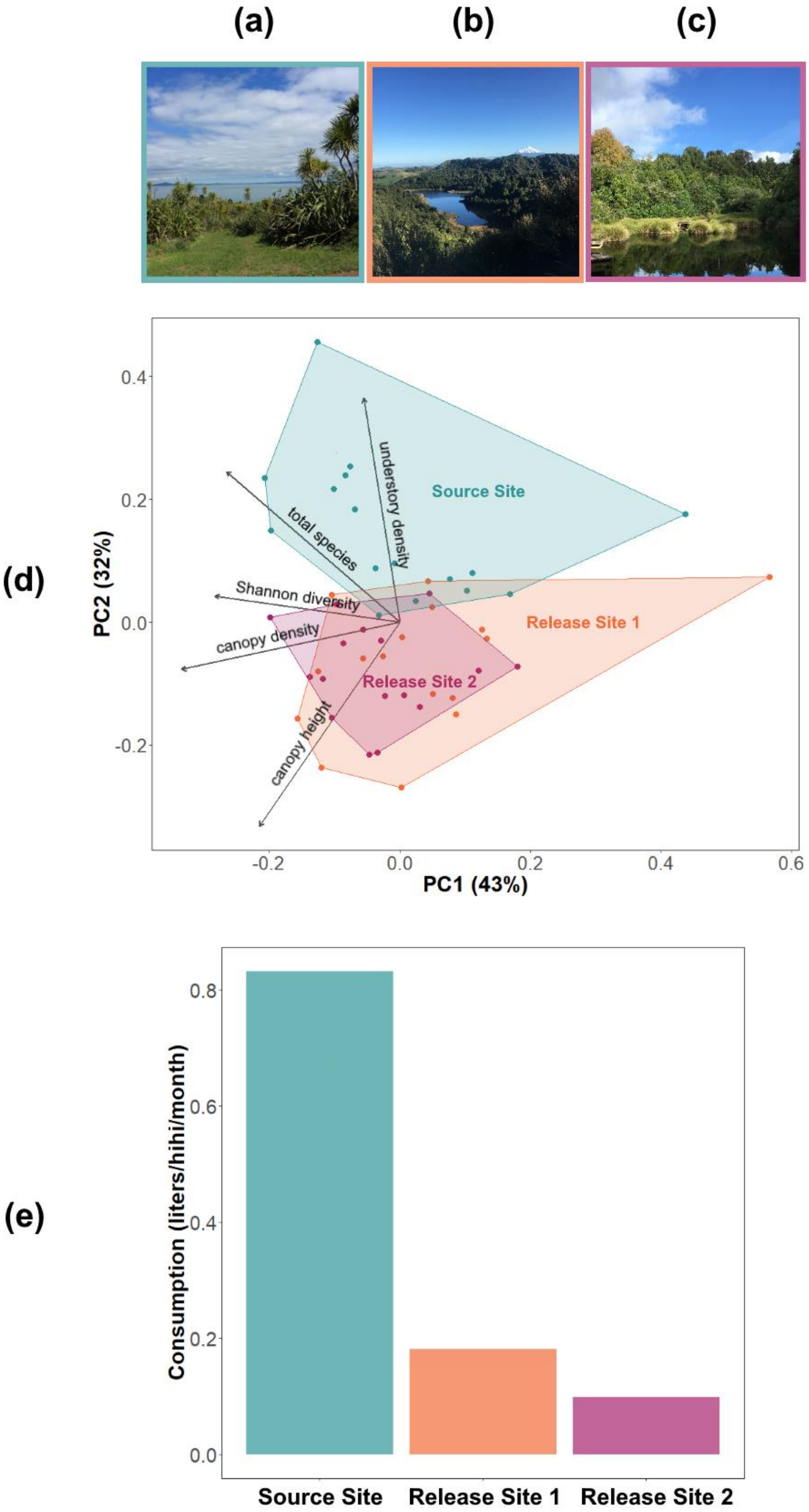

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Figure 4.3. The foraging landscapes of the three study sites: (a) the ‘Source Site’ (Tiritiri Matangi Island); (b) ‘Release Site 1’ (Rotokare Scenic Reserve); and (c) ‘Release Site 2’ (Bushy Park Tarapuruhi). (d) Biplot of the first two components of a Principal Component Analysis (Supplementary Materials 4.1) explaining variance in the structure and composition of habitat plots (points), which are grouped by site (shaded polygons). Axes are labeled with the percentage of variance explained by each component. Arrows represent habitat variable loadings. (e) Cross-site comparison of sugar water consumption (liters per hihi per month) from April–May 2017, one year prior to the main study period. Raw consumption data provided by the Hihi Conservation Charitable Trust (unpublished data) have been reduced by 85% at the Source Site to account for visitation by korimako (Chapter 3), but not at the two Release Sites, where only hihi use the feeders. Photo credit: CA.

Pre-translocation foraging observations

From 4th February–21st March 2018, a single observer conducted 230 hours of foraging observations at the Source Site by walking foraging transects that were evenly distributed around the island. Fourteen kilometers of transects through areas of high hihi presence (based on regular population monitoring) were walked three times weekly, while an additional 6 km through areas of low hihi presence were walked once weekly. Morning (c. 8:00–12:30) and afternoon (c. 12:30–16:30) sessions were balanced for each transect. During each session, the observer walked at a constant rate and stopped only when a hihi was seen or heard within 10 meters of the transect. If the bird could be located within 10 minutes, the observer began a focal follow of the individual, recording its band combination and any feeding events *ad libitum*. Each food eaten was classified as an invertebrate, fruit, or nectar; plant foods were identified to the species level, but invertebrates were too small to be classified more precisely. If multiple birds came into view, the group was scanned to capture as many foods eaten as possible. Focal individuals were abandoned if they moved too quickly to follow through the dense understory, or if they became inactive (preening or resting) or moved out of sight for 5 minutes.

Translocations

From 9th April–11th April 2018, 42 hihi were caught at the Source Site using mist nets and catching mechanisms at permanent supplementary feeding stations. Individuals were targeted for catching based on age and sex; typically, only juvenile hihi are translocated (Thorogood et al. 2013) to minimize demographic impact on the source population, and catching continues until an even sex ratio is achieved. After capture, individuals were distributed evenly among three 40 m^3 aviaries, where they were provided with food and water for four days while awaiting disease screening results (Ewen et al. 2018). At the end of this period, all birds had passed disease screening, and one surplus male and female were released. The remaining 40 individuals were transported to the mainland overnight by boat and van, with 30 released at Release Site 1 and 10 released at Release Site 2 the following morning (15th April).

Post-release observations

For six weeks following the translocation, foraging observations were collected at each of the three sites by a team of observers. All observers completed interobserver reliability testing to ensure food items were identified with 100% accuracy. At the Source Site, observations followed the pre-translocation methods and were collected by a single observer from 16th April–

24th May 2018, for a total of 105 observation hours. Observations at the two Release Sites were collected from 17th April–26th May 2018, with 230 hours at Release Site 1 (by two observers) and 125 hours at Release Site 2 (by one observer). The disparity in observation hours across sites was necessary to achieve similar sampling effort due to the challenging terrain and lower hihi density at Release Site 1. Both mainland sites contain a network of monitoring transects (spaced 50 m apart), which were walked about once weekly at Release Site 1 and twice weekly at Release Site 2. In September 2018, constant-effort population surveys (about 40 hours each) were conducted at all sites, during which an experienced observer attempted to sight as many individual hihi as possible.

Data analysis

All analyses were conducted in R (version 4.0.0; R Core Team 2020). When means are reported, they are accompanied by their estimated standard errors.

Accounting for uncertainty in dietary estimates

Within each site and time period (pre- or post-translocation), we tallied the number of foods eaten by type for each bird. To account for variation in the number of foods eaten per individual ($\bar{x}$ ± S.E. = 16.9 ± 1.1), we used a Bayesian adjustment (Coblentz et al. 2017; Chapter 2) to shift each individual's food counts toward the population's mean values by an amount inversely proportional to the individual's sample size of foods eaten. Previous work found that this adjustment helps to correct for the uncertainty in diets inferred from a small number of foraging observations and can produce reliable dietary estimates from as few as five foods eaten (Coblentz et al. 2017; Chapter 2), so we excluded individuals with fewer than five observed foods from all further analyses.

Testing the shared preferences and distinct preferences models

To determine whether the shared preferences or distinct preferences model explains dietary variation across our study populations, we compared the three sites only in the post-translocation period to eliminate seasonal effects. Using the WTdMC function in the R package RInSp (Zaccarelli et al. 2013), we used our Bayesian-adjusted food counts to calculate Roughgarden's Total Niche Width (TNW) for each population (Roughgarden 1972; Bolnick et al. 2002). For discrete food types, TNW is estimated using the Shannon diversity index (Shannon 1948) and can be divided into two components of variance: a within-individual (WIC) component representing the breadth of individuals' diets and a between-individual component

(BIC) representing the overlap between individuals' diets. The ratio of WIC/TNW indicates the level of dietary specialization in the population: values near 0 indicate a specialist population where individuals consume distinct, narrow diets, while values near 1 indicate a generalist population where individuals eat broader, overlapping diets.

Using the WTdMC function, we compared the WIC/TNW value of each population (Source Site, Release Site 1, Release Site 2) to 999 Monte Carlo permutations in which the population diet was randomly redistributed among individuals. This tested whether each population was significantly more specialized than expected by chance. However, there are no statistical tests to compare WIC/TNW values across populations, so we compared them qualitatively only. To assess the effects of age and residency on population-level dietary specialization, we also compared WIC/TNW values between subsets of each population: (i) adults versus juveniles (all sites); (ii) newly-translocated versus resident individuals (Release Sites only); and (iii) newly-translocated versus resident juveniles (Release Sites only).

Examining dietary responses to competitive release

Next, we assessed dietary changes across the translocation within smaller cohorts based on (i) age (juvenile or adult) and (ii) post-translocation site. This resulted in four cohorts: Source Site Adults, Source Site Juveniles, Release Site 1 Juveniles (translocated during the study), and Release Site 2 Juveniles (translocated during the study). Within each time period (pre- or post-translocation), we measured each individual's dietary specialization relative to other members of their cohort using the Proportional Similarity Index (PS_i). PS_i compares each individual's proportional use of foods (adjusted following the Bayesian correction outlined above) to the average cohort member's diet (Bolnick et al. 2002) and is calculated as:

$$1 - 0.5\sum_j \left|p_{ij} - q_j\right|,$$

where p_{ij} is the proportional use of food type *j* by individual *i*, and q_j is the proportional use of food type *j* by the average cohort member (Bolnick et al. 2002). A specialist on food type *j* receives a PS_i of q_j, while a generalist whose diet exactly matches the cohort average receives a PS_i of 1.

Because only six individuals translocated to Release Site 2 had sufficient observations in either time period (five foods eaten: see above), the Release Site 1 and Release Site 2 cohorts were pooled into a single cohort of 'Translocated Juveniles.' This allowed us to treat the two Release Sites as replicates while we focused on our hypotheses of interest. We then tested the effects of cohort (Source Site Adults, Source Site Juveniles, Translocated Juveniles) and time (pre- vs. post-translocation) on PS_i in a stepwise fashion using Likelihood Ratio Tests. A model containing an interaction between cohort and time was compared to a simplified model without the higher-order effect. Models were structured as Linear Mixed Models (LMM) with a random effect of individual bird identity and post-translocation site (to account for differences between the two Release Sites). The interaction was significant (see Results), so we conducted post-hoc *t*-test comparisons: (1) between cohort pairs before the translocation, (2) between cohort pairs after the translocation, and (3) within cohorts before vs. after the translocation. A fourth comparison tested whether cohorts differed in the change in mean dietary specialization experienced across the translocation.

Changes in dietary specialization at the cohort level could be explained by different patterns among individuals. For instance, if the cohort mean does not change, individuals' diets may have been stable across the translocation, or all individuals may have flipped to the opposite end of the specialist-generalist spectrum. Therefore, in our next analysis, we examined the consistency of individuals' dietary changes within each cohort. We first calculated each individual's PS_i change across the translocation (post-translocation PS_i minus pre-translocation PS_i), including only those individuals seen eating at least five foods in both periods. From a preliminary examination of the relationship between PS_i change and pre-translocation PS_i, we identified a potential regression-to-the-mean effect: across all cohorts, individuals with extreme diets tended to converge toward the cohort mean in their post-translocation measure. To account for this effect, we followed the methods of Barnett et al. (2004) to adjust individuals' post-translocation PS_is by their pre-translocation deviation from the cohort mean ('pre-translocation differential'). We then used a Likelihood Ratio Test to test whether individuals' post-translocation diets depended on an interaction between their pre-translocation differential and cohort. Because the interaction was not significant (see Results), we examined the significance of each factor in the additive model (pre-translocation differential + cohort) using *t*-tests. Models were structured as above but without a random effect of bird identity (each bird appeared only once in this dataset). This analysis measured the consistency of dietary changes within cohorts (represented by the slope). To test the direction of these changes, we compared the intercept for each cohort to its mean pre-translocation PS_i using a *z*-test.

Predicting post-release survival

Because dietary generalists were previously found to survive better than specialists over winter at the Source Site (Chapter 2), we tested whether this generalist advantage held in translocated individuals. However, we predicted that an individual's diet at the Source Site (i.e. pre-translocation PS_i) would not be the best predictor of its survival in a new environment, where there may be different selection pressures. Instead, we expected that translocated individuals' survival would depend on how they foraged in the initial period after release (i.e. post-translocation PS_i) or their dietary flexibility (i.e. change in PS_i across the translocation).

Because there were insufficient surveys at the Release Sites to conduct a more formal survival analysis, we instead used an individual's presence in the September 2018 survey (five months post-translocation) as a proxy for survival. This timeframe equates to recruitment into the next breeding season and overlaps with the interval previously examined at the Source Site (Chapter 2), but only juveniles were examined here to eliminate potential age effects. Although this analysis does not account for possible differences in detection based on diet, it provides a preliminary sense of which individuals would be most favorable to translocate; even if individuals not seen in the survey were actually alive, it could indicate undesired behaviors, such as dispersal away from the core protected areas of the reserve.

We conducted Likelihood Ratio Tests to assess whether an individual's presence in the September survey depended on its cohort (Source Site Juveniles or Translocated Juveniles) and three dietary metrics: (i) pre-translocation PS_i; (ii) post-translocation PS_i; and (iii) $\triangle PS_i$, calculated as:

$$\frac{(Post-translocation\ PS_i - Pre-translocation\ PS_i)}{Pre-translocation\ PS_i}.$$

Models containing the interaction of interest (cohort$*$dietary metric) were compared to successively simplified models without the higher-order effect. As the response variable was binary (present/absent), models were structured as Generalized Linear Mixed Models (GLMMs) with a binomial family and logit-link function. A random effect of post-translocation site was included to account for possible differences between the two Release Sites.

4.3 RESULTS

Testing the shared preferences and distinct preferences models

In the post-translocation period, all observed populations and cohorts were significantly more specialized than expected by chance (Monte Carlo simulations: $P < 0.001$). The three populations had similar Total Niche Widths, with a TNW of 1.97 at the Source Site (n = 61 individuals), 2.03 at Release Site 1 (n = 42 individuals), and 2.10 at Release Site 2 (n = 32 individuals). However, TNW was explained by different relative contributions of within- and between-individual variation at each site. WIC/TNW at the Source Site (0.35) was 44% lower than at Release Site 1 (0.62) and 36% lower than at Release Site 2 (0.55). This indicates greater dietary specialization at the more competitive Source Site, consistent with the shared preferences model of dietary variation.

Across sites, there were different effects of age and residency on specialization. Juveniles (*n* = 25) and adults (*n* = 36) were equally specialized at the Source Site (WIC/TNW = 0.38) but differed at the two Release Sites: juveniles (*n* = 29, WIC/TNW = 0.56) were more specialist than adults (*n* = 13, WIC/TNW = 0.78) at Release Site 1 and slightly more generalist than adults at Release Site 2 (juveniles: *n* = 12, WIC/TNW = 0.59; adults: *n* = 20, WIC/TNW = 0.55; Figure 4.4a). At Release Site 1, there were no major differences in specialization based on residency (translocated: *n* = 22, WIC/TNW = 0.62; resident: *n* = 20, WIC/TNW = 0.66), but newly-translocated individuals (*n* = 6; WIC/TNW = 0.70) were more generalist than residents (*n* = 26; WIC/TNW = 0.53) at Release Site 2 (Figure 4.4b). When only juveniles were considered, residents (Release Site 1: *n* = 7, WIC/TNW = 0.47; Release Site 2: *n* = 6, WIC/TNW = 0.56) tended to be 20–25% more specialist than newly-translocated individuals (Release Site 1: *n* = 22, WIC/TNW = 0.62; Release Site 2: *n* = 6, WIC/TNW = 0.70; Figure 4.4c) at both Release Sites.

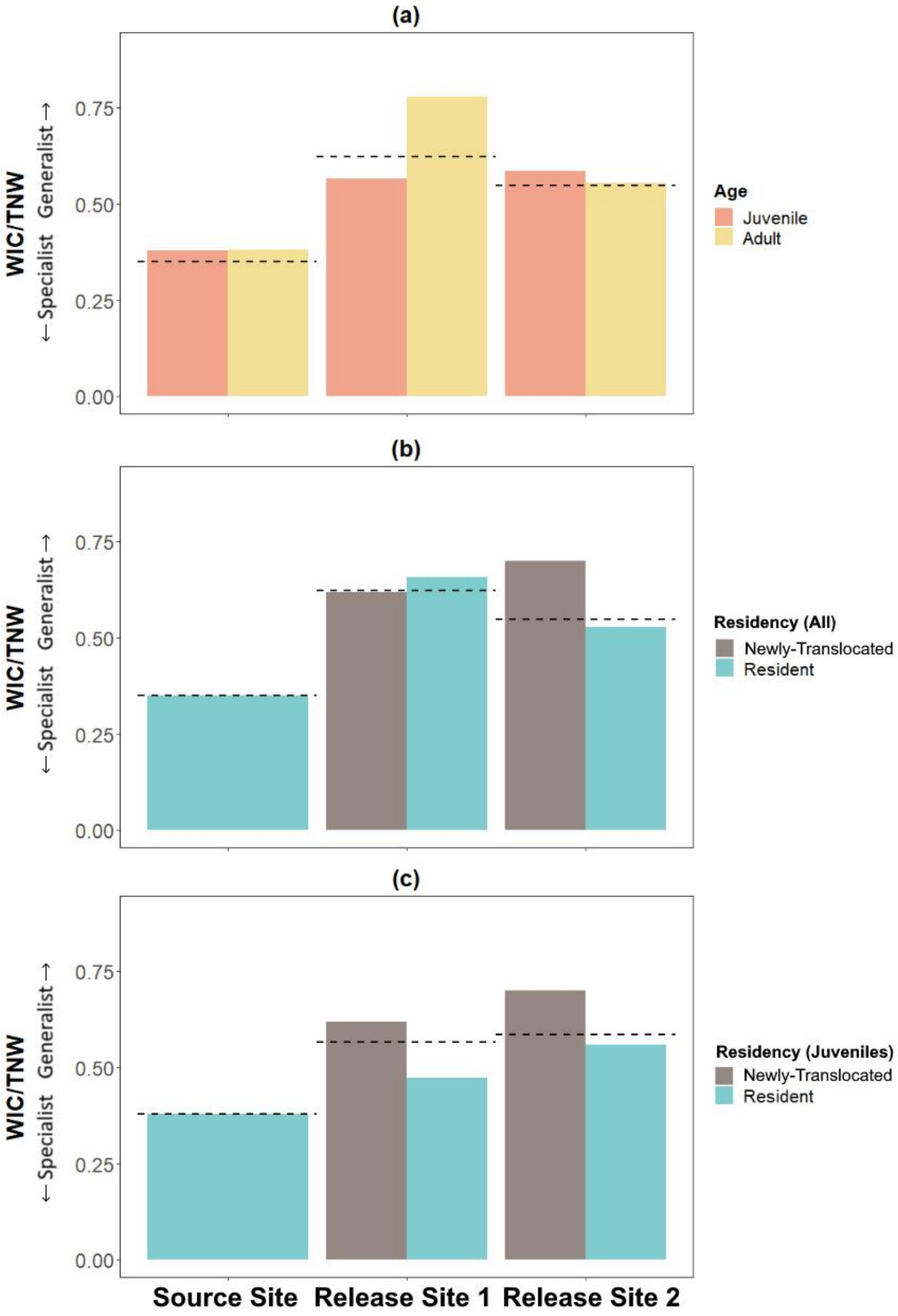

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Figure 4.4. Comparisons of dietary specialization in the post-translocation period between (a) age cohorts, (b) residency cohorts, and (c) juvenile residency cohorts within each site. Dietary specialization is represented by the proportion of the population's total niche width (TNW) that is explained by the dietary breadth of individuals (within-individual component of variation: WIC); lower values reflect a specialist population where individuals consume distinct, narrow diets, and higher values reflect a generalist population where individuals consume broad, overlapping diets. Dashed lines indicate WIC/TNW for (a–b) the full population or (c) the juvenile subset of the population.

Examining dietary responses to competitive release

Individual dietary specialization (PS_i) depended on an interaction between an individual's cohort and the time period (cohort∗time: $\chi^2 = 13.87$, df = 2, $P < 0.001$; Figure 4.5). Before the translocation, mean dietary specialization did not differ significantly among the three cohorts: Source Site Adults (n = 29, mean PS_i = 0.42 ± 0.02) were equally specialized as Source Site Juveniles (n = 21, mean PS_i = 0.37 ± 0.02) and Translocated Juveniles (n = 26, mean PS_i = 0.43 ± 0.02; Table 4.1a). However, after the translocation, all cohorts differed significantly: Source Site Adults were the most specialist (n = 27, mean PS_i = 0.33 ± 0.03), followed by Source Site Juveniles (n = 21, 0.43 ± 0.04) and Translocated Juveniles (n = 27, 0.51 ± 0.02; Table 4.1b). Within cohorts, Source Site Adults changed significantly across the translocation, becoming more specialist, while Translocated Juveniles became significantly more generalist (Table 4.1c). Meanwhile, Source Site Juveniles did not change significantly but trended weakly toward generalization (Table 4.1c); as a result, the change in PS_i across the translocation did not differ significantly between juvenile cohorts (Table 4.1d). Notably, compared to the other two cohorts, where individuals were distributed along a continuum of PS_is, Source Site Juveniles diverged after the translocation into being either more generalist or more specialist (Figure 4.5).

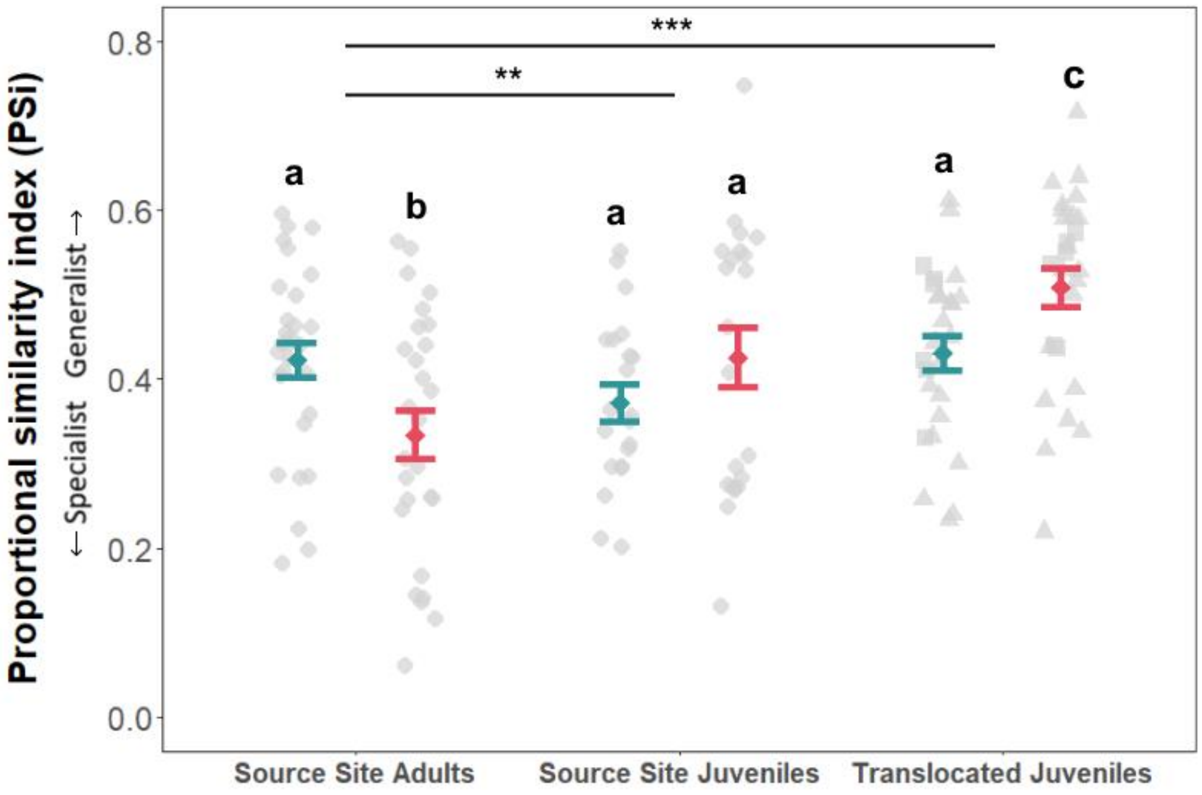

Figure 4.5. Change in mean dietary specialization (PS_i) across the translocation for each of the three focal cohorts: adults remaining at the Source Site, juveniles remaining at the Source Site, and juveniles translocated to one of the two Release Sites. Gray points are the raw data (PS_is calculated within cohort), with shape indicating the individual's location after the translocation (circle = Source Site; triangle = Release Site 1; square = Release Site 2). Means and standard error bars are colored to indicate the time period (blue = pre-translocation; red = post-translocation). Letters indicate significant differences between all mean PS_is, and stars indicate significant interactions (cohort∗time).

Table 4.1. Pre- and post-translocation PS_i comparisons within and between cohorts.

Comparison	Estimate ± S.E.	*t*	*P*-value	
(a) Between Cohorts: Pre-Translocation				
Source Site Adults vs. Source Site Juveniles	0.051 ± 0.035	1.448	0.150	
Source Site Adults vs. Translocated Juveniles	−0.008 ± 0.033	−0.241	0.810	
Source Site Juveniles vs. Translocated Juveniles	−0.059 ± 0.036	−1.636	0.104	
(b) Between Cohorts: Post-Translocation				
Source Site Adults vs. Source Site Juveniles	−0.091 ± 0.036	−2.572	**0.011**	*
Source Site Adults vs. Translocated Juveniles	−0.174 ± 0.033	−5.245	**<0.001**	***
Source Site Juveniles vs. Translocated Juveniles	−0.083 ± 0.036	−2.334	**0.021**	*
(c) Within Cohort: Pre- vs. Post-Translocation				
Source Site Adults	−0.089 ± 0.033	−2.708	**0.008**	**
Source Site Juveniles	0.054 ± 0.038	1.423	0.157	
Translocated Juveniles	0.078 ± 0.034	2.322	**0.022**	*
(d) Between Cohorts: Change in PS_i				
Source Site Adults vs. Source Site Juveniles	−0.142 ± 0.050	−2.849	**0.005**	**
Source Site Adults vs. Translocated Juveniles	−0.166 ± 0.047	−3.553	**<0.001**	***
Source Site Juveniles vs. Translocated Juveniles	−0.024 ± 0.050	−0.482	0.631	

Note: Results of pairwise comparisons from an LMM predicting dietary specialization (PS_i) from an interaction between cohort (Source Site Adults, Source Site Juveniles, Translocated Juveniles) and time (pre vs. post-translocation). Comparisons are made (a) between cohorts before the translocation; (b) between cohorts after the translocation; (c) within cohorts before vs. after the translocation; and (d) between dietary changes experienced by cohorts across the translocation. Significant *P*-values are indicated in bold.

Individuals' diets after the translocation differed by cohort but did not depend on their diet relative to the cohort mean before the translocation (cohort∗pre-translocation differential: $\chi^2 = 0.963$, df = 2, $P = 0.618$; pre-translocation differential: estimate = -0.135 ± 0.184, $t = -0.734$, $P = 0.466$). Regardless of whether they were more or less specialist than other cohort members before the translocation, adults remaining at the Source Site became significantly more specialist than the cohort mean after the translocation (intercept < mean pre-translocation PS_i; $z = -2.851$, $P = 0.004$). Translocated juveniles showed the opposite effect, becoming significantly more generalist than the cohort's starting mean (intercept > mean pre-translocation PS_i; $z = 2.072$, $P = 0.038$). Meanwhile, juveniles remaining at the Source Site were more split in their dietary changes; although they tended to become slightly more generalist, this trend was not significant ($z = 1.601$, $P = 0.109$; Figure 4.6).

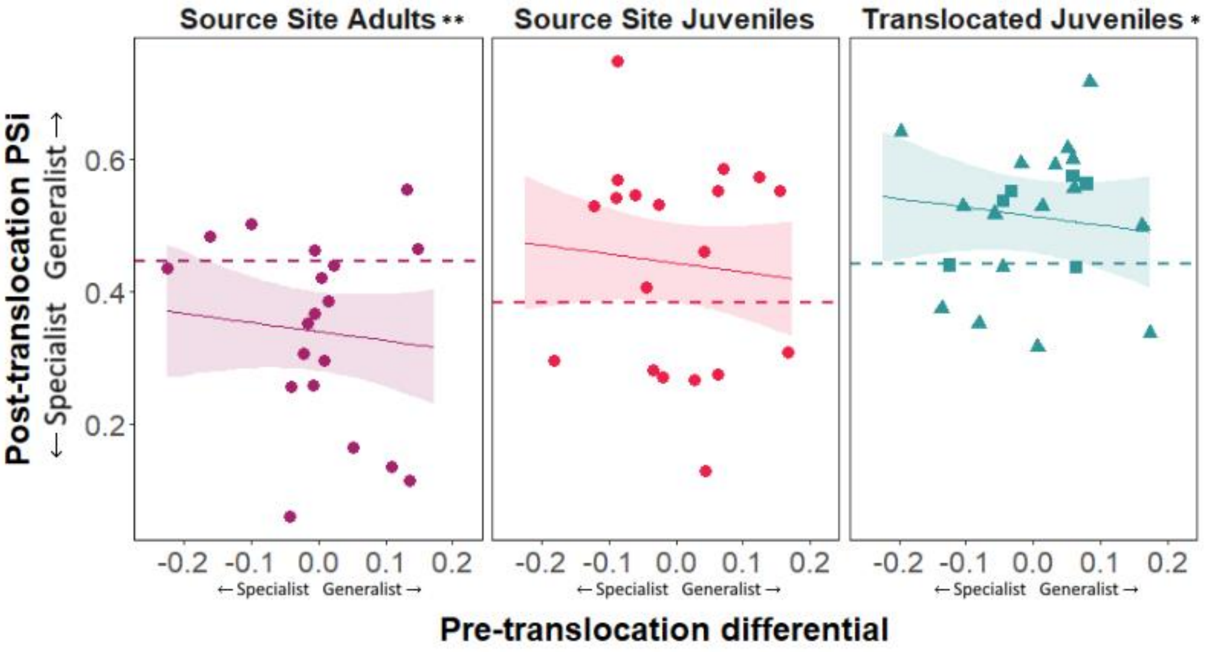

Figure 4.6. Relationship between individuals' post-translocation dietary specializations (PS_is) and their pre-translocation diet relative to the cohort mean ('pre-translocation differential'). Regression lines (solid lines) and 95% confidence regions (shaded areas) are extracted from an LMM with cohort and pre-translocation differential as additive fixed effects; slopes are not significant. Dashed horizontal lines represent each cohort's mean PS_i before the translocation, with significance stars next to the cohort name indicating that this mean differs significantly from the intercept of the regression line. Points are the raw data (PS_is calculated within cohort), with shape indicating the individual's post-translocation site (circle = Source Site; triangle = Release Site 1; square = Release Site 2).

Predicting post-release survival

There was a significant relationship between an individual's dietary specialization before the translocation and their five-month survival (sighting in September 2018 survey), but this depended on their cohort (pre-translocation PS_i*cohort: $\chi^2 = 15.73$, df = 1, $P < 0.001$; Figure 4.7a). For juveniles remaining at the Source Site ($n = 31$), individuals were more likely to survive if they were more generalist before the translocation (estimate = 15.4 ± 5.7, $z = 2.691$, $P = 0.007$). Among translocated juveniles ($n = 32$), there was a trend in the opposite direction, with specialists more likely to survive, but this was not quite significant (estimate = −6.5 ± 3.6, $z = -1.814$, $P = 0.070$). Survival was also predicted by the dietary change that an individual experienced across the translocation in interaction with their cohort ($\triangle PS_i*$cohort: $\chi^2 = 6.47$, df = 1, $P = 0.011$; Figure 4.7b). At the Source Site ($n = 19$), juveniles that shifted toward a more specialist diet ($\triangle PS_i < 0$) were more likely to survive than those that became more generalist (estimate = −4.5 ± 2.0, $z = -2.241$, $P = 0.025$), with no significant relationship in translocated juveniles ($n = 22$; estimate = 0.46 ± 1.15, $z = 0.398$, $P = 0.690$). Meanwhile, there was no significant relationship between survival and post-translocation PS_i ($\chi^2 = 0.085$, df = 1, $P = 0.771$) or cohort ($\chi^2 = 1.56$, df = 1, $P = 0.212$).

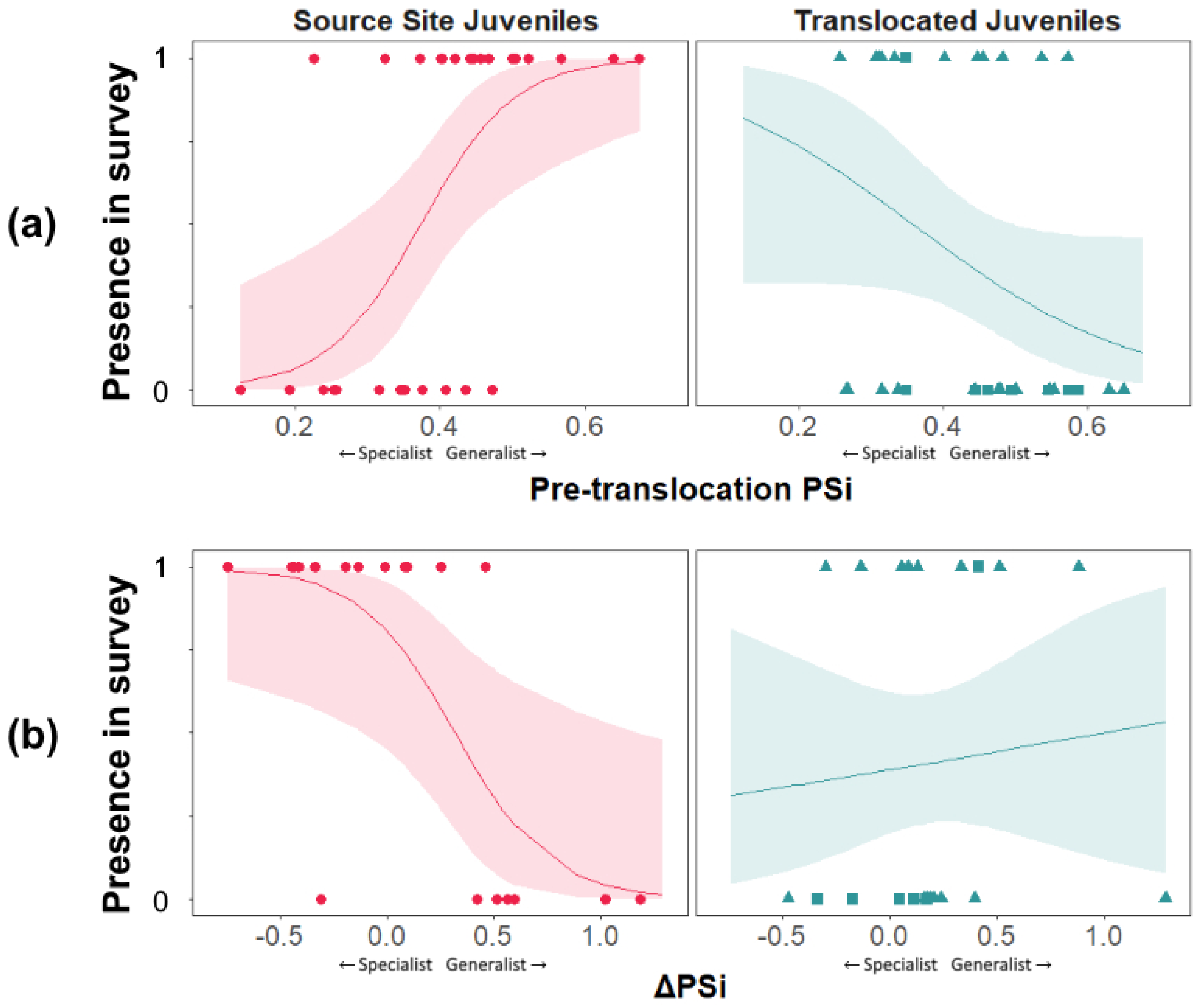

Figure 4.7. Relationship between individuals' presence in the September 2018 survey (five months post-translocation) and their (a) dietary specialization before the translocation (pre-translocation PS_i, calculated within cohort) or (b) proportional change in dietary specialization across the translocation ($\triangle PS_i$). Juveniles that remained at the Source Site are presented on the left, and juveniles translocated to one of the two Release Sites are presented on the right. Regression lines (solid lines) and 95% confidence regions (shaded areas) are extracted from a GLMM with an interaction between cohort and the respective dietary metric. Points are the raw data (PS_is calculated within cohort), with shape indicating the individual's post-translocation site (circle = Source Site; triangle = Release Site 1; square = Release Site 2).

4.4 DISCUSSION

Measuring dietary responses to competitive release can provide insight into the structure of a population's niche and the inherent preferences of individuals (Svanbäck and Bolnick 2005; Araújo et al. 2011; Bolnick et al. 2011). Here, we used two translocations of hihi, a threatened New Zealand passerine, to experimentally test how individuals' diets changed when they were moved from a highly competitive Source Site to two less competitive Release Sites. After the translocation, individuals at the Release Sites consumed broader, more overlapping diets than those remaining at the Source Site, suggesting that individuals share the same inherent resource preferences but must specialize to avoid competition in denser populations (Svanbäck and Bolnick 2005; Araújo et al. 2011). By tracking dietary changes across the translocation, we also found a consistent response to competitive release within the translocated cohort: translocated juveniles shifted consistently and significantly toward more generalist diets. Meanwhile, depending on their age, individuals remaining at the Source Site either did not change significantly (juveniles) or became more specialist (adults). There was also evidence that individuals' diets may have consequences for survival. Individuals that were generalist before the translocation exhibited higher five-month survival than specialists, but only if they remained at the Source Site; at the two Release Sites, generalists had lower survival than specialists. Overall, our study demonstrates that translocations can provide behavioral ecologists with a rare opportunity to test the causes and consequences of dietary variation, with potential implications for conservation.

Our results provide strong evidence that competition and resource limitation drive dietary differences among hihi. Consistent with the shared preferences model (Svanbäck and Bolnick 2005; Araújo et al. 2011), hihi consume generalist diets under low competition but differentiate into distinct dietary specializations under high competition. This pattern is consistent with past findings in a range of mammals (e.g. Tinker et al. 2008; Tinker et al. 2012; A. Robertson et al. 2015), fish (e.g. Svanbäck and Persson 2004; Svanbäck and Bolnick 2007; Araújo et al. 2014), birds (e.g. Pagani-Núñez et al. 2016) and reptiles (e.g. Santamaría et al. 2020), but the mechanisms by which hihi achieve specialization may differ from other species. In general, intraspecific competition tends to favor the expansion of a population's total niche as individuals broaden their diets to include foods that would normally be ignored (e.g. Svanbäck and Persson 2004; Svanbäck and Bolnick 2007). However, our three study populations all had similar total niche widths after the translocation. This suggests that specialization in hihi is shaped mainly by the expansion and contraction of individuals' niches, while the population's niche remains fixed. The high degree of interspecific competition at the Source Site could explain this result, as dominant heterospecifics can constrain a population’s niche by making certain resources unattainable (Araújo et al. 2011). If hihi must specialize to avoid competing with each other but are forced to do so within a restricted population niche, individuals may not be able to meet their dietary needs from their narrow specializations. This could potentially explain the source population’s high reliance on supplementary feeding (Thorogood et al. 2013).

There was also some evidence that diet depended not only on the social environment but on age. While only translocated juveniles’ diets changed significantly across the translocation, all juveniles trended toward more generalist diets. This could suggest that juveniles have a natural tendency to become more generalist in the post-translocation period, which is amplified by competitive release. Alternatively, it could show that, like their translocated peers, juveniles remaining at the Source Site also experienced a small degree of competitive release due to the translocation. While we know that removing 40 individuals has minimal impacts on the demographics of the source population (D. Armstrong and Ewen 2013), we may have underestimated the social impact, particularly for juveniles. Juvenile hihi aggregate after fledging in juvenile-dominated ‘gangs,’ largely isolating them from the adult social structure (Franks et al. 2020). Because only juveniles were translocated, removing 40 individuals (about 25% of the juvenile cohort) could have impacted the degree of competition experienced by juveniles, while adults remained largely unaffected. Furthermore, if translocated juveniles were selected non-randomly with respect to gang membership, some Source Site juveniles may have experienced a greater competitive release than others. This may be why Source Site juveniles clustered into two distinct dietary groups after the translocation—one more specialist and one more generalist—which may reflect the degree of competitive release they experienced. Unfortunately, our foraging observations did not measure social groupings in sufficient resolution to assess this, but it would be worthwhile to incorporate measures of social connectivity into future studies.

When using translocations to test foraging theory, it is important to consider that the translocation process itself imposes unique challenges on individuals (Dickens et al. 2010; IUCN/SSC 2013) that could influence foraging. After the translocation, we found distinct differences in dietary specialization between newly-translocated and resident juveniles at the Release Sites: both were more generalist than Source Site juveniles (as predicted by the shared preferences model), but the translocated birds were even more so. This suggests that the act of being translocated may have caused birds to shift beyond the level of generalization normally favored at their release site. Why might this be? Anecdotally, translocated birds concentrated in just a few small areas in the initial weeks after release. Remaining in a group could be beneficial to birds navigating an unfamiliar environment, because foraging socially can help individuals discover new food sources (Galef and Giraldeau 2001) and reduce predation risk (Sorato et al. 2012). Alternatively, these post-release aggregations could be a byproduct of our translocation methods; we released individuals in only two locations at each site, and translocated individuals sometimes exhibit strong site fidelity to release locations (Banks et al. 2002; Berger-Tal and Saltz 2014). Regardless of the cause, these post-release groupings may explain why newly-translocated individuals exhibited such generalist diets, as they were foraging on a common pool of resources in a small area. Over time, as they disperse and begin to form territories (typically within four weeks for hihi: Richardson and Ewen 2016; Metcalf et al. 2019), their generalization may decrease in line with residents' diets.

In addition to serving as a test of behavioral ecology theory, our study could also inform future translocation efforts. Habitat suitability and food limitation are major factors affecting translocation success (Magdalena Wolf et al. 1998; Berger-Tal et al. 2020), so selecting a release site that meets a species' dietary needs is a critical decision (Seddon et al. 2007; D. Armstrong and Seddon 2008; IUCN/SSC 2013; Seddon et al. 2014). Observing how individuals responded to competitive release helped to reveal inherent food preferences, which could guide the selection of release sites for future translocations of hihi. However, if diets shift in response to changing competition, then a population's needs may also change over time. As the population (and competition) grows, individuals may need to seek refuge through specialization, so there could be a longer-term need for diverse, less preferred resources to support dietary diversification. Thus, it is important to consider how individuals will respond not only to the immediate environmental changes associated with translocation (Owen-Smith 2003; Silver and Marsh 2003; Ewen and Armstrong 2007; B. Bell 2016) but also to longer-term changes associated with population establishment.

Another challenge for conservation biologists is how to select individuals for translocation to give them their best chance of success. In recent years, there has been increasing interest in using individuals' behaviors at the source site to predict their success after release (Arcese 2003; Sinn et al. 2014; May et al. 2016; Germano et al. 2017; Merrick and Koprowski 2017). However, while studies of captive-reared animals suggest that early-life diet can influence post-release survival (Whiteside et al. 2015), to our knowledge, diet has not yet been explored as a candidate trait for selecting wild-born individuals for translocations. Here, we found a benefit of translocating juvenile hihi with more specialist pre-translocation diets. Regardless of how their diets changed, these birds tended to be more likely to survive to their first breeding season than generalists. Meanwhile, specialists remaining at the Source Site were less likely to survive the same period, so selectively translocating them would not weaken the source population—

a common concern in translocations (D. Armstrong and Seddon 2008). Past work suggested that generalist hihi may have a competitive advantage over specialists at the Source Site (Chapter 3), but, in many species, competitively dominant individuals are less innovative than subordinates (Reader and Laland 2001; Thornton and Samson 2012; Aplin et al. 2013; Keynan et al. 2015). Thus, specialist hihi may be disadvantaged at the Source Site but better equipped to adapt to a novel foraging environment, increasing their chances of survival. Further investigation is needed to confirm that the survival result holds after accounting for differences in detection based on diet, as we did not have sufficient data to do so here.

Overall, our study suggests that competitive release drives hihi toward more generalist diets, in line with the shared preferences model of dietary variation. We have also demonstrated how translocations can provide behavioral ecologists with opportunities to test theories that might otherwise be challenging to examine in a natural setting. Translocations do have their limitations: they often involve small sample sizes, and, as conservation priorities take precedence, there may be little control over which individuals are translocated. In our case, translocating a greater number of individuals may have enabled us to detect a stronger effect of diet on survival, and translocating a mixed cohort of juveniles and adults may have allowed us to control for age effects. Nevertheless, a major benefit of using translocations to test theory is that it allows behavioral ecologists to contribute to conservation in novel ways. By setting shared goals from the beginning of a translocation program, these interventions may be designed so that behavioral ecologists and conservation biologists can both answer their questions of interest. Given the fragile state of biodiversity today, there has never been a more important time for these two fields to merge to their mutual benefit and to the benefit of the species we all value.

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Chapter 5

Flower power? Testing the ecological implications of individual traplining tendencies

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Intraspecific behavioral differences can shape individuals' fitness and population dynamics, but less is known about how this variation scales up to affect higher ecological levels. Here, we tested the consequences of behavioral variation for pollination, a mutualism with far-reaching effects on ecosystem health. Previously, several effective pollinator species have been found to exhibit a specialized foraging pattern called 'traplining,' where plants are checked for nectar in a systematic sequence. This can improve pollen diversity and dispersal distance, but it is unclear how much individuals vary in their traplining tendencies and whether this impacts pollination. Using the hihi, a threatened avian pollinator endemic to New Zealand, as a case study, we presented individuals with an open-field analogue of a radial arm maze consisting of a pentagonal array of novel feeders. Consistent with traplining, individuals tended to search the array systematically, favoring adjacent turns between feeders. They also avoided repeat visits to empty feeders, but males and older individuals did so more successfully than females and younger individuals. Meanwhile, females were more persistent in the task, continuing to search until they found food, while males gave up more frequently. These results show that individual hihi vary in traits previously found to predict pollination efficiency at the species level. Yet, when we measured pollination outcomes on individuals' territories, we found no evidence that performance in the foraging task predicted territory holders' contributions to pollination. Overall, our study provides a rare test of how individual variation can influence ecological function and suggests that traits known to be consequential at the species level may differ in their consequences at the individual level.

5.1 INTRODUCTION

With the knowledge that individuals within species often vary in their behaviors (Bolnick et al. 2003; Sih et al. 2004; Réale et al. 2007), ecologists are increasingly interested in determining the consequences of this variation. Most studies focus on linking behavioral variation to individual fitness (Dingemanse and Réale 2005; B. Smith and Blumstein 2008; Costa-Pereira et al. 2019). However, variation can also scale up to influence broader ecosystem dynamics (Bolnick et al. 2011; Wolf and Weissing 2012; Raffard et al. 2017), particularly when behaviors underlie key interspecific interactions. For instance, animal-plant mutualisms provide many opportunities for behavioral variation to impact ecological function. Plants that depend on these interactions, being immobile, effectively derive their own movement patterns and reproductive success from the behaviors of their animal mutualists (Snell et al. 2019); therefore, if individual pollinators or seed dispersers vary in their effectiveness, it could impact the fitness of the plants they encounter (Zwolak 2018; Snell et al. 2019). Through their influence on plants, animals can also drive long-lasting structural changes to the ecosystem, with cascading effects on other species. This effect has been underscored by the current biodiversity crisis; worldwide, declines of animal mutualists are threatening the stability of the ecosystems they contribute to (Kelly et al. 2010; Potts et al. 2010; Neuschulz et al. 2016). If individuals vary in their contributions to ecological function, conservation biologists could potentially harness this variation to improve the effectiveness of behavior-based interventions. However, this would require a better understanding of how individual differences translate into ecological consequences, and most work on this topic remains theoretical.

There has been a recent rise in studies investigating how variation across a range of behavioral traits affects seed dispersal quality (see Zwolak 2018 for a review). For instance, in small mammals, an individual’s boldness, docility, and stress response have been found to predict the distance it disperses seeds and the quality of sites where it deposits them (Brehm et al. 2019; Feldman et al. 2019). Meanwhile, most work on pollination remains focused on traits such as body size (Willmer and Finlayson 2014; Jauker et al. 2016), age, or sex (G. Smith et al. 2019; Fuster and Traveset 2020), with less attention given to behavior (but see: Thomson and Chittka 2009; Maruyama et al. 2016). This is somewhat surprising given that behavioral differences have long been used to explain variation across pollinator species, with many of these behaviors now known to vary at the individual level. Perhaps most prominently, several effective pollinator species exhibit a unique foraging pattern called ‘traplining,’ in which plants are checked for nectar in a systematic sequence (Janzen 1971; D. Anderson 1983). From the pollinator’s perspective, this strategy helps to maximize the efficiency of their route and minimize repeat visits to depleted flowers (Thomson 1996; Thomson et al. 1997; Williams and Thomson 1998; Ohashi et al. 2006; Saleh and Chittka 2007). From the plant's perspective, traplining enhances reproduction by increasing pollen diversity and dispersal distance (Ohashi and Thomson 2009). Another trait that can influence the amount of pollen transported is a pollinator's persistence (Laverty and Plowright 1988), or likelihood to continue searching until they find nectar. While some studies evaluating traplining have found evidence that individuals may vary (Thomson 1996; Saleh and Chittka 2007; Tello-Ramos et al. 2015), less is known about variation in persistence. Furthermore, differences in traplining and persistence have rarely been tested explicitly or evaluated to see whether they predict quantifiable pollination outcomes.

In this study, we tested for individual variation in pollination ability in a system where this information could inform conservation. The hihi (*Notiomystis cincta*) is a threatened passerine endemic to New Zealand, where it is thought to have been one of the most important pollinators (Craig et al. 1981; S. Anderson 2003; Kelly et al. 2006; S. Anderson et al. 2011) before habitat loss, predation, and disease nearly drove it to extinction in the late 1800s. Today, hihi exist in one remnant population on Te Hauturu ō Toi (Little Barrier Island Nature Reserve) and seven reintroduced populations across the North Island. The species' broad annual diet includes fruit, invertebrates, and nectar (Craig 1985; Rasch and Craig 1988; Chapter 2), but nectar dominates in spring (Gravatt 1971; Angehr 1984; Rasch and Craig 1988; Chapter 1), coinciding with the flowering period for most native plants. Many of these plants are threatened, themselves (Kelly et al. 2010). Thus, hihi translocations aimed primarily at species recovery often cite the restoration of pollination function as an added potential benefit (Smuts-Kennedy 2009; Frost 2012; Collins et al. 2015). However, these efforts typically assume that all hihi are equally effective at achieving restoration goals, when there is evidence for individual variation in dietary specialization (Chapter 2) and age differences in learning ability (Franks and Thorogood 2018). If behavioral variation drives differences in pollination ability, conservation biologists could promote ecosystem recovery by selectively translocating individuals with favorable pollinator traits, just as other translocations have used behavior to predict post-release survival (e.g. Sinn et al. 2014; May et al. 2016; Germano et al. 2017).

We first conducted a pollinator exclusion experiment across 50 hihi territories on Tiritiri Matangi Island, home to the main source population for hihi translocations (Thorogood et al. 2013). Hihi are socially monogamous, and males defend their territories from intra- and interspecific intruders during the breeding season (Ewen et al. 2004; Low 2005); thus, conducting the study on territories ensured that plant visitation by birds was limited to the two hihi territory holders as much as possible. After measuring birds' contributions to fruit set, we then examined whether these contributions were predicted by the territory holders' performance in a novel foraging task, presented in the following season to avoid disrupting natural foraging during the pollination experiment. The task consisted of an open-field analogue of a classic radial arm maze (Healy and Hurly 1995; Foreman and Ermakova 1997) and captured three key pollinator behaviors: an individual's search sequence and avoidance of depleted flowers (two components of traplining), and its persistence. Using these metrics, we (1) assessed the traplining abilities and persistence of hihi as a species; (2) evaluated age, sex, and individual differences; and then (3) investigated whether the most successful trapliners enhanced pollination to a greater degree on their territories. Through these questions, we aimed to conduct a rare assessment of whether individual differences in foraging behaviors link to measurable differences in pollination outcomes.

5.2 METHODS

Study site and population

Tiritiri Matangi Island (36°36'00.7"S 174°53'21.7"E) is a 220-hectare nature reserve home to a hihi population (~200 individuals) established through translocation in 1995. Located 3.5 km off the coast of the North Island mainland, the island was farmed for over a century but was extensively replanted in the 1980s. Today, it consists mainly of regenerating native bush, which supports a high density of remnant and reintroduced native bird species. Due to a shortage of natural tree cavities, all hihi on the island nest in artificial nest boxes, with two boxes (within 10 m of each other) per territory, and territories estimated to be at least 30 m apart (Ewen et al. 2018). Nest boxes are intensively monitored during the breeding season to identify territory holders and track breeding activities. At 21-days old, nestlings are sexed based on early signs of sexually dimorphic plumage (C. Smith et al. 2015) and uniquely color banded to facilitate individual identification after fledging. As in all other reintroduced populations (Chauvenet et al. 2012; Thorogood et al. 2013; Doerr et al. 2017), the hihi at this site rely on supplementary feeding to varying degrees throughout the year, with sugar water provided *ad libitum* in six feeder cages across the island.

Pollinator exclusion experiment

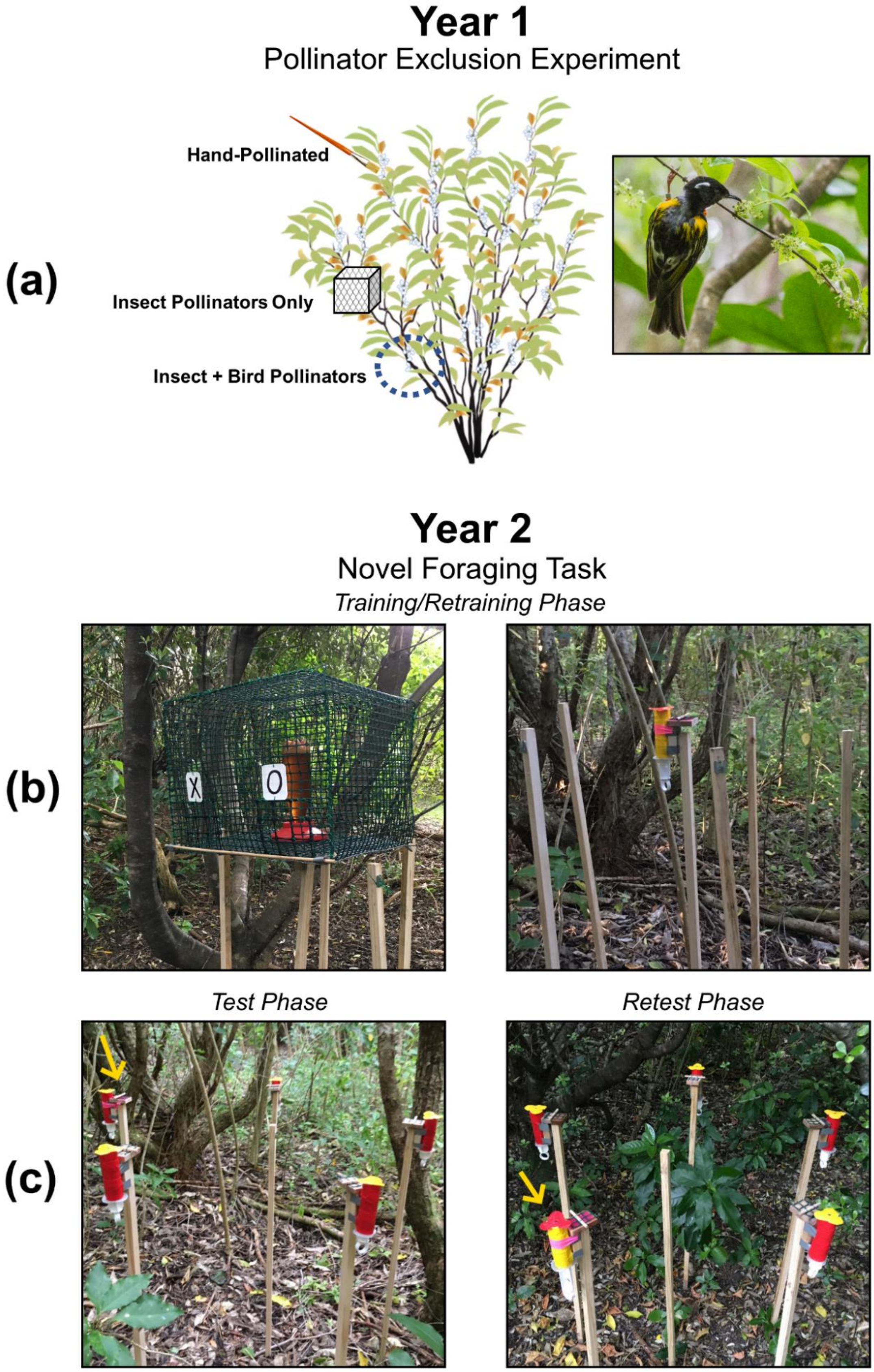
For the purposes of this study, we focused on pollination of hangehange (*Geniostoma ligustrifolium*), a gynodioecious (Rattenbury 1980) native understory shrub. Like many New Zealand plants, hangehange was long assumed to be insect-pollinated due to its small (< 4 mm), inconspicuous pale-green flowers. However, it is now known to receive much of its pollination from birds, including hihi (Castro and Robertson 1997; S. Anderson 2003). Hangehange is particularly suitable for experimentation on Tiritiri Matangi because it is widespread across the island and flowers during the hihi breeding season. During peak flowering in October, hangehange nectar makes up about 65% of the hihi diet (Chapter 1).

A pollinator exclusion experiment was set up from 14th September–20th September 2017, at the start of the hangehange flowering period and just prior to the start of the hihi breeding season. Fifty hihi territories with a high chance of occupancy based on trends over the last three breeding seasons were selected across the island. On each territory, up to five mature hangehange plants ($\bar{x}$ ± S.E.: 4.08 ± 0.21; for a total of 204 plants across the island) were selected within 20 m of the nest boxes. We attempted to select only female plants, which can be identified based on the presence of moderate to high numbers of dry fruit capsules remaining from the previous reproductive cycle. If we accidentally selected any hermaphrodite plants, self-pollination rates would be accounted for by our pollination metric (see below), which compared outcomes across branchlets within the same plant.

On each focal plant, we assigned one branchlet containing at least 10 unopened buds to each of the following pollinator conditions (Kearns and Inouye 1993; Figure 5.1a):

(1) Insect Pollinators Only: branchlet enclosed in a 2x2 cm wire mesh cage to exclude birds but allow insects (mesh size selected following S. Anderson 2003; continued insect visitation confirmed by Schmidt-Adam et al. 2009; no birds observed attempting to forage through mesh during anecdotal observations);
(2) Insect + Bird Pollinators: branchlet left open to natural pollination;
(3) Hand-Pollinated: branchlet left open to natural pollination and pollinated by hand during the receptive period (following the methods of S. Anderson 2003).

All territories were revisited once flowers were open and receptive (about three weeks later) to complete the hand-pollination treatment, once flowers had passed receptivity (about six weeks after the start of experiment) to remove coverings, and in late December 2017 to count fruits on each branchlet. Dividing this count by the original number of buds provided a measure of fruit set (proportion of buds that developed into fruits). We restricted this value to be below 1, as values greater than 1 suggest that additional buds formed after the initial bud count.



(*Figure caption on next page*)

Figure 5.1. Overview of the study phases. (a) In Year 1, a pollinator exclusion experiment was conducted on Tiritiri Matangi Island. Flowers on 204 hangehange plants were exposed to three pollination treatments: insect pollinators only (enclosed in wire mesh to exclude birds), insect+bird pollinators (left open), or hand-pollinated (left open and brushed with pollen during the receptive period). To isolate the effects of hihi (a, right) on pollination as much as possible, the experiment was conducted on 50 hihi territories. (b–c) In Year 2, a novel foraging task was introduced on 33 hihi territories. Territory holders were first trained using a familiar feeder (b, left) for 1.5 days, then introduced to a novel ‘flower’ feeder (b, right: Retraining Phase flower) for up to two hours. The novel flower was then replaced by an array of five flowers (c, left: Test Phase; c, right: Retest Phase), with a single rewarding flower (yellow arrow) moved randomly within the array each time a hihi visited over a five hour period. Image credits: bush adapted from public domain image, hihi photo by Martin Sanders, all other photos by CA.

Novel foraging task

From 20th September–13th November 2018, a novel foraging task was presented on 33 hihi territories on Tiritiri Matangi. We targeted individuals who, in the previous season, had been resident on territories involved in the pollinator exclusion experiment. Many now resided on new territories with different partners. Even if they did not have pollination data, we included these new partners in the task to increase our sample size for assessing species-level traplining tendencies and differences across age-sex classes. Each territory had an active nest throughout each phase of the task.

Training Phase

In early afternoon (c. 15:00), a 0.1 m^3 feeder cage was placed on the focal territory at least 10 m from both nest boxes. The cage was supported by 1 m tall wooden posts and was built from 2x2 cm plastic mesh, with two 4x4 cm holes (marked with an ‘X’ and ‘O’ for another study) on one side allowing birds to enter. Inside was a hummingbird-style feeder consisting of a red base topped with a 1.5 L translucent brown bottle containing 20% sugar solution. Some territory holders had encountered this feeder design (Figure 5.1b) in a previous study (Franks et al. 2018), and all had experience feeding on the same sugar solution at the island’s permanent supplementary feeding stations.

The training feeder was left in place the entire next day to allow territory holders to associate the location with a reward. On the following morning (c. 8:00), the feeder was removed and replaced by five 1 m tall wooden posts in a pentagonal array of 0.6 m radius. An additional post at the center of the pentagon was topped with a ‘novel flower’ feeder (Figure 5.1b) consisting of a red plastic tube (12 cm high, 5 cm diameter). The bottom of the tube was sealed with a plunger. The top opening was covered in yellow duct tape, with three yellow ‘petals’ (4 cm diameter half-circles of duct tape) around the edges and a 0.75 cm diameter hole in the center, large enough to allow feeding but small enough to prevent visual inspection of the tube’s contents. A perch consisting of a 7 cm long dowel (0.75 cm diameter) resting on a small wooden platform (4.5x6 cm, covered in plastic mesh for traction) was affixed 3 cm below the top of the tube. As part of another study on visual cue learning, the tube was tied with a small piece of pink flagging tape, and the perch platform was colored pink; however, no birds learned to associate these cues with food during the Test Phase.

The observer filled the tube with 20% sugar solution, then sat under cover of vegetation at least 5 m away. Of the 33 territories, 31 completed training, which varied in length due to weather and logistical constraints. On 27 territories, one (female only: n = 9; male only: n = 9) or both (*n* = 9) territory holders fed from the novel flower within 79 minutes ($\bar{x}$ ± S.E. = 23 ± 4) and proceeded to the Test Phase. On four territories, neither territory holder fed within 93 minutes (54 ± 15), but these territories progressed to the Test Phase because territory holders were highly active in the vicinity of the novel flower. Two territories were excluded from the Test Phase, because neither territory holder fed from, or came within proximity of, the novel flower within two hours. At the end of the Training Phase, the novel flower was removed, leaving the central post bare.

Test Phase

The observer randomly placed the novel flower from the Training Phase on one of the five posts in the pentagonal array and topped it up with sugar solution. This became the ‘rewarding flower’ in the Test Phase. An additional flower was placed on each of the four remaining posts, oriented with the perch side closest to the center of the array (Figure 5.1c). These ‘unrewarding flowers’ were identical to the rewarding flower, except they were not marked with pink flagging tape or a pink perch base, and they remained empty throughout the Test Phase.

The observer returned to the hide and waited for a territory holder to arrive and land on one of the flowers, marking the start of a trial. During each trial, the observer recorded the sequence in which the focal bird landed on each flower and whether they probed it (dipped beak into the hole). The trial ended when the bird moved at least 5 m away and began another activity (e.g. natural foraging or visiting the nest box), remained within view but did not return to the array within two minutes, or flew out of sight. The observer then approached the array, topped up the rewarding flower (if needed), and repositioned it to one of the other posts. The new position was determined from a pseudorandom sequence, which avoided placing the rewarding flower on the same post more than twice in a row. While intended to ensure that no bird experienced a long run with the rewarding flower in the same position (which could influence their search strategy), territory holders often alternated their visits to the array, so birds occasionally received more than two successive trials with the rewarding flower in the same position (across 1,291 trials: *n* = 8 runs of 3 successive trials, *n* = 3 runs of 4 successive trials). The non-rewarding flowers were also randomly repositioned to avoid cue use based on subtle visual differences among the flowers. The observer then returned to the hide and waited for the next bird’s arrival. Testing continued for five hours on all territories except one, where testing was abandoned after neither territory holder visited the array in the first 1.5 hours.

Retraining and Retest Phases

Twenty of the territories involved in the Training Phase were retrained following the same methods four to six weeks later, with the feeder cage in the same location. For the concurrent study on cue use, the rewarding flower now had inverted coloration, with a yellow tube and red petals, while the nonrewarding flowers remained red with yellow petals (Figure 5.1c). Eighteen territories completed retraining. On 16 territories, one (female only: *n* = 5; male only: *n* = 4) or both (*n* = 7) territory holders fed from the novel flower within 25 minutes (12 ± 2 S.E.). On two territories, neither territory holder fed within 15 minutes, but the territory progressed to the Retesting Phase because territory holders were highly active near the novel flower and had participated in the initial Training and Test Phases. Two other territories that had participated in the initial Test Phase were excluded from retesting, because neither territory holder fed from, or came within proximity of, the novel flower during two hours of retraining. Retesting followed the Test Phase procedure and lasted for five hours, except on one territory, where retesting was abandoned after neither territory holder came into view within the first 30 minutes.

Control for scent cues

In the concurrent study on visual cue use, seven birds (4 males, 3 females) probed the rewarding flower first on seven of ten consecutive trials in the Retest Phase, indicating they had learned to associate the yellow tube with a reward. This necessitated an adjustment during data analysis (see below) but also provided an opportunity to control for scent cues. On these birds' territories, at the end of the Retest Phase, the rewarding flower was repositioned and replaced with an identical flower that had never contained sugar water. Six of the seven birds probed the yellow flower first on their next visit, suggesting that hihi in this task rely primarily on visual (rather than scent) cues. This was also supported by the fact that empty flowers accounted for 67% of the 3,557 flowers probed throughout the study, suggesting that birds needed to probe the flowers to determine if they were empty.

Data Analysis

All analyses were conducted in R (version 4.0.0; R Core Team 2020). Where means are presented, they are accompanied by their estimated standard errors.

Evaluating performance in the novel foraging task

For birds that met the learning criterion in the concurrent study on visual cue use (*n* = 7; see above), all trials (17.14 ± 1.72 trials/bird) from the point of learning onward were excluded from further analyses so as not to bias other performance metrics. From the remaining trials (*n* = 1,171), we calculated three metrics related to traplining for each bird (*n* = 51) that participated in the task. First, an individual's search sequence was determined by classifying each movement between two probed flowers as 'adjacent' (moving to one of the two nearest flowers in the array) or 'non-adjacent' (moving to one of the two farthest flowers) across all trials in the Test and Retest Phases. Birds searching the array randomly would be expected to make 50% adjacent and 50% non-adjacent turns, while those searching systematically could favor either adjacent or non-adjacent turns. Second, to quantify avoidance of empty flowers, we categorized each instance in which an empty flower was probed as a 'known empty' (focal bird had probed that flower earlier in the same trial) or 'unknown empty' (focal bird had not probed that flower already). Third, as a measure of persistence, we counted the total number of trials in which the focal bird probed the rewarding flower at least once (i.e. persisted) and the number of trials in which they never probed the rewarding flower (i.e. did not persist). Here, we excluded trials in which the rewarding flower was probed first (5.53 ± 0.57 trials/bird), because persistence requires observing whether an individual continues to search the array after probing an empty flower.

Using a one-sample *t*-test, we tested whether hihi searched the array systematically by comparing the mean proportion of adjacent turns made by each bird to 50% (chance expectation). Two males and two females were excluded from this analysis because they had no recorded turns as a result of probing only one flower per trial. We then assessed variation in each metric qualitatively using histograms and tested for effects of age and sex using Generalized Linear Mixed Models (GLMMs). Each response variable was a weighted proportion: (i) the number of adjacent turns as a proportion of all turns made by the focal bird, (ii) the number of known empty flowers as a proportion of all empty flowers visited by the focal bird, and (iii) the number of trials in which the focal bird persisted as a proportion of all trials in which they did not probe the rewarding flower first. For the first two metrics, the focal bird's total number of trials was included as an additive fixed effect in all models to account for a possible effect of visitation rate on performance (this never explained a significant amount of variation; result not presented); this was not needed for the third metric because it was already accounted for in the response variable. All models used a binomial family and logit link function and included territory ID as a random effect. For each metric, we used Likelihood Ratio Tests to compare a model with the interaction of interest (age∗sex) against successively simplified models and tested the significance of each effect using z-tests.

Predicting pollination outcomes from traplining performance

Of the 204 plants included in the pollinator exclusion experiment, 45 were excluded from further analyses due to the territory being unoccupied by hihi during the breeding season (*n* = 11 territories), 34 due to total fruit set failure (no fruit set in insect, insect+bird, and hand-pollination conditions), and eight due to plant damage. For the remaining 117 plants (territories: *n* = 37; 3.16 ± 0.21 plants/territory), the contribution of birds to fruit set was estimated by calculating a bird pollination index (BPI):

$$1 - \frac{fruit\ set_{insect}}{fruit\ set_{insect+bird}}.$$

When a plant set more fruit in the insect condition than insect+bird condition (suggesting birds reduced fruit set; *n* = 18 plants) or did not set fruit in either condition (indicating neither insects nor birds improved fruit set; *n* = 16 plants), we reassigned BPI (negative or undefined in the calculation) a value of 0. As a result, the value of BPI can be interpreted as the proportional contribution of birds to fruit set, ranging from 0 (birds did not benefit fruit set) to 1 (birds were responsible for all fruit set). A preliminary examination of the distribution of BPIs found a mean value of 0.42 ± 0.04, suggesting birds were responsible for 42% of fruit set on the average plant. However, there was bimodality around extreme values, so we transformed BPI into a binary variable indicating whether birds did (1) or did not (0) benefit fruit set. Original BPIs equal to 0 (*n* = 58 plants) were left unadjusted, but those greater than 0 (*n* = 59 plants) were reassigned a value of 1.

Lastly, we investigated whether individuals’ performance in the novel foraging task predicted pollination outcomes on their territories. Unfortunately, only 39 plants from 12 territories had foraging task data for the male territory holder, so we restricted analyses to females. This resulted in a dataset of 65 plants from 21 territories. GLMMs were used to test the effect of each traplining or persistence metric on BPI. A Likelihood Ratio Test was used to compare a model containing the metric of interest against a null model, and a z-test was used to examine the significance of the effect. Because BPI is binary, models used a binomial family and logit link function. A random effect of territory ID was included in all models to account for differences in pollination outcomes across territories. In the systematic search analysis, three plants (from two territories) were excluded because the female territory holder had no recorded turns as a result of probing only one flower per trial.

5.3 RESULTS

Of the 33 males and 33 females presented with the novel foraging task, 26 males and 25 females from 30 territories (male and female: $n = 21$; male only: $n = 5$; female only: $n = 4$) participated, for an average of 22.96 ± 1.87 trials per individual (excluding post-learning trials; see Methods). Overall, hihi exhibited strong traplining tendencies. Participants deviated from a 50-50 ratio of adjacent to nonadjacent turns expected if they were searching the array randomly ($t = 17.36$, df = 46, $P < 0.001$). Instead, they appeared to search systematically, making 86% ± 2% of turns to adjacent flowers (Figure 5.2a); all but one individual favored adjacent turns. Individuals also exhibited a strong tendency to avoid empty flowers they had already probed; only 4.0% ± 0.7% of empty flowers probed had already been probed earlier in the same trial (Figure 5.2b). Furthermore, when they began a trial by probing an empty flower, individuals persisted in their search until they found food on 65% ± 4% of trials (Figure 5.2c).

Individuals varied in their traplining tendencies and persistence. In the case of systematic search, individual differences could not be explained by age or sex; a null model was best supported (age vs. null: $\chi^2 = 1.928$, df = 1, $P = 0.165$; sex vs. null: $\chi^2 = 0.425$, df = 1, $P = 0.515$; Figure 5.2d). However, there was evidence that an individual's avoidance of empty flowers depended on both age and sex (age+sex vs. age: $\chi^2 = 19.58$, df = 1, $P < 0.001$; age+sex vs. sex: $\chi^2 = 10.35$, df = 1, $P = 0.001$; Figure 5.2e). Across all ages, males re-probed about half as many empty flowers as females (sex: estimate = −0.885 ± 0.209, $z = -4.240$, $P < 0.001$). Meanwhile, older individuals re-probed fewer empty flowers than younger individuals (age: estimate = −0.317 ± 0.108, $z = -2.945$, $P = 0.003$), although this effect was less certain because most individuals were either 2 ($n = 15$) or 3 ($n = 18$) years old (younger: $n = 2$; older: $n = 16$). There was also a small but significant effect of sex on persistence (sex vs. null: $\chi^2 = 11.57$, df = 1, $P < 0.001$; Fig 5.2f), with males persisting on approximately 66% of trials and females on approximately 78% of trials (sex: estimate = −0.611 ± 0.181, $z = -3.385$, $P < 0.001$).

Across the 21 territories with pollination data and female traplining data, half of plants measurably benefited from bird pollination (BPI = 1, $n = 33$ plants) and half did not (BPI = 0, $n = 32$). On average, bird pollination improved fruit set on 48% ± 6% of plants on each territory. Despite this variation, we could not detect any significant consequences of females' performance in the novel foraging task for pollination outcomes on their territories. Birds did not contribute to pollination to any greater degree on territories where the female searched more systematically (proportion of adjacent turns vs. null: : $\chi^2 = 1.293$, df = 1, $P = 0.256$; estimate: −4.977 ± 4.477, $z = -1.112$, $P = 0.266$; Figure 5.2g), avoided empty flowers better (proportion repeat empty flowers probed vs. null: $\chi^2 = 0.318$, df = 1, $P = 0.573$; estimate: −2.267 ± 4.026, $z = -0.563$, $P = 0.573$; Figure 5.2h), or persisted more often (proportion of trials persisted vs. null: $\chi^2 = 1.869$, df = 1, $P = 0.172$; estimate: 1.045 ± 0.777, $z = 1.345$, $P = 0.179$; Figure 5.2i) in the novel foraging task.

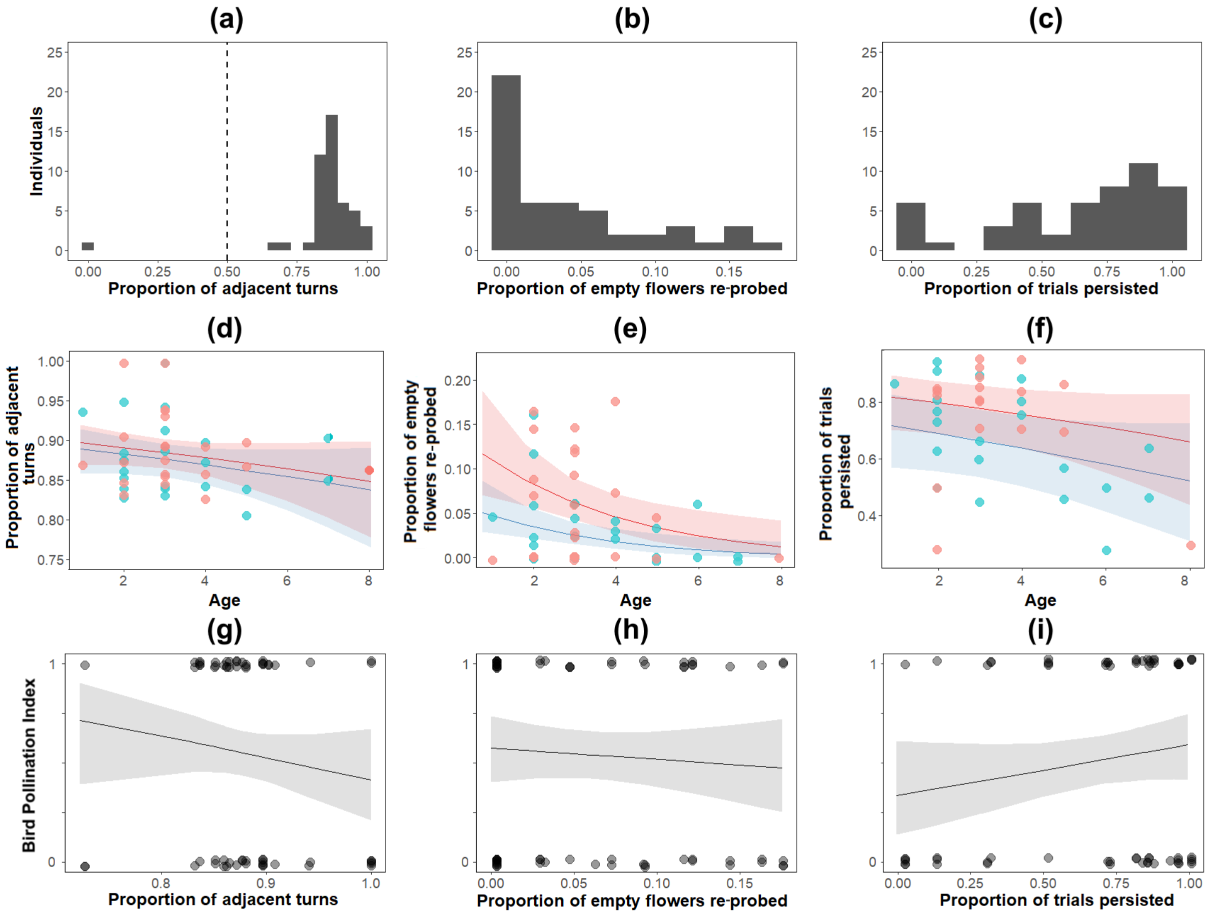


Figure 5.2. Results from the novel foraging task and pollinator exclusion experiment. (a–c) Individuals varied in (a) their systematic search of the novel flower array (deviating from the 50% of adjacent turns expected by chance); (b) their avoidance of empty flowers; and (c) the proportion of trials in which they persisted until they found food. (d–f) Each of these metrics was then tested for effects of age and sex. Solid lines are regression lines (with 95% confidence intervals) from a model including additive effects of age and sex (red = females; blue = males); each point represents one individual. Neither variable significantly predicted (d) an individual's systematic search, but (e) both had significant effects on avoidance of empty flowers, and (f) sex had a significant effect on persistence. (g–i) For each female with data from the pollinator exclusion experiment, her performance in the novel foraging task was then used to predict whether plants benefited (Bird Pollination Index = 1) or did not benefit (BPI = 0) from bird pollination on her territory. Regression lines are from a model including only the effect labeled on the x-axis, and points indicate one plant. None of these relationships were significant.

5.4 DISCUSSION

While most traplining studies examine bees (e.g. Ohashi et al. 2006; Buatois and Lihoreau 2016; Klein et al. 2017) or hummingbirds (e.g. Temeles et al. 2006; Tello-Ramos et al. 2015, 2019), our study adds hihi to a short list of other taxa (e.g. primates: Janson et al. 1981; bats: Lemke 1984) known to exhibit behaviors characteristic of traplining. In the novel foraging task, hihi searched systematically rather than randomly (favoring adjacent turns, as in Thomson et al. 1997; Tello-Ramos et al. 2015) and avoided repeat visits to empty flowers (as in Pyke 1979; Healy and Hurly 1995). In most trials, they also persisted until they found food (as in Laverty and Plowright 1988). All of these behaviors can improve pollination quality (Laverty and Plowright 1988; Ohashi and Thomson 2009), suggesting that hihi are specialized for pollination not only through their diet (Castro and Robertson 1997; S. Anderson 2003) and morphology (i.e. brush-tipped tongues: Kelly et al. 2010) but through their behavior. More work is needed to determine whether hihi fully qualify as trapliners, however, as our study was not long enough to track whether individuals develop repeatable search sequences, a defining feature of traplining (Thomson et al. 1997).

Despite their strong performance on average, individuals varied in their success in our novel foraging task, with key differences emerging between age-sex classes. Males and older birds avoided revisiting empty flowers more successfully than females and younger individuals, which could indicate superior spatial memory. Similar results have been found in scatterhoarding species (reviewed in: Zwolak 2018): spatial memory is often better in males than females (Galea et al. 1996; Dunlap et al. 2006; Barkley and Jacobs 2007) and can be positively correlated with age if it improves with ontogeny and experience (Clayton 1992; Clayton 1994) or is subject to natural selection (Sonnenberg et al. 2019). Alternatively, these trends could be caused by differences in attention rather than cognition. Female and juvenile hihi are more vulnerable to predation and aggression than males (Craig 1985; Castro et al. 1996; Low and Pärt 2009), and the stress from these perceived risks can impede spatial memory (Mastrangelo et al. 2009). Sex also predicted individuals' persistence in the task: males were more likely than females to give up before finding food. According to Optimal Foraging Theory, individuals tend to give up faster if they are satiated or perceive higher resource availability (Charnov 1976; Gill and Wolf 1977). Female hihi have high energetic demands across all breeding stages, as they build the nest and incubate eggs without assistance (Ewen and Armstrong 2000) and provision nestlings three times more often than males (Castro et al. 1996); these demands could have increased their threshold for satiation and persistence in our foraging task. Because these behaviors require frequent visitation to the nest box, their foraging may also be restricted to a smaller area than males', reducing perceived resource availability. Nevertheless, the magnitude of this sex difference was small and may be less biologically meaningful than the one for individuals' avoidance of empty flowers.

Combined with the results of our novel foraging task, our pollinator exclusion experiment calls into question some of the common assumptions about the ecological implications of traplining. Hihi appeared to be strong trapliners overall, and bird pollination improved fruit set by 42% on average, in line with the global average of 46% for bird-pollinated plants (Ratto et al. 2018). However, while half of plants in our study relied mostly or entirely on birds, the other half showed no benefit of bird pollination. Such bimodality could arise if pollinators fail to visit certain plants altogether or visit all plants but pollinate some ineffectively; thus, trapliners may not benefit all plants equally. A similar pattern could also arise if individual trapliners vary in their effectiveness, as has been suggested in other species (Thomson 1996; Saleh and Chittka 2007; Tello-Ramos et al. 2015). However, despite individual variation in our novel foraging task, we found no evidence that a female's traplining tendencies or persistence predicted pollination outcomes on her territory. This could indicate that these traits are not consequential in our study system, perhaps because traplining does not vary substantially enough in hihi to drive differences in pollination efficiency. Any benefits of enhanced traplining ability could also be neutralized if traplining has detrimental effects on other aspects of plant reproduction (Ohashi and Thomson 2009), such that stronger trapliners bring no net benefit to pollination.

While our results suggest that individual traplining tendencies and persistence do not affect pollination, some uncertainty remains. First, the small size of our dataset may have limited our power to detect a significant relationship in females and prevented us from conducting a similar analysis in males. Second, conducting the study on territories may have helped to isolate the effects of individual birds, but potentially also excluded important sources of variation. Territoriality has emerged as a key influence on seed dispersal quality (Zwolak 2018), with non-territorial individuals tending to disperse seeds farther than territorial individuals (Rawsthorne et al. 2010; Jadeja et al. 2013). Seed dispersal can also differ greatly between areas used by multiple individuals (e.g. leks) and areas defended by a single individual (e.g. territories; Krijger et al. 1997; Karubian and Durães 2009; Karubian et al. 2012). Recent evidence suggests similar effects in pollinators, with territory intruders depositing more compatible pollen than territory holders (Maruyama et al. 2016). Given the potential benefits of intruders to pollination, territory holders that defend their territories more successfully may actually reduce pollination, even if they are effective trapliners. Thus, future work should consider how pollination outcomes might arise from the additive effects of different behavioral traits and from interactions among individual pollinators.

To conclude, while we could not explain differences in pollination outcomes across hihi territories, their strong performance in the novel foraging task indicates that the species is behaviorally specialized for pollination. Testing traplining abilities across a wider range of species, using more consistent methodology, could help us assess how rare these abilities are. If hihi are unique in their traplining tendencies among endemic avian pollinators, it could underscore their value to the ecosystem. Nevertheless, the variation in pollination outcomes across territories warrants further investigation. If these differences arise from behavior, conservation biologists may need to account for behavioral variation when predicting the success of ecosystem recovery efforts. In translocations aimed at restoring lost pollination function, success may depend on which individuals are translocated and which survive. However, behavioral variation could also serve as a tool for enhancing ecosystem recovery if individuals can be selected for translocation based on favorable pollinator traits. Given the degraded state of mutualisms worldwide (Kelly et al. 2010; Potts et al. 2010; Neuschulz et al. 2016), targeted interventions like these could prove invaluable for restoring lost functions more efficiently.

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The pollinator exclusion experiment in this chapter was improved by advice on methodology from Sandra Anderson.

Chapter 6

Does translocation of a lost avian pollinator restore ecosystem function?

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Given escalating threats to biodiversity worldwide, there is an increasing need for conservation interventions that promote broader ecosystem restoration alongside species recovery goals. Translocation is a common intervention with the potential to promote ecosystem health by restoring lost ecological functions. However, few translocation programs explicitly state or monitor function as a fundamental objective, limiting our ability to learn from past efforts and design more effective interventions. Here, we tested whether translocations of hihi (*Notiomystis cincta*), a threatened New Zealand passerine, achieve their implicit goal of restoring lost pollination function. Through a pollinator exclusion experiment, we attempted to isolate the contribution of hihi to pollination by measuring fruit set and seed quality across sites with and without hihi. Results suggested that hihi improved the germination probability of viable seeds, but plants at non-hihi sites appeared to shift their reproductive investment to produce a greater quantity of low-quality fruits. As a result, the same proportion of seeds germinated overall, regardless of hihi presence. Therefore, although our study confirms that hihi bring unique benefits to the ecosystem by improving seed quality, it also raises important questions about the complexity of ecological functions. If ecosystems can partially compensate for the loss of a mutualist, it is even more important that functional objectives are stated and monitored in conservation programs so that future interventions can be targeted at ecosystems with the most need and potential to benefit.

6.1 INTRODUCTION

The decline of one species can have cascading impacts on many others through the disruption of important ecological functions (Soulé et al. 2003; Tylianakis et al. 2008; Kelly et al. 2010; Brodie et al. 2014). This raises the stakes for conservation, but it also presents an opportunity: because species are so interconnected, interventions that target single species can also be used to achieve broader ecological objectives (Simberloff 1998). Conservation translocations typically focus on single-species recovery, but also offer an opportunity to promote ecosystem health by restoring lost mutualisms, reintroducing keystone species, or introducing ecological replacements (Lipsey and Child 2007; Seddon 2010; Ewen et al. 2012; IUCN/SSC 2013; Lunt et al. 2013; Seddon et al. 2014). For example, lost seed dispersal functions have been restored successfully through the reintroduction of brown howler monkeys (*Alouatta guariba clamitans*: Genes et al. 2018) and red-rumped agoutis (*Dasyprocta leporine*: Mittelman et al. 2020) in Brazil and the ecological replacement of extinct giant tortoises by extant species in Mauritius (Griffiths et al. 2011) and the Galápagos (Hunter et al. 2013). Given translocation's potential as a tool for ecosystem recovery, however, it is surprising that the number of translocations asking ecological questions has not increased in recent decades (Taylor et al. 2017). IUCN guidelines highlight ecological function as an important consideration for translocations (IUCN/SSC 2013), but only 6% of recently reviewed case studies explicitly state ecosystem restoration as an objective (Seddon and Armstrong 2019; see also: Chauvenet et al. 2016; Taylor et al. 2017), and those that do rarely evaluate whether this objective is achieved (Ewen et al. 2014). In practice, more emphasis seems to be placed on the harms that a translocated species may bring to an ecosystem rather than its potential ecological benefits (D. Armstrong and Seddon 2008; Polak and Saltz 2011).

One possibility for why ecological function is rarely stated or monitored explicitly is because it is assumed to be a byproduct of more focused species recovery goals. Species recovery, however, may not always equate to ecosystem recovery. Populations that achieve minimum viable sizes, a common benchmark for species recovery (Shaffer 1981; Gilpin and Soulé 1986; but see: Flather et al. 2011) are not always large enough to carry out their ecological functions effectively (Conner 1988; McConkey and Drake 2006; Sanderson 2006; Akçakaya et al. 2018; Brodie et al. 2018; Akçakaya et al. 2020). Evaluating translocation success only by species benchmarks could therefore result in a 'half-empty forest' (Redford and Feinsinger 2001), or one in which species have technically recovered but key functions remain missing. Additionally, many threatened species declined so long ago that we may not fully understand their ecological roles (e.g. Culliney et al. 2012; Gordon and Letnic 2016). If the environment has changed, they may no longer be able to fulfill these roles, or another species may have replaced them and repaired the functional deficiency (Akçakaya et al. 2020). Translocations are costly and not without risk (D. Armstrong and Seddon 2008; IUCN/SSC 2013; Berger-Tal et al. 2020), so, if ecological function is an objective, then stating and monitoring it explicitly could help ensure these interventions are targeted at places with the most need and potential for restoration.

Animal-mediated pollination is one mutualism that is currently facing serious threats worldwide, putting the stability of many ecosystems at risk (Potts et al. 2010). Yet, of the 291 faunal reintroduction case studies published by the IUCN (Soorae 2008, 2010, 2011, 2013, 2016, 2018), only two mention that the translocated species is a known pollinator, and neither sets the restoration of pollination function as a core objective or measured outcome. Translocations have long been used to restore floral species threatened by pollinator declines (Abeli and Dixon 2016), but few have explored the possibility of translocating the pollinators themselves (Cariveau et al. 2020; but see LaBar et al. 2014 for a theoretical exploration). Conservation biologists may be hesitant to translocate pollinators due to the relative costliness (Dixon 2009) and complexity of manipulating animals versus plants (Morton and Rafferty 2017). Predicting restoration success could be difficult, because plant visitation does not always translate into high-quality pollination (King et al. 2013; Hervías-Parejo and Traveset 2018; Bestea et al. 2019); thus, translocated species would need to be selected carefully to ensure they not only visit target plants but also pollinate them effectively. Furthermore, the loss of a pollinator can be compensated by plant adaptations (Schleuning et al. 2016) or increased visitation by other pollinators (e.g. Hallett et al. 2017), including non-native species (Pattemore and Wilcove 2011), so the ecological need for restoration must be evaluated carefully.

Despite these challenges, translocation will likely become a necessary tool for restoring pollination as it grows increasingly difficult for extirpated pollinators to recolonize areas without assistance. Perhaps nowhere is this more evident than in New Zealand, where rapid declines of native birds due to disease, deforestation, and predation by introduced mammals have coincided with devastating declines of native plants (Kelly et al. 2010). Historically, birds were thought to make only incidental contributions to pollination, as the majority of native plants appear entomophilous (Godley 1979; Clout and Hay 1989). However, more recent studies have found several native birds to be important (S. Anderson 2003; Kelly et al. 2010) and, in some cases, essential (e.g. S. Anderson et al. 2011) to pollination. Translocations are frequently used to restore native bird populations, and many are motivated at least in part by ecosystem restoration goals (Parker 2013), but few actively test whether these ecological goals are realized.

The hihi (*Notiomystis cincta*), a threatened endemic bird, is thought to have been one of the most important pollinators in New Zealand before its widespread decline and near-extinction in the late 1800s (Craig et al. 1981; S. Anderson 2003; Kelly et al. 2006; S. Anderson et al. 2011). Frequent translocations to establish new populations cite the restoration of pollination function as a potential benefit (Smuts-Kennedy 2009; Frost 2012; Collins et al. 2015) but do not include it as a fundamental objective or assess whether it is achieved. Thus, questions remain about:

(1) The species' role:
    How much do hihi contribute to pollination compared to other species?
(2) The ecological need:
    How significantly is pollination reduced at sites where hihi are absent?
(3) Translocation's effectiveness:
    How successfully do hihi translocations restore pollination function?

While these questions could be examined by comparing ecological function immediately before and after a translocation, ecological restoration may require more time to become evident (Choi 2004; Hilderbrand et al. 2005; Pullin et al. 2013). Thus, we employed an alternative strategy, the 'elimination approach' (Akçakaya et al. 2020), in which ecological function is compared across sites with different densities of a species to evaluate its importance to the ecosystem. Through a pollinator exclusion experiment, we compared pollination outcomes across sites where hihi have been reintroduced and sites where they remain absent. To ensure our monitoring protocol captured the various ways that hihi could potentially influence pollination, we monitored outcomes at three levels: fruit set, seed viability, and seed germination. If past assumptions about the benefits of hihi translocations hold true, we would expect that plants at sites with hihi would (i) be less pollen-limited (more maximally pollinated) and (ii) receive a greater proportion of their pollination from birds compared to plants at sites without hihi.

6.2 METHODS

Study species

The hihi is the sole extant member of the Notiomystidae family (Driskell et al. 2007; Figure 6.1a). Although they were once widespread throughout the North Island of New Zealand, they became reduced to a single remnant population on Te Hauturu ō Toi (Little Barrier Island Nature Reserve) by 1890. Since the 1990s, translocations have been used to establish seven additional populations at sites where introduced mammalian predators have been excluded (Thorogood et al. 2013; Franks et al. 2019). All reintroduced populations depend on supplementary provisioning of sugar water to varying degrees throughout the year (Chauvenet et al. 2012; Thorogood et al. 2013; Doerr et al. 2017). However, hihi preferentially select natural foods when they are sufficiently available and eat a broad diet of invertebrates, fruit, and nectar (Craig 1985; Rasch and Craig 1988; Roper 2012; Walker et al. 2014; Chapter 2). Nectar use peaks at ~56% of their diet in spring (Rasch and Craig 1988), coinciding with the hihi breeding season and the flowering season for many native plants.

For the purposes of this study, we chose to focus on the mutualistic relationship between hihi and hangehange (*Geniostoma ligustrifolium*), a gynodioecious (Rattenbury 1980) native understory shrub. Hangehange is common, making it amenable to cross-site comparisons, but it is nonetheless thought to be pollen-limited (McNutt 1998), suggesting a potential need for pollination to be restored. Its flowers form in inflorescences in spring and are small (<4 mm), scented, and pale green, so it was long assumed to be pollinated primarily by insects, including beetles (Coleoptera), flies (Diptera), butterflies and moths (Lepidoptera), and bees (Hymenoptera: Norton 1984; S. Anderson 2003). It has since been shown to depend heavily on birds, including hihi and the two native honeyeaters: tūī (*Prosthemadera novaeseelandiae*) and korimako (*Anthornis melanura*). Among these species, hihi are presumed to be the primary pollinators; only hihi and korimako have the potential to meet their energetic demands while foraging on hangehange (Castro and Robertson 1997), and hihi visit it more frequently (Roper 2012) and probe more flowers per visit than korimako (Castro and Robertson 1997). A fourth species, the tauhou (*Zosterops lateralis*), has been suggested to be another important pollinator (Burns 2013), but its preference for forest edges (Barbaro et al. 2012) may make it less likely to encounter hangehange, and its recent colonization of New Zealand (c. 1856) means its role in pollination may be less likely to represent an evolved mutualism.

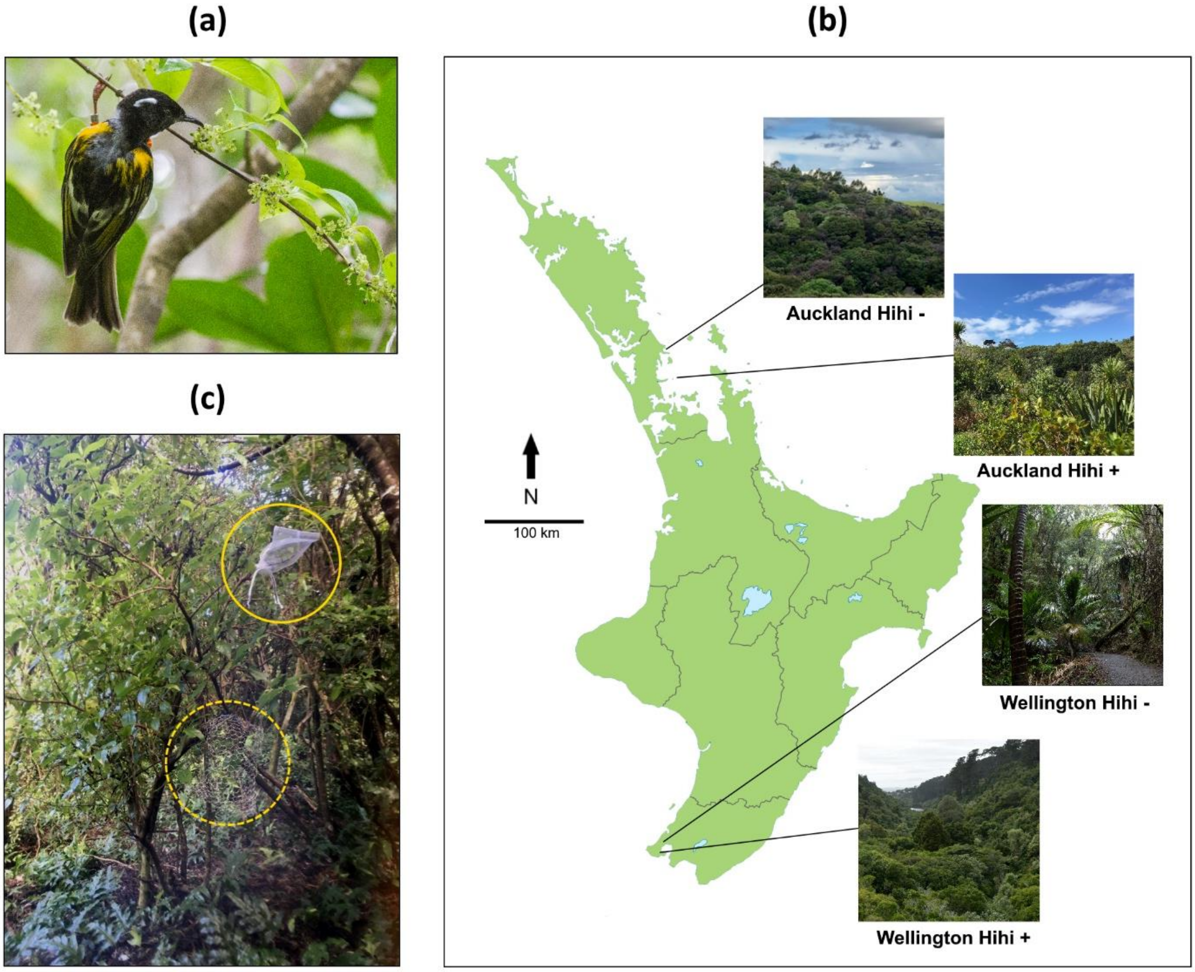

Figure 6.1. (a) A male hihi foraging on hangehange (Photo: Martin Sanders). (b) Map of the North Island of New Zealand showing the locations of the four study sites (Photos: Auckland Hihi+: CA, Hihi−: Sharon Kast; Wellington: Christopher Stephens). (c) A hangehange plant in the pollinator exclusion experiment showing the two pollinator-exclusion treatments: self-pollination (all pollinators excluded by a fine mesh bag: solid circle) and insect-only pollination (bird pollinators excluded by a 2x2 cm wire cage: dashed circle; Photo: CA).

Study sites

The study was conducted in the Auckland and Wellington regions of New Zealand's North Island, approximately corresponding to the northern and southern extremes of the hihi's historic range. Within each region, we selected one nature reserve containing hihi (Hihi+) and a second that did not contain hihi (Hihi−) but was otherwise ecologically similar. Each site consists primarily of regenerating broadleaf forest with small patches of remnant mature native bush, reflecting a long history of farming followed by intensive habitat restoration over the last ~40–100 years. Relative abundances of hihi, the other main avian pollinators of hangehange, and kākāriki, a known nectar robber (*Cyanoramphus novaezelandiae:* Kelly et al. 2010) are noted for each site in Table 6.1.

Table 6.1. Estimated relative abundances of hangehange pollinators and a known nectar robber (kākāriki) at each of the four study sites. Values reflect the number of times each species was seen or heard in transect surveys (Auckland Hihi+: Feb.–Mar. 2018, Stewart and Milton 2018; Wellington Hihi−: Sept. 2013, Greater Wellington Regional Council, unpublished data) or five-minute bird counts (Auckland Hihi−: Jan. 2018, M. Maitland and T. Lovegrove, Auckland Council, unpublished data; Wellington Hihi+: Sept. 2013, Zealandia Ecosanctuary, unpublished data) as a proportion of the total times any of the five focal species were seen or heard.

	Auckland		**Wellington**	
	Hihi+	**Hihi−**	**Hihi+**	**Hihi−**
Hihi	0.18	0.00	0.18	0.00
Korimako	0.53	0.54	0.02	0.02
Tūī	0.13	0.35	0.62	0.70
Tauhou	0.01	0.10	0.10	0.28
Kākāriki	0.15	0.01	0.08	0.00

In Auckland, the Hihi+ site was Tiritiri Matangi Island (36°36'00.7"S 174°53'21.7"E; Figure 6.1b), a 220-hectare nature reserve located 3.5 km offshore. After being farmed for over a century, the island was extensively replanted in the 1980s, and introduced mammalian predators were eliminated in 1993. Today, the island provides sanctuary to many native birds. A population of hihi was established with a translocation from Te Hauturu ō Toi in 1995 and numbered ~150 adults during our study. The Auckland Hihi− site was Tāwharanui Regional Park (36°22'12.6"S 174°49'54.9"E; Figure 6.1b), a 588-hectare reserve located 25 km north of the Auckland Hihi+ site. Tāwharanui is considered a 'mainland island' (Saunders and Norton 2001), as it is a peninsula separated from adjacent land by a predator-exclusion fence, protecting native wildlife from all introduced mammalian predators except mice.

Another mainland island served as the Hihi+ site for the Wellington region. Located in Wellington city center, Zealandia Ecosanctuary (41°17'24.4"S 174°45'13.4"E; Figure 6.1b) is a 225-hectare forest surrounded by a predator-exclusion fence. The forest has been regenerating since farming ended in the early 1900s and contains a large reservoir that was once an important part of the city's water catchment area. A hihi population was established through translocation in 2005 and numbered ~120 adults during our study. Approximately 15 km northeast, Belmont Regional Park (41°12'07.2"S 174°52'32.0"E; Figure 6.1b) was chosen as the corresponding Hihi− site. Although much larger than Zealandia at 3,500 hectares, Belmont is dominated by pastureland with small patches of regenerating and remnant native bush. Our study was carried out in the Korokoro Dam area, which is similar to Zealandia in its forest structure and history as a water catchment area. Unlike the other two mainland sites, Belmont is unfenced, but site managers use bait stations and traps to control introduced mammalian predators. At the start of our study, tracking rates (percent of tracking tunnels with evidence of mammalian predators) in the study area were ~20% for rats and ~22% for mice (Uys 2017a, 2017b).

Pollinator exclusion experiment

At each of the four study sites, 30 mature hangehange plants were selected for a pollinator exclusion experiment. An additional 18 plants were included at the Auckland Hihi+ site to account for the island's drier climate, as we anticipated that water stress could lead to total fruit set failure in some plants (reducing our usable dataset). As hangehange is gynodioecious and hermaphrodite individuals set seed only rarely (Rattenbury 1980), we attempted to select only female plants. Prior to the flowering season, females can be identified reasonably based on the presence of moderate to high numbers of dry fruit capsules remaining from the previous reproductive cycle. However, to account for potential identification errors, we also quantified and controlled for self-pollination rates within each plant (see below).

Focal plants were distributed evenly across 10 territories at each site, with three to five plants per territory at the Auckland Hihi+ site and three per territory at all other sites. At the Hihi+ sites, selecting plants on hihi breeding territories helped limit bird visitation to hihi as much as possible; hihi are known to chase intra- and interspecific intruders off their territories (Ewen et al. 2004; Low 2005). At both Hihi+ sites, almost all hihi nest in intensively monitored nest boxes, so breeding territories were defined conservatively as a 20 m radius around a nest box. Because plants were selected prior to the start of the hihi breeding season, site managers were consulted to ensure that selected territories had a high chance of occupancy based on trends over the past three breeding seasons. At the Hihi− sites, focal plants were located on 10 plots of 20 m radius chosen for their ecological similarity to hihi territories.

Following established methods (Kearns and Inouye 1993), for each focal plant we assigned one branchlet containing at least 10 unopened buds to each of the following pollinator conditions:

1. Self-Pollination: branchlet enclosed in a fine organza bag to exclude all pollinators;
2. Insect Pollinators Only: branchlet enclosed in a 2x2 cm wire mesh cage to exclude birds but allow insects (mesh size selected following S. Anderson 2003; continued insect visitation confirmed by Schmidt-Adam et al. 2009; no birds observed attempting to forage through mesh during anecdotal observations at the study sites);
3. Insect + Bird Pollinators: branchlet left open to natural pollination;
4. Hand-Pollinated: branchlet left open to natural pollination and pollinated by hand during the receptive period (following the methods of S. Anderson 2003).

All sites were visited at the start of the flowering season in September 2017 to select branchlets, count buds, and apply coverings for the pollinator-exclusion conditions (Figure 6.1c). Sites were revisited approximately three weeks later (once flowers were open and receptive) to complete the hand-pollination treatment. Six to eight weeks after coverings were first applied, all flowers had passed receptivity, so coverings were removed. Wellington sites were always visited about 2–3 weeks after Auckland sites to account for latitudinal differences in phenology.

Site assessments

To evaluate regional habitat differences and test our assumption that paired Hihi+/Hihi− sites were ecologically similar, we conducted a habitat assessment on each focal territory. We focused on understory vegetation, because hangehange is an understory plant and hihi generally forage in the understory (Gravatt 1971; Roper 2012). On each territory, we designated five 20 m transects radiating evenly from a central point. At five sampling points along each transect, we counted and identified (to species level) every mature plant intersecting an imaginary cylinder of 1 m radius extending from the ground to a height of 2 m. Summing these counts across all 25 sampling points and dividing by the total sampling area (25π m^2) provided an estimate of understory density and hangehange density. As a measure of species richness and evenness, we calculated a Shannon diversity index (Shannon 1948) as:

$$-\sum_{i=1}^{R} p_i ln p_i,$$

where R is the total number of unique species present and p_i is the proportion of plants belonging to species i. Lastly, we completed a vertical habitat assessment (adapted from Scott 1965; Makan et al. 2014) at each sampling point by extending an imaginary cylinder of 10 cm radius from the ground to the canopy, identifying all species with intersecting foliage, and estimating the canopy height. Combined with the data from our understory assessments, this provided a count of the total number of unique species and an average canopy height for the territory.

Pollinator visitation rates were assessed at each site during five hour-long sessions conducted during the period of flower receptivity. Observations were conducted over three days at the Auckland Hihi+ site and one day at all other sites, with sessions spread evenly throughout the morning and afternoon. During each session, an observer sat quietly under cover of vegetation on one of the focal territories with five mature hangehange plants in view and at least 5 m away. Each bird that visited one of the plants and foraged (probed or consumed flowers) was counted and identified to species level. At the end of the session, the number of flowers on each plant was estimated by multiplying the number of open flowers (estimated to the nearest 10) on one branchlet by the number of branchlets (estimated to the nearest 5) on the plant. These counts were used to calculate a visitation rate for each bird species, which was standardized to visits per hour per 10,000 flowers.

Pollination outcomes

All sites were visited in late December 2017 to count fruits on each treated branchlet. Comparing this count to the original number of buds provided a measure of fruit set (proportion of buds that developed into fruits). For a subset of plants (11 per site), fruits were also collected from the insect and/or insect+bird conditions in mid-February (Auckland) to early March (Wellington). These were placed in paper bags and transported to the Wellington Botanic Garden for germination and seed viability testing. After being stored at room temperature for up to two months, fruits were removed from each bag and rubbed on a paper towel to separate the seeds from the capsules. Across all fruits collected from a treated branchlet, 80 seeds (where available) were selected randomly so that eight replicate germination tests of 10 seeds each could be performed; where fewer seeds were available (13/56 branchlets), all seeds ($\bar{x}$ ± S.E. = 33.6 ± 6.5) were taken and divided among replicates. Seeds were plated on 1% water agar in 90 mm plastic petri dishes divided into four sections (each containing one replicate). Dishes were incubated at 15/25°C alternating temperature in a 16/8 hour dark/light cycle and were inspected every 14 days for contamination and agar desiccation. At least four weeks after plating, seeds were inspected for germination (radical protrusion of at least 1 mm; Supplementary Figure 6.1a), and ungerminated seeds were dissected to assess viability. Seeds were considered viable if they contained a structured endosperm and unviable if they were mushy or lacking a clear structure (Supplementary Figure 6.1b-c). These data provided up to eight replicate measures per sampled plant of seed viability (proportion of all seeds which were viable), germination probability of viable seeds (proportion of viable seeds which germinated), and germination probability of all seeds (proportion of all seeds which germinated; see Supplementary Table 6.1 for replicate sample sizes).

Data analysis

All analyses were conducted in R (version 4.0.0; R Core Team 2020).

Assessing habitat differences

We first conducted a Principal Component Analysis (PCA) to quantify the ecological similarity of our four study sites. Habitat variables measured on focal territories were pooled across sites and standardized prior to analysis to account for the variables' different scales. The minimum number of components needed to explain at least 70% of the variance were examined visually using biplots, with convex hulls drawn around all datapoints (territories) belonging to each site. Using the vegan package (Oksanen et al. 2019), site differences were then tested quantitatively with a permutational multivariate analysis of variance using Euclidean distance matrices (M. Anderson 2001). As this analysis indicated significant differences among sites (see Results), post-hoc pairwise comparisons between sites were performed using a pairwise permutation MANOVA (PERMANOVA) with 1,000 permutations (RVAideMemoire package: Hervé 2020). Our study design assumed paired Hihi+/Hihi− sites to be ecologically similar, so, to avoid increasing the likelihood of Type II errors, we did not correct the resulting *P*-values; thus, our results may overestimate differences among sites.

While PCA is useful for visualizing and quantifying the degree of similarity between groups, it can make it difficult to interpret which variables are responsible for group differences (Jolliffe and Cadima 2016). Therefore, we followed our PCA with a conditional inference tree analysis. The ctree function (party package: Hothorn et al. 2020) performs a binary recursive partitioning procedure. Here, we used it to test the dependence of site on each of the habitat variables, performed a binary split of the data based on the variable with the strongest significant association with site, and continued until site was no longer associated with any of the remaining variables (Hothorn et al. 2006).

Comparing pollination outcomes

Before comparing pollination outcomes across conditions and sites, a few modifications were needed for our data. From our original dataset of 138 plants, 31 were excluded due to total fruit set failure (insect+bird and hand-pollinated conditions yielded no fruit). As predicted based on its drier climate, a greater proportion (16/48) of plants were excluded at the Auckland Hihi+ site compared to the other sites (Auckland Hihi−: 2/30; Wellington Hihi+: 5/30; Wellington Hihi−: 8/30). For each branchlet, the fruit count was truncated so it did not exceed the original number of buds, which would suggest that extra buds formed after the initial bud count. Within each plant, if proportional fruit set was lower for the hand-pollinated condition than the insect+bird condition (suggesting an error in the hand-pollination treatment: Larson and Barrett 2000), the hand-pollinated fruit count was raised to make the two fruit sets equal; if this resulted in a decimal, the fruit count was rounded up, as whole numbers were needed for analyses.

We assessed the significance of our main hypotheses in a stepwise fashion using Likelihood Ratio Tests, where we compared a model containing the interaction of interest (pollination condition∗hihi presence) against a simplified model without the higher-order effect (pollination condition+hihi presence). If the interaction was not significant, we tested the significance of each factor in the additive model using *z*-tests. For models testing fruit set as the pollination outcome, fruit count was the response variable with an offset of log(bud count), and negative binomial models were used to account for overdispersion (glmmTMB package: Brooks et al. 2017). For seed-level outcomes, response variables were proportions (accounting for the number of seeds in each replicate), and models were structured as Generalized Linear Mixed Models (GLMMs) with a binomial family, logit link function, and bound optimization by quadratic approximation (BOBYQA) optimizer to reduce convergence errors. Regardless of the pollination outcome being tested, all models contained region as a covariate (to account for regional differences) and individual plant ID, territory, and site as random effects. An observation-level random effect was included in seed viability models to correct for overdispersion (Harrison 2014).

The self-pollination condition produced fruits in only six focal plants, so this condition was excluded from the initial fruit set analyses. To check that self-pollination rates did not affect our results, we repeated analyses with fruit counts for the insect and insect+bird conditions reduced in proportion to the plant’s self-pollination rate; the hand-pollination condition was not adjusted, as it was intended to represent maximal pollination, including selfing. Results were quantitatively similar, so we present analyses with the full dataset.

All figures present predicted values from the minimal model. Predicted fruit counts were converted to proportions by dividing by the original number of buds on each treated branchlet and truncating, if needed, to restrict values between 0 and 1. Reported means for each condition were derived from the model predictions and are accompanied by their estimated standard errors. These means were also used to calculate a pollen limitation index (PLI: Larson and Barrett 2000), calculated as:

$$1 - \frac{fruit\ set_{insect+bird}}{fruit\ set_{hand-pollinated}}.$$

PLI is bounded between 0 and 1, with a value of 0 indicating that plants receive maximal pollination and higher values suggesting that plants are pollen-limited. We used a similar approach to quantify the proportion of fruit set attributable to bird pollination, or ‘Bird Pollination Index’ (BPI), calculated as:

$$1 - \frac{fruit\ set_{insect}}{fruit\ set_{insect+bird}}.$$

A BPI of 0 indicates that bird pollinators do not improve fruit set, while a value of 1 indicates that they are responsible for all fruit set.

6.3 RESULTS

Site comparisons

The Principal Component Analysis identified strong associations between habitat variables measured across all sites. PC1 and PC2 explained a cumulative 70% of the variance among territories (Table 6.2). All habitat variables loaded positively on PC1, with total species and hangehange density having the strongest loadings. Understory density had a strong negative loading on PC2, while Shannon diversity and canopy height loaded positively. A biplot of PC1 and PC2 (Figure 6.2a) identified a strong positive correlation between canopy height and Shannon diversity.

The habitat differed significantly across sites (ADONIS: $R^2 = 0.45$, $P < 0.001$). Although paired Hihi+/Hihi− sites were selected to be as ecologically similar as possible, only the two Wellington sites could not be distinguished (PERMANOVA: $P = 0.072$; Auckland sites: $P = 0.001$). A visualization of the PCA (Figure 6.2a) identified understory density as the primary difference between the Auckland sites, which was confirmed by the conditional inference tree analysis: the Auckland Hihi+ site had a consistently denser understory (>0.993 plants/m^2; $P < 0.001$) than any of the other sites (Figure 6.2b). Meanwhile, the two Wellington sites were distinguished from the Auckland Hihi− site by their lower canopy (≤6.92 m; $P = 0.002$; Figure 6.2b).

Plant watches confirmed that hangehange visitation rates (standardized to visits per hour per 10,000 flowers) were higher at each Hihi+ site compared to its corresponding Hihi− site and that hihi were the primary visitors where they were present. At the Auckland Hihi+ site, hihi visited hangehange twice as often (0.66 visits/h) as korimako (0.33 visits/h). Visitation at the Auckland Hihi− site was less frequent and was restricted to korimako (0.08 visits/h). In Wellington, only hihi were observed visiting hangehange at the Hihi+ site (0.11 visits/h), while no visits by any species were observed at the Hihi− site.

Table 6.2. Results of the Principal Component Analysis (PCA) of habitat variables measured on focal territories across the four study sites. The first two components explained a cumulative 70% of variance among territories, while the three remaining components (PC4 and PC5 not presented) explained only 30% of variance. Variables with the strongest loadings on each component are indicated in bold.

	PC1	**PC2**	**PC3**
Total species	**0.58**	−0.25	0.09
Understory density	0.39	**−0.70**	−0.06
Shannon diversity	0.39	**0.46**	**0.70**
Hangehange density	**0.49**	0.15	−0.09
Canopy height	0.36	**0.47**	**−0.70**
Eigenvalue	2.30	1.20	0.74
Proportion of variance explained	0.46	0.24	0.15

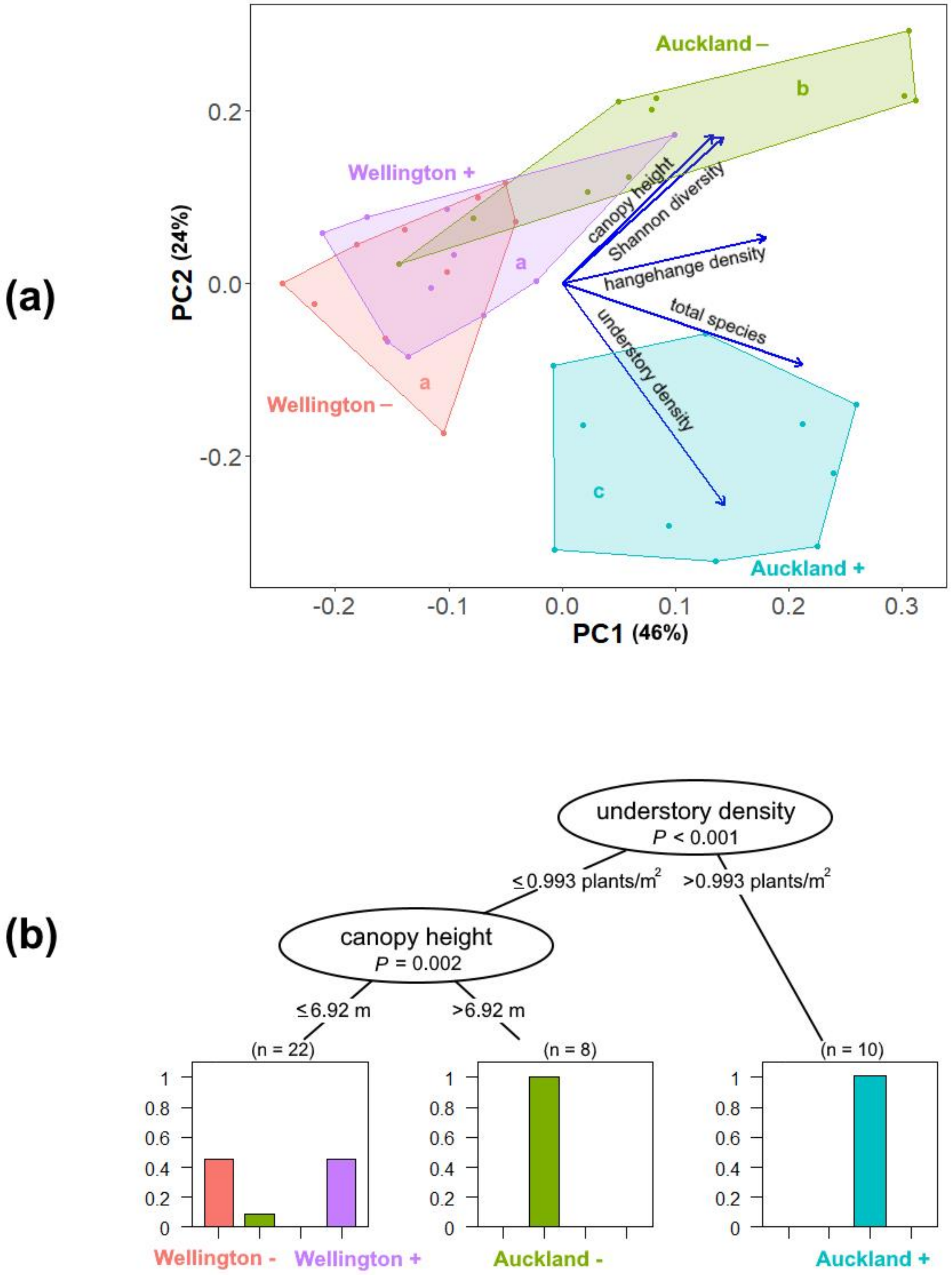

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Figure 6.2. Habitat comparisons across the four study sites. Sites are labeled by region and hihi presence (+) or absence (−). (a) Biplot of the first two components from the Principal Component Analysis (PCA), with axes labeled with the percentage of variance explained by the component. Arrows represent the loadings for the habitat variables, which have been scaled prior to analysis. Points represent territories grouped by site (shaded polygons). Letters within polygons indicate significant differences among sites (PERMANOVA, see Results). (b) Results of a conditional inference tree analysis confirming ecological similarity between the two Wellington sites and a significant difference based on understory density between the two Auckland sites. *P*-values within each oval indicate the significance of each binary split of the data. Histograms indicate the proportion of data points (y-axis) at the terminal node belonging to each site (x-axis).

Pollination outcomes

In the pollinator exclusion experiment, the treatment conditions affected fruit set as expected. Across all sites, only six plants (Auckland Hihi+: 4; Wellington Hihi+: 2) set fruit in the self-pollination condition. In the other conditions, fruit set was lowest for flowers exposed to insects only (Hihi+: 0.26 ± 0.02; Hihi−: 0.11 ± 0.01), was improved by bird visitation (Hihi+: 0.41 ± 0.03; Hihi−: 0.38 ± 0.03), and was highest for hand-pollinated flowers (Hihi+: 0.57 ± 0.03; Hihi−: 0.53 ± 0.03). There was a significant relationship between fruit set and pollination condition depending on hihi presence (condition∗hihi: $\chi^2 = 11.92$, df = 2, $P = 0.003$; Figure 6.3). Although natural (insect+bird) fruit set did not differ significantly between Hihi+ and Hihi− sites, the relative contributions of birds and insects varied based on hihi presence. In contrast to the prediction that reintroducing hihi restores pollination function, bird visitation explained a greater proportion of fruit set at Hihi− sites (BPI = 0.71) than Hihi+ sites (BPI = 0.36; Table 6.3a). Furthermore, while we predicted that plants would be more pollen-limited at sites without hihi, hand pollination did not improve fruit set significantly more at Hihi− sites than Hihi+ sites (Table 6.3a). In other words, plants experienced an equal degree of pollen limitation (PLI: Hihi+ = 0.28, Hihi− = 0.29) regardless of hihi presence.

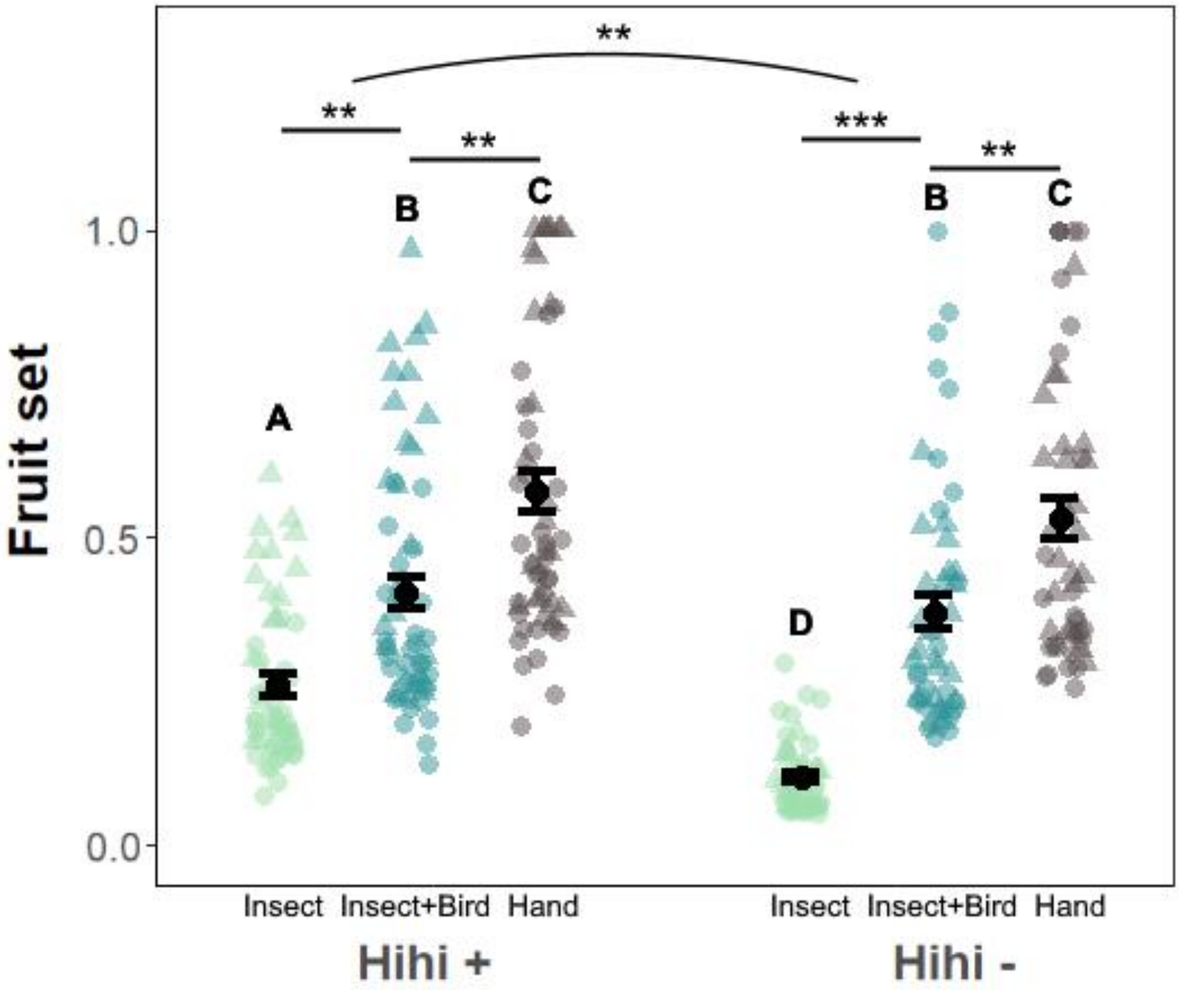

Figure 6.3. Differences in fruit set (proportion of buds which set fruit) by pollination condition and hihi presence (+/−). Means and standard error bars are presented, with letters indicating significant differences across all means, and stars indicating significant differences between conditions (lines) and interactions with hihi presence (arcs). The shape of each data point indicates the region (circle = Auckland, triangle = Wellington).

Table 6.3. Results of a GLMM using pollination condition, hihi presence (+/−), and region to predict (a) fruit set, (b) seed viability, (c) germination of viable seeds, and (d) germination of all seeds. Predictor estimates are from the minimal model identified through a Likelihood Ratio Test (a, c, d: condition∗hihi+region; b: condition+hihi+region). In all cases, results are presented for an intercept of insect+bird (natural pollination) and Auckland Hihi+ site. Significant *P*-values are indicated in bold.

Predictor	**Estimate**	**S.E.**	***z***	***P*-value**
(a) Fruit set				
(Intercept)	−1.19	0.17	−7.05	**<0.001 *****
condition[insect]	−0.47	0.14	−3.25	**0.001 ****
condition[hand-pollinated]	0.39	0.12	3.18	**0.002 ****
hihi[−]	−0.07	0.21	−0.34	0.731
region[Wellington]	0.27	0.18	1.54	0.124
condition[insect]:hihi[−]	−0.80	0.26	−3.08	**0.002 ****
condition[hand-pollinated]:hihi[−]	−0.01	0.18	−0.06	0.952
(b) Seed viability				
(Intercept)	1.49	0.33	4.50	**<0.001 *****
condition[insect]	−0.49	0.08	−5.77	**<0.001 *****
hihi[−]	1.24	0.39	3.21	**0.001 ****
region[Wellington]	−0.75	0.39	−1.93	0.054
(c) Germination of viable seeds				
(Intercept)	2.16	0.33	6.57	**<0.001 *****
condition[insect]	−0.74	0.16	−4.72	**<0.001 *****
hihi[−]	−0.80	0.38	−2.09	**0.037 ***
region[Wellington]	−1.31	0.37	−3.54	**<0.001 *****
condition[insect]:hihi[−]	0.67	0.23	2.97	**0.003 ****
(d) Germination of all seeds				
(Intercept)	0.88	0.33	2.71	**0.007 ****
condition[insect]	−0.62	0.10	−6.38	**<0.001 *****
hihi[−]	0.01	0.38	0.02	0.989
region[Wellington]	−1.23	0.38	−3.26	**0.001 ****
condition[insect]:hihi[−]	0.48	0.16	3.04	**0.002 ****

Patterns of seed viability also contrasted with the prediction that hihi improve pollination. Birds at Hihi+ sites did not improve seed viability significantly more than birds at Hihi− sites (condition*hihi: $\chi^2 = 10^{-4}$, df = 1, $P = 0.99$; Figure 6.4a; Table 6.3b). Regardless of pollination condition, seed viability was also significantly higher at Hihi− sites than Hihi+ sites (Table 6.3b). However, benefits of hihi visitation were evident in terms of seed germination. Viable seeds were more likely to germinate at Hihi+ sites than Hihi− sites, and birds made significantly greater contributions to this probability at the Hihi+ sites (condition∗hihi: $\chi^2 = 8.53$, df = 1, $P = 0.004$; Figure 6.4b). At Hihi+ sites, viable seeds that had been pollinated by birds had a 21% greater chance of germinating than those that had been exposed to insects only (Table 6.3c). At Hihi− sites, bird pollinators did not improve viable seed germination (estimate = 0.07 ± 0.16, $z = 0.41$, $P = 0.68$); additionally, there was much more variability in germination probabilities at Hihi− sites compared to Hihi+ sites (Figure 6.4b). Overall, however, although viable seeds were less likely to germinate at Hihi− sites, because a greater proportion were viable to begin with, the same proportion of all seeds germinated as at Hihi+ sites (Table 6.3d). Nevertheless, birds were responsible for a significantly greater portion of germination (BPI = 0.26) at the Hihi+ sites (condition*hihi: $\chi^2 = 9.19$, df = 1, $P = 0.002$; Figure 6.3c) than at the Hihi− sites (BPI = 0.11), where birds did not improve germination significantly (estimate = 0.14 ± 0.13, $z = 1.13$, $P = 0.3$).

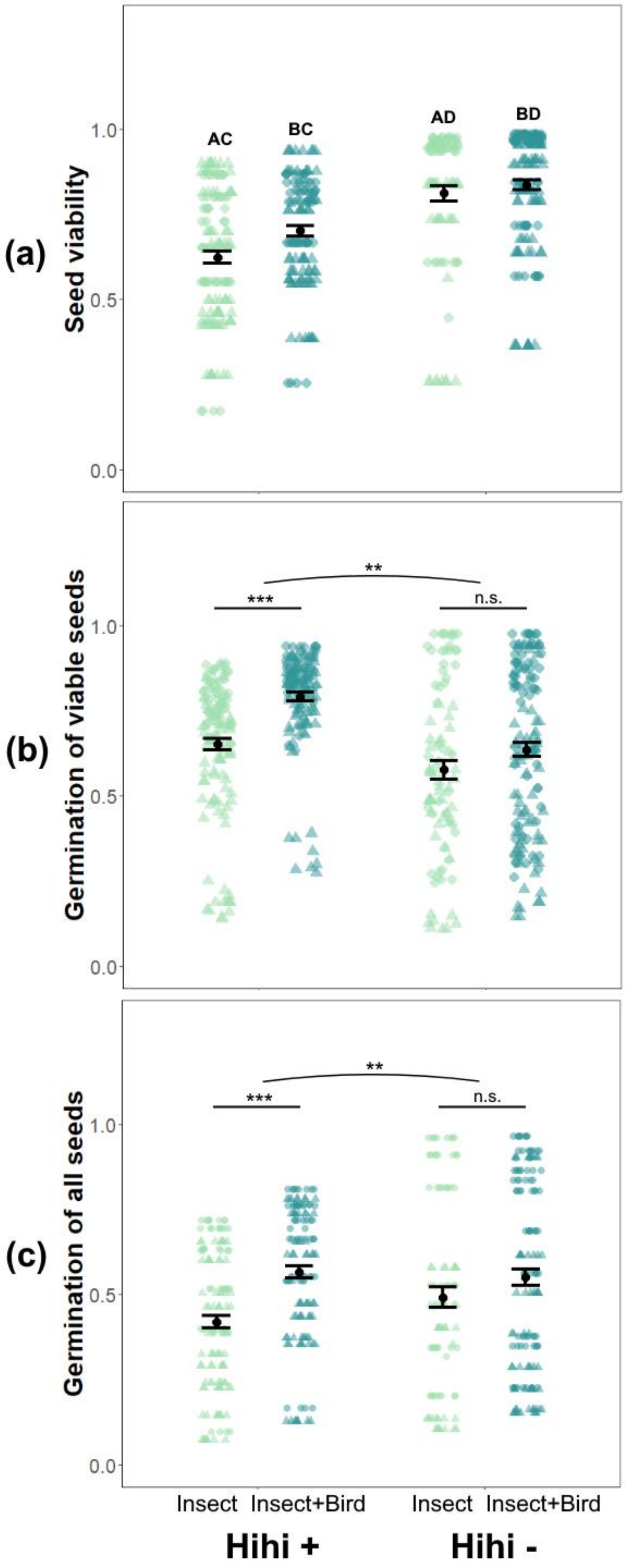

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Figure 6.4. Differences in seed-level pollination outcomes by pollination condition and hihi presence. Means and standard errors bars are presented, with the shape of each data point indicating the region (circle = Auckland, triangle = Wellington). (a) Seed viability. Letters indicate significant differences by pollination condition (AB) and hihi presence (CD). (b) Germination probability of viable seeds. Stars indicate significant differences between conditions (lines) and interactions with hihi presence (arcs). (c) Germination probability of all seeds. Stars indicate significance as in (b).

6.4 DISCUSSION

Despite their value as a tool for broader ecosystem restoration, translocations rarely state and monitor ecological goals explicitly (Ewen et al. 2014; Chauvenet et al. 2016; Taylor et al. 2017; Seddon and Armstrong 2019). Even when restoration is an implicit objective, translocations often rely on assumptions about how much an ecological function needs to be restored and how well translocated species can achieve this goal. Therefore, here we tested whether past assumptions about the ecological benefits of translocations hold true for the hihi, a threatened New Zealand passerine suggested to be a key pollinator missing from native habitats (Craig et al. 1981; S. Anderson 2003; Kelly et al. 2006). Using a pollinator exclusion experiment on hangehange, a common native plant, we found that birds made greater contributions to seed quality at sites where hihi have been reintroduced, primarily by improving germination of viable seeds. However, at sites without hihi, seeds were more likely to be viable to begin with, such that the same proportion of all seeds germinated. Furthermore, fruit set was equally pollen-limited regardless of hihi presence, and birds had a greater effect on fruit set at the non-hihi sites.

Our results suggest that hihi bring unique benefits to pollination by improving seed quality, but interpreting their overall effectiveness as pollinators is less straightforward. On average, plants at hihi sites experienced only a 36% reduction in fruit set when birds were excluded, compared to 71% for plants at non-hihi sites and 46% for bird-pollinated plants globally (Ratto et al. 2018). Thus, the differential effects of hihi on fruit set and seed quality could cancel out such that no net benefit is achieved. However, species can compensate for their deficiency at one stage of an ecological process by benefiting a more consequential stage. For example, in Bolivia, the purplish jay (*Trochocercus cyanomelas*) appears to be a lower-quality seed disperser than the chestnut-eared araçari (*Pteroglossus castanotis*) based on its shorter dispersal distances, but it promotes plant population growth more successfully overall by improving seedling emergence and depositing seeds in higher quality habitats (Loayza and Knight 2010). The positive impact of hihi on seed quality could therefore make them important drivers of plant populations, despite their relative unimportance to fruit set. Nevertheless, to further clarify the benefits of hihi to the system, future work should trace their effects through to later stages of plant recruitment (e.g. seedling survival) and consider other benefits they bring to the system as dual-mutualists (pollinators and seed dispersers; see Burns 2013).

While we attempted to isolate the effects of hihi on pollination as much as possible, mutualists occur in complex ecosystems where their effects may be masked by other species (Bronstein et al. 2003). Therefore, some of our results suggesting conflicting contributions of hihi could instead be the result of unexpected impacts of antagonistic species. Hihi are particularly sensitive to habitat quality, so they tend to be reintroduced to sites that have already undergone extensive restoration (Ewen and Armstrong 2007). For instance, the kākāriki, a known nectar robber (Kelly et al. 2010), is similarly sensitive to habitat quality so may become more prevalent at restored sites through translocation (Ortiz-Catedral and Brunton 2010) or unassisted recolonization (Ortiz-Catedral et al. 2009). Indeed, anecdotal observations at the Auckland hihi site included kākāriki foraging destructively on flowers, so it is possible that hihi do benefit fruit set, but this benefit is negated by kākāriki. This may call into question how we view restored ecosystems; if restoration promotes both mutualistic and antagonistic species, overall functionality at these sites may be no greater than at sites where both species remain absent. However, antagonists likely benefit the ecosystem in other ways, so this may underscore the need for restoring historic assemblages in their entirety to ensure that the negative effects of antagonists are balanced by mutualists.

Just as ecosystems change with restoration, ‘broken’ ecosystems are also dynamic and, in some cases, may be able to recover lost functions without intervention. Several studies have found that diminished pollination function can be restored at least partially through increased visitation by other native (e.g. Hallett et al. 2017) or introduced species (e.g. Pattemore and Wilcove 2011; Stavert et al. 2018; O’Rourke et al. 2020). Similar compensatory visitation could explain why functionality was unexpectedly high at the non-hihi sites. Although not detected in our plant watches, tauhou seem the most likely candidates, as they have been found to visit hangehange more frequently than hihi at sites with both species (Burns 2013). However, our results suggest that the species replacing hihi may provide lower-quality pollination, because birds improved fruit set but not seed quality at the non-hihi sites. Particularly for plants with multi-seeded fruits (such as hangehange), individuals exposed to a range of pollination qualities often preferentially invest in setting fruit and seed from high-quality pollination. Meanwhile, plants will set fruit and seed even from low-quality pollination if this is all that is available (Winsor et al. 1987; Craig and Stewart 1988; Vaughton and Carthew 1993), but resulting seeds may exhibit lower quality (Stephenson 1981), seedling growth (Schmidt-Adam et al. 2000), or seedling survival (A. W. Robertson et al. 2011). This mirrors the results we observed: plants at hihi sites appeared to preferentially invest in bird-pollinated seeds, while those at non-hihi sites set similar quality seed regardless of the pollination received. Thus, the functional similarity observed across sites may reflect hangehange’s ability to compensate for the loss of its primary pollinator by changing its reproductive investments, rather than the effective replacement of hihi. Moreover, the higher viability of seeds, regardless of pollination condition, at non-hihi sites suggests that these plants may also benefit from better water or nutrient availability than those at hihi sites, which they use to further maximize their fitness.

Given that pollination may be able to partially recover without a hihi translocation, our study raises important considerations for how we assess the ecological need for restoration. Conservation biologists increasingly debate whether ecosystems need to be restored to their natural state if functionality can be achieved through other means (Perring et al. 2015; Corlett 2016). Recently, it has also been argued that historic species assemblages may not always be able to restore natural function, particularly if they require ongoing support themselves (Heinen et al. 2020). For example, supplementary feeding could interfere with a species' ability to restore lost pollination and seed dispersal functions by dividing its attention between natural and artificial food sources (Heinen et al. 2020). All reintroduced hihi populations depend on supplementary feeding (Chauvenet et al. 2012; Thorogood et al. 2013), so it could be argued that this prevents hihi from reaching their full potential as pollinators. However, supplementary feeding is also what enables hihi to exist within damaged ecosystems. If artificial support allows hihi to benefit plants in the short-term, it might also be what enables them to gradually shape their own ideal ecosystems, such that supplementary feeding is no longer needed, and pollination is restored to a fully natural state.

Overall, our study suggests that the return of a lost pollinator via translocation can bring measurable benefits to an ecosystem. However, it also highlights the challenges of predicting how effectively one species can restore an ecological process and how well conservation interventions can promote functional restoration. Ecological functions are complex processes that species can influence at many stages (Schupp et al. 2017), and they occur in complex ecosystems where multiple species can have conflicting effects (Bronstein et al. 2003). Additionally, the beneficiaries of a function are not passive bystanders. When the providers of a function are lost, the receivers may be able to compensate, such that 'broken' ecosystems may not be as broken as they once were. The difficulty of predicting, and then monitoring, species' contributions to ecological function may explain why it is so rarely done. However, given ecological function is increasing as a justification for translocation, it should be treated explicitly. Making predictions and evaluating outcomes against defined objectives are essential steps for conservation decision-making (Ewen and Armstrong 2007; Seddon et al. 2007; Nichols and Armstrong 2012) and would allow the success of functional objectives to be improved through adaptive management (Canessa et al. 2016).

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This chapter involved contributions from Sandra Anderson (guidance on methodology) and Karin van der Walt (laboratory work).

Chapter 7

General discussion

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In this thesis, I explored the causes and consequences of dietary variation through a case study of the hihi, a threatened New Zealand passerine. I first used Bayesian statistics to improve the reliability of existing dietary specialization metrics, making them more amenable to small, observational datasets (Chapter 2). Using these improved metrics, I then found evidence for a link between diet and social factors: individuals' diets predicted the size of their foraging groups (Chapter 3), and competitive release brought on by translocation caused individuals to shift toward more generalist diets (Chapter 4). Across these studies, diet predicted survival, with generalists surviving better than specialists when they remained at their natal site (Chapters 2 and 4) but an opposite trend among translocated individuals (Chapter 4). I then asked whether the consequences of foraging extend to higher ecological levels. When presented with a novel foraging task, individual hihi varied in their search patterns and persistence, with key differences emerging between age-sex classes (Chapter 5). While this variation did not predict pollination outcomes at the territory level (Chapter 5), further work confirmed that reintroducing hihi to damaged ecosystems brings measurable benefits to pollination function by improving seed quality (Chapter 6).

In this chapter, I revisit the ecological feedback loop first presented in Chapter 1 (updated in Figure 7.1) to ask how the results of this thesis inform our understanding of the links between diet and social factors and the consequences of foraging for the ecosystem. I then conclude by considering the implications of this research for conservation, while also reflecting on how the fields of behavioral ecology and conservation biology can come together more effectively, to their mutual benefit.

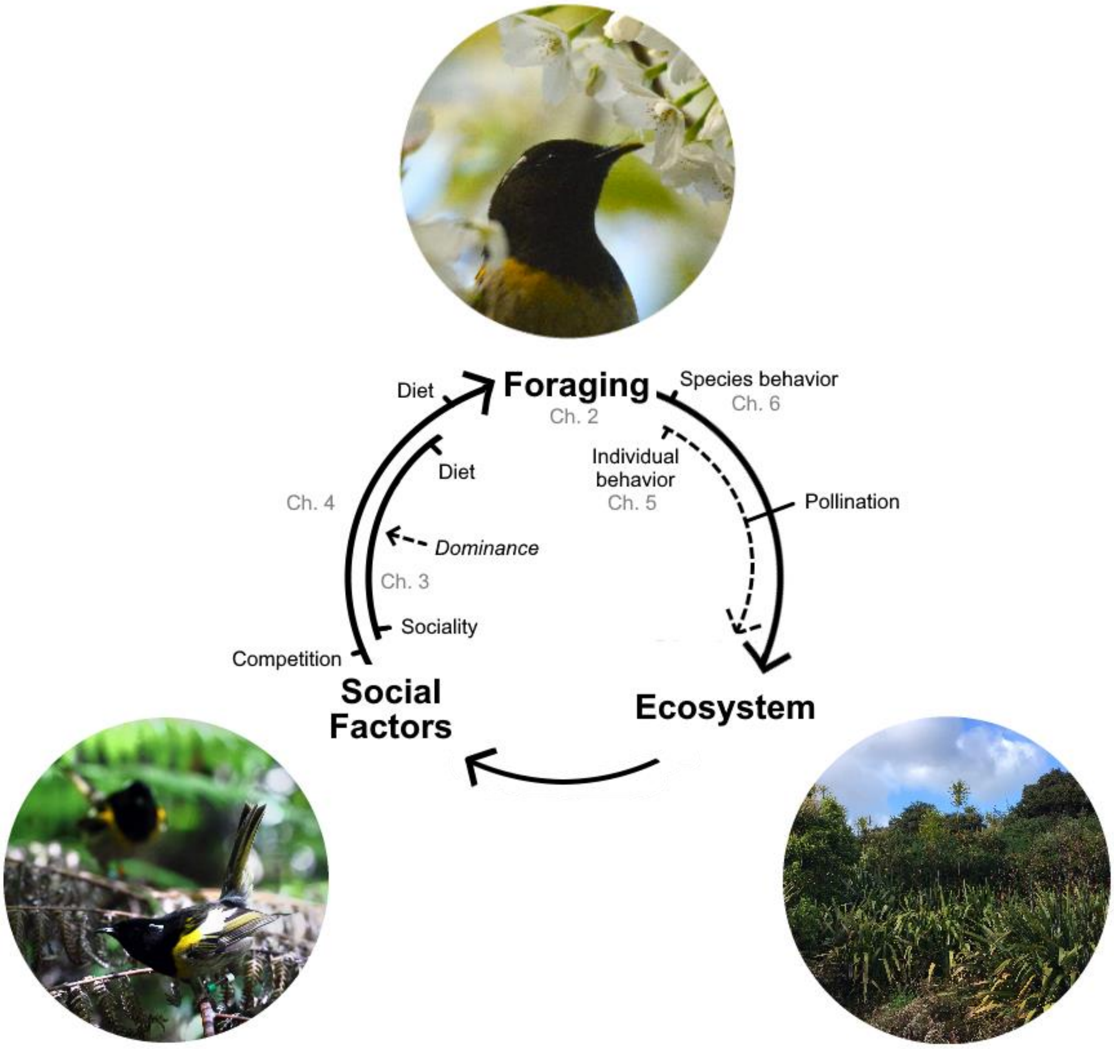

Figure 7.1. Evidence gathered in this thesis in support of an ecological feedback loop connecting social factors, foraging, and the ecosystem. Using dietary specialization metrics developed in Chapter 2, Chapter 3 showed that individual sociality and diet are linked through a possible mediating factor of dominance. Chapter 4 found that competition shapes dietary specialization. Chapters 5 and 6 explored the impacts of foraging on the ecosystem through a case study of pollination. A species' foraging behaviors can lead it to have unique impacts on the ecosystem through pollination (Chapter 6). While there is some evidence that individuals vary in their pollination efficiency, the traits underlying these differences are yet to be identified (Chapter 5). The effects of pollinators on plants could, in turn, shape the competitive landscape by altering the abundance and distribution of resources. Photo credits: Christopher Stephens (top), Stuart Attwood (bottom left), CA (bottom right).

7.1 HOW DOES DIET LINK TO SOCIAL FACTORS?

In Chapter 3, I found a relationship between dietary specialization and foraging group size. Generalists were more gregarious than specialists, but only among small-bodied individuals. Because body size is a proxy for dominance in many birds (e.g. Koenig et al. 2011; Funghi et al. 2015), I proposed that these findings could suggest that diet is linked to sociality through a dominance-related behavioral syndrome (Sih et al. 2004). For instance, Toscano et al. (2016) previously conceptualized how dominance, diet, and sociality could all be linked as downstream effects of personality: an individual's inherent sociability and boldness can shape its dominance and gregariousness, which can give rise to differences in resource selection (see Figure 1 in Toscano et al. 2016). A similar syndrome has been found in great tits (*Parus major*), where an individual's exploratory tendency explains both its resource selection (Serrano-Davies et al. 2017) and gregariousness (Aplin et al. 2014). However, consistency across contexts is a hallmark of behavioral syndromes (Sih et al. 2004). In my study, diet and sociality were not linked in a more competitive context at supplementary feeding stations, which could suggest that there is no syndrome in hihi. Nevertheless, artificial food sources can disrupt natural sociality (as in Szekely et al. 1989), so perhaps there is a syndrome but it is limited to natural contexts. Linking traits to behavioral syndromes can give deeper insight into their causes and consequences (Sih et al. 2004; Dall et al. 2012; Brommer and Class 2017), so further investigation into the relationship between diet and sociality in other natural foraging contexts would be beneficial.

Regardless of whether a syndrome exists, the dominance effect that I observed could help elucidate the mechanisms linking diet and sociality. I suggested two main possibilities, both drawing on my earlier finding that generalist diets appear to confer a survival advantage (Chapter 2). If small-bodied (likely subordinate) individuals are generalist while foraging in groups, it could suggest that foraging socially enables them to obtain higher-quality diets, or that consuming a better diet helps them to endure the competitive costs of group living. Meanwhile, the diets of dominant individuals should be less dependent on group size, because they typically have preferential resource access regardless of the competitive context (Cody 1974; Whitten 1983; Gustafsson 1988; Sol et al. 2005). Without a better understanding of the costs and benefits of group foraging in hihi, it is difficult to disentangle these two possibilities. However, my findings add to a growing literature on the role of dominance in behavioral correlations (Réale et al. 2007; Toscano et al. 2016) by demonstrating how the strength of these correlations can differ between dominant and subordinate individuals. In another recent study, Rudin et al. (2017) found that behavioral correlations can also depend on the stability of dominance hierarchies; correlations disappear in individuals that have undergone a recent change in status. Thus, there are many more questions to be explored about how dominance affects not only the direction of behavioral correlations but their strength and stability.

As a correlative study, Chapter 3 could not determine causality between diet and social factors but identified this link as worthy of further investigation. Therefore, in Chapter 4, I set out to explicitly test causality using conservation translocations as a rare opportunity to observe individual responses to changing social conditions. I tracked individuals' dietary changes as they either remained at their natal site or were moved to a less competitive release site and found that translocated juveniles immediately shifted toward more generalist diets. Although this effect appeared to arise partly from a natural, seasonal shift toward generalization, it was amplified by the competitive release experienced across the translocation. When individuals become more generalist in response to competitive release, it suggests that they share the same inherent resource preferences ('shared preferences model': Svanbäck and Bolnick 2005; Araújo et al. 2011) but must specialize to avoid competition in highly competitive environments (as in Tinker et al. 2012; Pagani-Núñez et al. 2016; Santamaría et al. 2020). This finding provides important insight into the inherent dietary preferences of individuals and the role of competition in shaping dietary specialization. Furthermore, while past studies of competitive effects on diet have mostly compared populations living under different competitive conditions (e.g. Tinker et al. 2012), tracking dietary responses within individuals allowed me to demonstrate that dietary variation can be highly plastic and responsive to competitive changes.

The translocation study also provided insight into the selective pressures acting on dietary specialization. Although generalist hihi survived better than specialists when they remained at the source site (Chapter 2), specialists became more generalist and survived better when translocated (Chapter 4). This was somewhat surprising, given that studies of diet at the species level suggest that generalists are better equipped to respond to environmental changes (Devictor et al. 2008; Börschig et al. 2013; Beever et al. 2017). However, other research shows that individuals that are competitively disadvantaged under normal conditions may be better prepared to tackle novel foraging challenges. For instance, in Arabian babblers (*Turdoides squamiceps*), subordinates exhibit a higher degree of innovativeness in a novel foraging task compared to dominants (Keynan et al. 2015). Similarly, in blue tits (*Cyanistes caeruleus)*, juvenile females are the most likely to learn new foraging skills, and subordinate males learn more successfully than dominant males (Aplin et al. 2013). Therefore, specialist hihi, who are disadvantaged in a familiar environment, may have traits that make them better able to cope with sudden challenges. Future research should explore whether dietary specialization is associated with innovativeness or other traits that would be beneficial in a novel environment.

Overall, Chapters 3 and 4 demonstrated that individual sociality links to diet through a possible mediating factor of dominance (Chapter 3; Figure 7.1) and that dietary specialization is shaped by competitive conditions (Chapter 4). These results confirm that there are, indeed, social effects on diet (Figure 7.1) and highlight the complex links between diet and individual sociality as an important direction for future research.

7.2 HOW DOES FORAGING INFLUENCE THE ECOSYSTEM?

The next two chapters examined how foraging behaviors can affect the ecosystem, using the hihi's role in pollination as a case study (Craig et al. 1981; S. Anderson 2003; Kelly et al. 2006; S. Anderson et al. 2011). In Chapter 5, I presented hihi with a novel foraging task derived from a radial arm maze (Foreman and Ermakova 1997) and found that they exhibited several traits common in high-quality pollinator species: they persisted until they found food (Laverty and Plowright 1988), searched systematically rather than randomly (Janzen 1971; D. Anderson 1983), and avoided repeat visits to empty flowers (Pyke 1979; Healy and Hurly 1995). Although individuals varied in their performance (explained, in part, by age and sex), none of these metrics predicted pollination outcomes on females' territories (males could not be examined due to a small sample size). This result illustrates that traits that make a species an effective pollinator may not necessarily influence pollination efficiency at the individual level. Thus, as behavioral ecologists look to use intraspecific behavioral variation to explain individuals' roles in the ecosystem (Thomson and Chittka 2009; Zwolak 2018; Snell et al. 2019), they should explicitly test whether these traits translate into measurable differences in ecological outcomes. While my study explored only a few behaviors known to influence pollination function, it provides a framework for putting the ecological consequences of behavioral variation to the test and could be used to explore other candidate traits in the future.

In Chapter 6, I broadened out to consider how a species' foraging behaviors can influence ecosystem function. By comparing pollination outcomes across sites with and without hihi (as in the 'elimination approach': Akçakaya et al. 2020), I found that hihi bring measurable benefits to the ecosystem by improving germination of viable seeds. However, other pollination outcomes, such as fruit set and seed viability, were surprisingly low at sites with hihi. On the one hand, this could indicate that hihi have conflicting effects on different pollination outcomes. Many species' contributions to ecological functions are far from binary; in extreme cases, species classified as antagonists have been found to bring positive effects when outcomes are examined at different levels or when they promote the behavior of mutualists (Maloof 2001;

Richardson 2004; Mayer et al. 2014). On the other hand, these results may reflect contributions by other actors, suggesting that my methodology did not isolate the effects of hihi as successfully as intended. First, nectar robbers were more abundant at hihi sites than non-hihi sites, so they could have canceled out the benefits of hihi by destroying flowers (Traveset et al. 1998) or deterring hihi from visiting plants (Varma et al. 2020). Additionally, introduced pollinators may have partially repaired the functional deficiency at the non-hihi sites, as non-native birds and mammals have done in other New Zealand forests (Pattemore and Wilcove 2011). Lastly, there was some evidence that plants at the non-hihi sites partly compensated for the absence of hihi by shifting reproductive investment, such that fruits were produced even from low-quality pollination (Winsor et al. 1987; Craig and Stewart 1988; Vaughton and Carthew 1993). Thus, a pollinator's influence may be shaped by many extrinsic factors, including the presence of other species and the compensatory abilities of the ecosystem.

Chapters 5 and 6 highlighted the challenges of isolating the effects of one actor (individual or species) on ecological function, particularly in complex ecosystems (Strauss 2014). While I attempted to minimize external effects by conducting my pollinator exclusion experiments on hihi territories, which are highly defended (Ewen et al. 2004; Low 2005), other methods may be worth exploring for future studies. Some common approaches, such as measuring functional roles in captivity (e.g. Culliney et al. 2012; Feldman et al. 2019), allow for greater environmental control but may not be feasible in threatened species like the hihi. Instead, proxies such as the volume and diversity of pollen loads carried on bills (S. Anderson 2003) could be used to attribute pollination to individuals more precisely *in situ*; however, this would still require individuals to be caught and would require an understanding of the relationship between these proxies and pollination outcomes (Mitchell 1997; Niesenbaum 1999; Quesada et al. 2001). To quantify the functional role of a species, comparing ecological outcomes immediately before versus after a reintroduction may make it easier to attribute changes to the reintroduced species, although this may not always allow enough time for large-scale changes to become evident (Choi 2004; Hilderbrand et al. 2005; Pullin et al. 2013). Selecting Tāwharanui as one of the non-hihi sites for my study was fortuitous, because it has been proposed as the next site for a hihi reintroduction; thus, my data could provide a baseline measure of pollination function, which can be used for comparison once hihi are reintroduced.

Overall, Chapters 5 and 6 show that species can influence the ecosystem by bringing unique benefits to mutualisms such as pollination (Chapter 6; Figure 7.1). There is also some evidence that individuals may differ in their contributions to these mutualisms, but more work is needed to determine whether these differences are driven by behavioral variation (Chapter 5; Figure 7.1).

7.3 IMPLICATIONS FOR CONSERVATION

While the central questions of my thesis were motivated by behavioral ecology theory, studying them in a threatened species allowed me to explore their potential implications for conservation. Translocation has become a vital tool for species recovery in hihi (Thorogood et al. 2013) and many other taxa (Sarrazin and Barbault 1996; D. Armstrong and Seddon 2008; Ewen et al. 2012; IUCN/SSC 2013), but success rates are estimated to be low overall (Griffith et al. 1989), particularly for species reintroductions (as low as 23%: Fischer and Lindenmayer 2000). Many failures have been attributed to individuals being behaviorally unsuited to their new habitat (B. Bell 2016; Caro 2016; Berger-Tal et al. 2020), which can increase their risk of predation (Banks et al. 2002), starvation (Dickens et al. 2010), and dispersal (Stamps and Swaisgood 2007). Thus, some studies have begun exploring whether behavioral variation can be used as a tool to predict which individuals will be most likely to survive and thrive in a novel environment. Most focus on personality traits (e.g. Bremner-Harrison et al. 2004; Sinn et al. 2014; Germano et al. 2017), but diet may be another trait worthy of consideration, because it is a critical variable affecting an individual’s ability to adapt to an unfamiliar environment (Kamil et al. 1981; Stephens et al. 2007).

The results of my thesis suggest that dietary specialization may be a promising tool for species recovery. Hihi with specialist pre-translocation diets survive better than generalists when translocated (Chapter 4), but worse when they remain at the source site (Chapter 2). These opposing effects are crucial, because maintaining a stable source population is a major concern in translocations (D. Armstrong and Seddon 2008). Nevertheless, more work is needed to determine whether specialists survive better than generalists at all release sites. Studies linking other traits to post-release survival have found that the favorability of these behaviors can be highly context specific. For example, while bold individuals often survive translocation better than shy ones (e.g. Sinn et al. 2014; May et al. 2016), boldness can be harmful in environments where individuals need to be cautious of unfamiliar predators or anthropogenic threats (e.g. Bremner-Harrison et al. 2004). Another important consideration is the mix of behavioral types in a translocated cohort; translocating individuals of a single type may not always be beneficial. If the behavior is genetically based, translocating diverse cohorts could help to minimize bottleneck effects that often reduce the viability of translocated populations (Letty et al. 2007; Berger-Tal et al. 2020). Sometimes, individuals also benefit from being around conspecifics with different traits. For instance, in translocated sandhill cranes (*Grus canadensis pulla*), hand-reared individuals exhibit higher survival than parent-reared individuals, but all individuals fare better when translocated in a mixed cohort (Ellis et al. 2000).

These types of patterns can arise out of ‘skill pool’ (Giraldeau 1984) or ‘pool of competence’ effects (Morand-Ferron and Quinn 2011), where individuals learn or otherwise benefit from the skills and knowledge of individuals with different behavioral tendencies. Thus, if it is compatible with conservation priorities, selecting cohorts of varying dietary compositions for future translocations would be beneficial to test whether this affects outcomes.

Behavioral variation could also be used to achieve broader-scale ecosystem recovery objectives if individuals’ contributions to ecological function depend on their behavioral types (Bolnick et al. 2011; Sih et al. 2012; Raffard et al. 2017). Although we were unable to explain individual hihi’s effectiveness as pollinators by their behaviors in Chapter 5, the fact that pollination outcomes varied across territories warrants further investigation. If a trait can be identified that reliably predicts high-quality pollination, individuals with that trait could be selectively translocated to promote the ecosystem recovery goals often cited in hihi translocations (Smuts-Kennedy 2009; Frost 2012; Collins et al. 2015). However, once again, having a diversity of behaviors in a population might be preferred; diversity in pollinator traits across species has been found to improve pollination function (Fontaine et al. 2006; Hoehn et al. 2008; Martins et al. 2015). It may also be vital to examine whether behaviors that promote ecological function are compatible with species recovery objectives, as some behaviors can have conflicting effects. For instance, in translocations, dispersal is generally viewed as a barrier to population establishment (Letty et al. 2007; Berger-Tal et al. 2020), but individuals with high dispersal tendencies can be beneficial in translocations aimed at promoting population connectivity (Le Gouar et al. 2012). Thus, using behaviors as selection criteria for translocations may require balancing different, potentially competing, objectives.

Despite the uncertainty surrounding individual differences in pollination efficiency (Chapter 5), the results of Chapter 6 confirm that hihi, as a species, bring unique benefits to pollination. This validates long-held assumptions about the value of hihi reintroductions for ecosystem recovery (Ewen and Armstrong 2007). However, the fact that sites without hihi may be able to achieve similar functionality through alternative means highlights the resilience of ecosystems and raises important questions about the value we place on historic species assemblages (Choi 2004; Hilderbrand et al. 2005; Perring et al. 2015; Corlett 2016). Several new approaches to conservation largely ignore species identity; for example, rewilding aims to restore lost ecological functions using the most effective species, even if they are not native (Seddon et al. 2014; Pettorelli et al. 2019). Nevertheless, it is important to consider the many known and unknown benefits that historic assemblages may offer the ecosystem. For example, if the mutualism between hihi and hangehange evolved to promote seed quality over other outcomes, then this effect may be important to prioritize even if plant reproduction can be achieved in other ways; native species often fulfill multiple functional roles (Kelly et al. 2010; Burns 2013; Fuster and Traveset 2020), so the behaviors that enable hihi to promote seed quality may also serve other vital functions that we do not yet understand. Replacing native species with functional substitutes, or allowing the ecosystem to compensate for their loss, may superficially repair one functional deficiency without capturing the full scope of the original role.

Overall, this thesis underscores the benefits that can be gained by uniting the fields of behavioral ecology and conservation biology. This collaboration has long been called for by both fields (Curio 1996; Caro 2007; B. Smith and Blumstein 2013; Caro 2016) but has struggled to gain traction. One reason, as suggested by Caro (2007), may be that behavioral ecologists are deterred by the small sample sizes that often come from working with threatened species. Yet, these challenges may be offset by the unique opportunities that conservation interventions can provide to observe individuals' responses to dramatic environmental changes not normally seen in natural settings (as in Chapter 4). Meanwhile, conservation biologists might not always recognize the benefit of behavioral ecology theory to conservation. However, including behavioral ecologists early in the process of conservation planning can ensure that the relevance to conservation is clear, theory is used to inform predictions, and monitoring programs are designed to maximize learning (Taylor et al. 2017; Durant et al. 2019). This type of collaboration can enable behavioral ecologists to explore complex, multi-level questions, such as the ecological feedback loop explored in this thesis (Figure 7.1). A better understanding of feedback loops like this one can also provide important insight about the risks and opportunities that conservation biologists face. When behavior is entwined with ecological function and the environment, any threat to one of these stages can have cascading impacts on the others. At the same time, this interconnectedness presents opportunities for conservation biologists to intervene at one stage to bring far-reaching benefits across multiple ecological levels (e.g. Watters et al. 2003).

7.4 SUMMARY

In summary, my thesis has shown how variation in foraging behavior is nested within an ecological feedback loop alongside social factors and the ecosystem. Social factors correlate with and directly shape individual dietary variation, and variation in foraging at the species (and possibly individual) level can influence the ecosystem through effects on animal-plant mutualisms; the ecosystem, in turn, is known to shape social factors. I have also examined these questions in a species in which this knowledge could have conservation implications, and proposed ways that variation in diet and foraging behaviors can be used to promote species and ecosystem recovery. Together, my results suggest that a better understanding of the causes and consequences of behavioral variation can be beneficial not only for behavioral ecology but for conservation, highlighting the value of merging these two fields.

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Appendix 1

Supplementary materials

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A1.1 CHAPTER 2 SUPPLEMENT

Supplementary Table 2.1. Habitat types recorded during foraging observations.

	Habitat type	Dominant species	Typical canopy height (m)	Description
1	Bracken	*Phormium tenax, Muehlenbeckia australis*	0 – 3	Open areas dominated by New Zealand flax and ground-cover plants
2	High Māhoe	*Melicytus ramiflorus, Coprosma robusta, Dysoxylum spectabile*	8 – 10	Continuous canopy predominantly consisting of mature māhoe; variably dense understory
3	Immature Kohekohe	*Dysoxylum spectabile, Melicytus ramiflorus*	8 – 12	Patchy canopy dominated by immature kohekohe trees; dense mixed understory
4	Kānuka	*Kunzea ericoides, Coprosma robusta, Myrsine australis*	10 – 12	Patchy canopy of kānuka; open mid- to upper-understory; dense lower-understory with dominant māpou
5	Low Māhoe	*Melicytus ramiflorus, Phormium tenax, Geniostoma ligustrifolium*	4 – 6	Largely open canopy punctuated by immature māhoe trees; dense understory and ground cover
6	Mature Kohekohe	*Dysoxylum spectabile, Melicytus ramiflorus, Metrosideros excelsa*	10 – 14	Continuous canopy dominated by mature kohekohe and other large species in places; sparse understory
7	Nīkau	*Rhopalostylis sapida*	8 – 10	Groves of nīkau trees
8	Pōhutukawa	*Metrosideros excelsa, Melicytus ramiflorus, Coprosma robusta*	8 – 10	Pōhutukawa dominated areas with variably dense understory

Note: The eight predefined, visually-distinct habitat types recorded for each foraging event and used to assess the relative availability of food plant species through habitat assessment plots.

Supplementary Table 2.2. Known hihi food species monitored during the study period.

Scientific name	***Māori*** **name**	**Fruit**		**Nectar**	
		2017	**2018**	**2017**	**2018**
(a)					
Coprosma rhamnoides	karamu	✓	✓		
Coprosma robusta	karamu	✓	✓		
Cordyline australis	tī kōuka	✓	✓		
Dysoxylum spectabile	kohekohe	0	✓		✓[+]
Elingamita johnsonii	–	0	✓*		
Geniostoma ligustrifolium	hangehange	✓	✓		
Hebe stricta	koromiko			0	✓
Ipomoea cairica	pōwhiwhi			0	✓*
Kunzea ericoides	kānuka	0	✓	✓	✓
Macropiper excelsum	kawakawa	✓	✓		
Melicytus ramiflorus	māhoe	✓	✓	✓	✓
Muehlenbeckia australis	pohuehue	–	✓	✓	✓
Myrsine australis	māpou	✓	✓	0	–
Parsonsia heterophylla	kaihua			0	✓*
Pseudopanax arboreus	puahou	✓	✓		
Pseudopanax lessonii	houpara			✓*	✓*
Rhopalostylis sapida	nīkau			✓	–
Sophora chathamica	kōwhai	0	✓*		
Vitex lucens	pūriri	0	0	✓	✓
(b)					
Alseuosmia macrophylla	toropapa	–	–	–	–
Coprosma propinqua	mingimingi	0	0	–	–
Dodonaea viscosa	akeake			–	–
Hedycarya arborea	porokaiwhiria			–	–
Hoheria populnea	houhere			–	–
Myoporum laetum	ngaio	0	0	0	–
Phytolacca octandra	–	0	0		
Pittosporum crassifolium	karo	0	0		
Pittosporum umbellatum	haekaro			0	0

Rhabdothamnus solandri	taurepo			0	0
Schefflera digitata	patē	–	–	–	–

Note: All known hihi food plant species present on Tiritiri Matangi Island and expected to have fruits or flowers available during the 2017 and 2018 study periods (determined from Perrott and Armstrong 2000 and personal communications with site managers). All species in (a) and (b) were monitored, but only species in (a) were observed being consumed by hihi. Checkmarks (✓) indicate food types that were observed being eaten; those with pluses (+) were consumed despite going undetected in phenology surveys, and those with asterisks (*) have not (to our knowledge) previously been reported in the literature as known hihi foods. Foods that were expected to be eaten by hihi but were not observed being eaten are indicated by zeros (0) if they were detected in phenology surveys and dashes (–) if they were not detected. Blank cells indicate food types that were not expected to be eaten by hihi, either because they were out of season during the study period or because hihi are not known to eat them and would not be expected to based on their morphology.

Supplementary Table 2.3. PS_i model selection with age and sex.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**	**Cumulative Weight**
PS_i ~				
age $*$ sex	1215.58	0.00	0.50	0.50
1	1216.98	1.40	0.24	0.74
sex	1218.68	3.10	0.11	0.85
age	1218.70	3.12	0.10	0.95
age + sex	1220.24	4.65	0.05	1.00

Note: Results from a model selection explaining dietary specialization (PS_i) by all combinations of age and sex.

Supplementary Table 2.4. Monthly survival and resighting probability model selections for 2017.

Model	$QAIC_c$	$\triangle QAIC_c$	Model Likelihood	Number of Parameters
(a) Original PS_is				
$\phi(.)\rho(PS_i * \text{time})$	109.84	**0.00**	1.00	5
$\phi(\text{time})\rho(PS_i * \text{time})$	112.02	2.18	0.34	7
$\phi(PS_i)\rho(PS_i * \text{time})$	112.25	2.41	0.30	6
$\phi(.)\rho(\text{time})$	113.23	3.39	0.18	4
$\phi(\text{time})\rho(\text{time})$	113.38	3.54	0.17	5
$\phi(.)\rho(PS_i + \text{time})$	114.06	4.22	0.12	5
$\phi(PS_i * \text{time})\rho(\text{time})$	114.20	4.36	0.11	7
$\phi(PS_i + \text{time})\rho(PS_i * \text{time})$	114.63	4.79	0.091	8
$\phi(PS_i)\rho(\text{time})$	115.19	5.35	0.069	5
$\phi(PS_i)\rho(PS_i + \text{time})$	116.43	6.59	0.037	6
$\phi(\text{time})\rho(PS_i + \text{time})$	117.02	7.18	0.028	7
$\phi(PS_i + \text{time})\rho(\text{time})$	117.89	8.05	0.018	7
$\phi(PS_i + \text{time})\rho(PS_i + \text{time})$	119.55	9.71	<0.01	8
$\phi(PS_i * \text{time})\rho(PS_i)$	122.89	13.05	<0.01	4
$\phi(PS_i * \text{time})\rho(PS_i + \text{time})$	124.03	14.19	<0.01	10
$\phi(\text{time})\rho(.)$	124.60	14.76	<0.01	3
$\phi(PS_i * \text{time})\rho(.)$	125.57	15.73	<0.01	5
$\phi(\text{time})\rho(PS_i)$	125.78	15.94	<0.01	4
$\phi(PS_i * \text{time})\rho(PS_i * \text{time})$	126.09	16.25	<0.01	12
$\phi(PS_i + \text{time})\rho(.)$	126.54	16.70	<0.01	4
$\phi(.)\rho(.)$	127.67	17.83	<0.01	2
$\phi(PS_i + \text{time})\rho(PS_i)$	127.99	18.15	<0.01	5
$\phi(.)\rho(PS_i)$	128.55	18.71	<0.01	3
$\phi(PS_i)\rho(.)$	129.60	19.76	<0.01	3
$\phi(PS_i)\rho(PS_i)$	130.73	20.89	<0.01	4
(b) Uncertainty-Corrected PS_is				
$\phi(\text{time})\rho(PS_i * \text{time})$	112.31	**0.00**	1.00	7
$\phi(.)\rho(\text{time})$	113.23	**0.92**	0.63	4
$\phi(.)\rho(PS_i + \text{time})$	113.27	**0.95**	0.62	5

$\phi(PS_i)\rho(\text{time})$	113.28	**0.96**	0.62	5
$\phi(\text{time})\rho(\text{time})$	113.38	**1.07**	0.59	5
$\phi(PS_i)\rho(PS_i + \text{time})$	114.51	2.20	0.33	6
$\phi(PS_i + \text{time})\rho(\text{time})$	116.03	3.72	0.16	7
$\phi(\text{time})\rho(PS_i + \text{time})$	116.53	4.21	0.12	7
$\phi(.)\rho(PS_i * \text{time})$	116.54	4.23	0.12	7
$\phi(PS_i)\rho(PS_i * \text{time})$	116.80	4.48	0.11	8
$\phi(PS_i + \text{time})\rho(PS_i + \text{time})$	117.75	5.43	0.067	8
$\phi(PS_i + \text{time})\rho(PS_i * \text{time})$	120.03	7.71	0.021	10
$\phi(PS_i * \text{time})\rho(\text{time})$	120.80	8.49	0.014	10
$\phi(PS_i * \text{time})\rho(PS_i + \text{time})$	121.67	9.35	<0.01	10
$\phi(\text{time})\rho(.)$	122.39	10.08	<0.01	2
$\phi(\text{time})\rho(PS_i)$	124.48	12.16	<0.01	4
$\phi(PS_i * \text{time})\rho(PS_i * \text{time})$	124.81	12.49	<0.01	12
$\phi(PS_i + \text{time})\rho(.)$	125.29	12.97	<0.01	4
$\phi(PS_i + \text{time})\rho(PS_i)$	126.02	13.70	<0.01	5
$\phi(PS_i * \text{time})\rho(.)$	126.15	13.84	<0.01	5
$\phi(.)\rho(PS_i)$	126.35	14.03	<0.01	3
$\phi(PS_i * \text{time})\rho(PS_i)$	127.63	15.31	<0.01	6
$\phi(.)\rho(.)$	127.67	15.36	<0.01	2
$\phi(PS_i)\rho(PS_i)$	128.12	15.80	<0.01	4
$\phi(PS_i)\rho(.)$	128.16	15.84	<0.01	3

Note: Results from model selections explaining monthly survival probability (ϕ) and resighting probability (ρ) in the 2017 survey periods (February 2017–February 2018) by (a) our original Bayesian PS_is and (b) Bayesian PS_is corrected to account for the uncertainty inherent to each individual's sample size of foods eaten. $\triangle QAIC_c$s values are bolded for the best supported models ($\triangle QAIC_c < 2$).

Supplementary Table 2.5. Monthly survival and resighting probability model selections for 2018.

Model	**AIC$_c$**	**$\triangle$AIC$_c$**	**Model Likelihood**	**Number of Parameters**
(a) Original PS$_i$s				
$\phi(PS_i)\rho(time)$	390.71	**0.00**	1.00	6
$\phi(PS_i)\rho(PS_i + time)$	392.49	**1.78**	0.41	7
$\phi(.)\rho(PS_i * time)$	394.80	4.09	0.13	9
$\phi(PS_i)\rho(PS_i * time)$	395.19	4.48	0.11	10
$\phi(.)\rho(PS_i + time)$	396.00	5.30	0.071	6
$\phi(.)\rho(time)$	396.46	5.75	0.056	5
$\phi(PS_i + time)\rho(PS_i * time)$	396.83	6.12	0.047	11
$\phi(PS_i + time)\rho(time)$	396.93	6.22	0.045	9
$\phi(time)\rho(PS_i + time)$	397.85	7.14	0.028	7
$\phi(PS_i + time)\rho(PS_i + time)$	398.80	8.10	0.018	10
$\phi(time)\rho(PS_i * time)$	398.84	8.14	0.017	11
$\phi(time)\rho(time)$	400.42	9.71	<0.01	7
$\phi(PS_i * time)\rho(time)$	401.08	10.37	<0.01	11
$\phi(PS_i * time)\rho(PS_i + time)$	403.15	12.44	<0.01	12
$\phi(PS_i * time)\rho(PS_i * time)$	403.34	12.63	<0.01	14
$\phi(PS_i)\rho(PS_i)$	444.47	53.76	<0.01	2
$\phi(time)\rho(PS_i)$	447.34	56.63	<0.01	2
$\phi(.)\rho(PS_i)$	447.34	56.63	<0.01	2
$\phi(PS_i + time)\rho(PS_i)$	450.08	59.38	<0.01	4
$\phi(PS_i * time)\rho(PS_i)$	450.08	59.38	<0.01	4
$\phi(time)\rho(.)$	452.24	61.53	<0.01	2
$\phi(PS_i)\rho(.)$	453.74	63.04	<0.01	3
$\phi(.)\rho(.)$	453.88	63.17	<0.01	2
$\phi(PS_i + time)\rho(.)$	454.42	63.71	<0.01	5
$\phi(PS_i * time)\rho(.)$	458.62	67.91	<0.01	7
(b) Uncertainty-Corrected PS$_i$s				
$\phi(PS_i)\rho(time)$	390.76	**0.00**	1.00	6
$\phi(PS_i)\rho(PS_i + time)$	391.86	**1.10**	0.58	7
$\phi(.)\rho(PS_i * time)$	393.17	2.40	0.30	9

$\phi(PS_i)\rho(PS_i \ast time)$	393.94	3.18	0.20	10
$\phi(.)\rho(PS_i + time)$	394.69	3.93	0.14	6
$\phi(time)\rho(PS_i \ast time)$	394.91	4.15	0.13	10
$\phi(PS_i + time)\rho(PS_i \ast time)$	395.61	4.85	0.089	11
$\phi(.)\rho(time)$	396.46	5.70	0.058	5
$\phi(time)\rho(PS_i + time)$	396.46	5.70	0.058	7
$\phi(PS_i + time)\rho(time)$	397.02	6.26	0.044	9
$\phi(PS_i \ast time)\rho(PS_i \ast time)$	397.74	6.97	0.031	12
$\phi(PS_i + time)\rho(PS_i + time)$	398.33	7.57	0.023	10
$\phi(time)\rho(time)$	400.42	9.65	<0.01	7
$\phi(PS_i \ast time)\rho(time)$	400.81	10.05	<0.01	11
$\phi(PS_i \ast time)\rho(PS_i + time)$	402.55	11.79	<0.01	12
$\phi(PS_i)\rho(PS_i)$	446.05	55.29	<0.01	2
$\phi(.)\rho(PS_i)$	446.05	55.29	<0.01	2
$\phi(time)\rho(PS_i)$	446.05	55.29	<0.01	2
$\phi(PS_i + time)\rho(PS_i)$	449.17	58.41	<0.01	4
$\phi(PS_i \ast time)\rho(PS_i)$	451.29	60.52	<0.01	5
$\phi(time)\rho(.)$	452.24	61.47	<0.01	2
$\phi(PS_i + time)\rho(.)$	452.47	61.70	<0.01	4
$\phi(PS_i \ast time)\rho(.)$	453.28	62.51	<0.01	5
$\phi(PS_i)\rho(.)$	453.77	63.00	<0.01	3
$\phi(.)\rho(.)$	453.88	63.11	<0.01	2

Note: Results from model selections explaining monthly survival probability (ϕ) and resighting probability (ρ) in the 2018 survey periods (February 2018–February 2019) by (a) our original Bayesian PS_is and (b) Bayesian PS_is corrected to account for the uncertainty inherent to each individual's sample size of foods eaten. $\triangle AIC_c$ values are bolded for the best supported models ($\triangle AIC_c < 2$).

A1.2 CHAPTER 3 SUPPLEMENT

Supplementary Table 3.1. Results of an AIC_c model selection explaining dietary specialization (PS_i) by intrinsic factors expected to influence dominance. All models included year as a covariate.

Model	AIC_c	$\triangle AIC_c$	AIC_c Weight
~ 1	−196.98	0.00	0.28
~ age	−196.07	0.91	0.18
~ tarsus	−195.20	1.78	0.11
~ sex	−194.95	2.03	0.10
~ age + sex	−194.82	2.16	0.10
~ age + tarsus	−194.21	2.77	0.07
~ sex + tarsus	−193.15	3.83	0.04
~ age + sex + tarsus	−192.93	4.05	0.04
~ age ∗ tarsus	−192.64	4.34	0.03
~ age ∗ tarsus + sex	−191.34	5.64	0.02
~ sex ∗ tarsus	−191.20	5.78	0.02
~ sex ∗ tarsus + age	−191.01	5.97	0.01
~ age ∗ tarsus + sex ∗ tarsus	−189.08	7.90	0.01

Supplementary Table 3.2. Results of an AIC$_c$ model selection explaining the number of feeder watch sessions an individual was observed entering the feeder. All models included year as a covariate.

Model	AIC$_c$	$\triangle$AIC$_c$	AIC$_c$ Weight
~ PS$_i$ + sex + age	609.08	0.00	0.23
~ PS$_i$ + sex	609.83	0.74	0.16
~ PS$_i$ + sex + tarsus	610.40	1.32	0.12
~ PS$_i$ $*$ sex + age	610.87	1.79	0.09
~ PS$_i$ $*$ sex	611.31	2.23	0.08
~ PS$_i$ $*$ age + sex	611.61	2.52	0.07
~ sex $*$ tarsus + PS$_i$	612.14	3.05	0.05
~ PS$_i$ $*$ sex + tarsus	612.26	3.18	0.05
~ PS$_i$ $*$ tarsus + sex	612.46	3.38	0.04
~ PS$_i$ $*$ sex + PS$_i$ $*$ age	612.87	3.78	0.03
~ PS$_i$ $*$ sex + sex $*$ tarsus	613.99	4.91	0.02
~ PS$_i$ $*$ tarsus + sex $*$ tarsus	614.34	5.26	0.02
~ PS$_i$ $*$ sex + PS$_i$ $*$ tarsus	614.41	5.33	0.02
~ PS$_i$ $*$ sex + PS$_i$ $*$ tarsus + sex $*$ tarsus	616.27	7.19	0.01
~ PS$_i$ + age	616.70	7.62	0.01
~ PS$_i$ + age + tarsus	617.54	8.46	<0.01
~ PS$_i$ $*$ sex $*$ tarsus	618.26	9.18	<0.01
~ age $*$ tarsus + PS$_i$	618.73	9.64	<0.01
~ PS$_i$ $*$ age	618.93	9.85	<0.01
~ PS$_i$ $*$ tarsus + age	619.63	10.55	<0.01
~ PS$_i$ $*$ age + tarsus	619.79	10.71	<0.01
~ PS$_i$ $*$ tarsus + age $*$ tarsus	620.80	11.71	<0.01
~ PS$_i$ $*$ age + age $*$ tarsus	621.03	11.95	<0.01
~ PS$_i$ $*$ age + PS$_i$ $*$ tarsus	621.92	12.84	<0.01
~ 1	622.37	13.29	<0.01
~ PS$_i$ $*$ age + PS$_i$ $*$ tarsus + age $*$ tarsus	623.14	14.06	<0.01
~ PS$_i$	624.00	14.91	<0.01
~ PS$_i$ + tarsus	624.67	15.59	<0.01
~ PS$_i$ $*$ age $*$ tarsus	625.42	16.34	<0.01
~ PS$_i$ $*$ tarsus	626.52	17.43	<0.01

Supplementary Table 3.3. Results of an AIC_c model selection explaining the number of times an individual was observed entering the feeder across all sessions (including individuals observed entering the feeder at least once). All models included year as a covariate.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**
~ 1	598.07	0.00	0.27
~ PS_i + sex + age	599.95	1.88	0.10
~ PS_i	600.24	2.17	0.09
~ PS_i + sex	600.47	2.40	0.08
~ PS_i ∗ sex + age	601.10	3.03	0.06
~ PS_i + age	601.39	3.32	0.05
~ PS_i ∗ sex	601.64	3.57	0.04
~ PS_i + tarsus	601.72	3.65	0.04
~ PS_i + sex + tarsus	602.14	4.07	0.03
~ PS_i ∗ age + sex	602.19	4.12	0.03
~ PS_i ∗ sex + PS_i ∗ age	602.71	4.64	0.03
~ PS_i + age + tarsus	602.74	4.66	0.03
~ PS_i ∗ sex + tarsus	603.28	5.21	0.02
~ sex ∗ tarsus + PS_i	603.47	5.39	0.02
~ PS_i ∗ age	603.60	5.53	0.02
~ PS_i ∗ tarsus	604.01	5.93	0.01
~ PS_i ∗ tarsus + sex	604.51	6.44	0.01
~ PS_i ∗ sex + sex ∗ tarsus	604.68	6.61	0.01
~ PS_i ∗ tarsus + age	605.03	6.96	0.01
~ PS_i ∗ age + tarsus	605.06	6.99	0.01
~ age ∗ tarsus + PS_i	605.11	7.04	0.01
~ PS_i ∗ sex + PS_i ∗ tarsus	605.72	7.65	0.01
~ PS_i ∗ tarsus + sex ∗ tarsus	605.85	7.77	0.01
~ PS_i ∗ sex + PS_i ∗ tarsus + sex ∗ tarsus	607.16	9.09	<0.01
~ PS_i ∗ age + PS_i ∗ tarsus	607.43	9.36	<0.01
~ PS_i ∗ tarsus + age ∗ tarsus	607.45	9.38	<0.01
~ PS_i ∗ age + age ∗ tarsus	607.51	9.43	<0.01
~ PS_i ∗ sex ∗ tarsus	609.15	11.08	<0.01
~ PS_i ∗ age + PS_i ∗ tarsus + age ∗ tarsus	609.93	11.86	<0.01
~ PS_i ∗ age ∗ tarsus	611.83	13.76	<0.01

Supplementary Table 3.4. Results of an AIC_c model selection explaining the number of korimako entrances to the feeder observed per hour in a given feeder watch session. All models included year as a covariate.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**
~ korimako to korimako aggression	1266.54	0.00	1
~ 1	1280.95	14.40	<0.01
~ hihi to hihi aggression	1281.71	15.16	<0.01
~ hihi to korimako aggression	1283.09	16.55	<0.01
~ korimako to hihi aggression	1283.11	16.57	<0.01

Supplementary Table 3.5. Results of an AIC_c model selection explaining an individual’s grouping tendency (proportion of focal follows observed with at least one conspecific) while foraging on natural food sources. All models included year as a covariate.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**
~ PS_i ∗ tarsus + age	397.09	0.00	0.42
~ PS_i ∗ tarsus + age ∗ tarsus	398.77	1.68	0.18
~ PS_i ∗ age + PS_i ∗ tarsus	399.21	2.11	0.14
~ PS_i + age + tarsus	400.25	3.16	0.09
~ PS_i ∗ age + PS_i ∗ tarsus + age ∗ tarsus	400.99	3.89	0.06
~ PS_i ∗ age + tarsus	402.26	5.17	0.03
~ age ∗ tarsus + PS_i	402.33	5.23	0.03
~ PS_i ∗ age ∗ tarsus	402.49	5.40	0.03
~ PS_i ∗ age + age ∗ tarsus	404.40	7.31	0.01
~ PS_i + age	405.35	8.26	0.01
~ PS_i + sex + age	406.77	9.67	<0.01
~ PS_i ∗ age	407.46	10.37	<0.01
~ PS_i ∗ sex + age	408.69	11.60	<0.01
~ PS_i ∗ age + sex	408.93	11.83	<0.01
~ PS_i ∗ sex + PS_i ∗ age	410.56	13.46	<0.01
~ PS_i ∗ tarsus	418.21	21.12	<0.01
~ PS_i ∗ tarsus + sex	418.53	21.43	<0.01
~ PS_i ∗ sex + PS_i ∗ tarsus	420.03	22.94	<0.01
~ PS_i ∗ tarsus + sex ∗ tarsus	420.32	23.22	<0.01
~ PS_i ∗ sex + PS_i ∗ tarsus + sex ∗ tarsus	421.68	24.59	<0.01
~ PS_i + tarsus	422.34	25.25	<0.01
~ PS_i + sex + tarsus	422.69	25.60	<0.01
~ PS_i ∗ sex ∗ tarsus	423.52	26.43	<0.01
~ sex ∗ tarsus + PS_i	423.83	26.74	<0.01
~ PS_i ∗ sex + tarsus	424.24	27.14	<0.01
~ 1	425.21	28.12	<0.01
~ PS_i ∗ sex + sex ∗ tarsus	425.23	28.14	<0.01
~ PS_i	427.31	30.22	<0.01
~ PS_i + sex	427.54	30.45	<0.01
~ PS_i ∗ sex	429.08	31.98	<0.01

Supplementary Table 3.6. Results of an AIC$_c$ model selection explaining whether an individual entered the feeder with at least one conspecific already inside the feeder. All models included year as a covariate.

Model	**AIC$_c$**	**$\triangle$AIC$_c$**	**AIC$_c$ Weight**
~ PS$_i$ + age + tarsus	1298.46	0.00	0.12
~ PS$_i$ + tarsus	1299.05	0.59	0.09
~ PS$_i$ ∗ tarsus + age	1299.94	1.47	0.06
~ PS$_i$ ∗ age + tarsus	1299.96	1.50	0.06
~ PS$_i$	1299.98	1.51	0.06
~ PS$_i$ + age	1300.24	1.77	0.05
~ 1	1300.27	1.80	0.05
~ PS$_i$ ∗ tarsus	1300.30	1.84	0.05
~ PS$_i$ ∗ sex + tarsus	1300.38	1.91	0.05
~ age ∗ tarsus + PS$_i$	1300.44	1.97	0.04
~ PS$_i$ + sex + tarsus	1300.46	2.00	0.04
~ PS$_i$ ∗ sex	1301.05	2.59	0.03
~ PS$_i$ ∗ age + PS$_i$ ∗ tarsus	1301.42	2.95	0.03
~ PS$_i$ + sex	1301.43	2.96	0.03
~ PS$_i$ ∗ age	1301.55	3.09	0.03
~ PS$_i$ ∗ tarsus + sex	1301.78	3.32	0.02
~ PS$_i$ ∗ tarsus + age ∗ tarsus	1301.84	3.37	0.02
~ PS$_i$ ∗ sex + age	1301.86	3.40	0.02
~ PS$_i$ ∗ age + age ∗ tarsus	1301.90	3.43	0.02
~ PS$_i$ ∗ sex + PS$_i$ ∗ tarsus	1301.91	3.45	0.02
~ PS$_i$ + sex + age	1302.17	3.71	0.02
~ PS$_i$ ∗ sex + sex ∗ tarsus	1302.24	3.78	0.02
~ sex ∗ tarsus + PS$_i$	1302.25	3.79	0.02
~ PS$_i$ ∗ age + PS$_i$ ∗ tarsus + age ∗ tarsus	1303.27	4.80	0.01
~ PS$_i$ ∗ tarsus + sex ∗ tarsus	1303.46	4.99	0.01
~ PS$_i$ ∗ age + sex	1303.51	5.05	0.01
~ PS$_i$ ∗ sex + PS$_i$ ∗ tarsus + sex ∗ tarsus	1303.69	5.23	0.01
~ PS$_i$ ∗ sex + PS$_i$ ∗ age	1303.84	5.37	0.01
~ PS$_i$ ∗ age ∗ tarsus	1305.17	6.70	<0.01
~ PS$_i$ ∗ sex ∗ tarsus	1305.47	7.00	<0.01

Supplementary Table 3.7. Results of an AIC_c model selection explaining whether an individual entered the feeder with at least one conspecific already inside the feeder, also accounting for the number of heterospecifics inside the feeder. All models included year as a covariate.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**
~ PS_i + age + tarsus + heterospecifics	1299.25	0.00	0.11
~ PS_i + tarsus + heterospecifics	1299.56	0.31	0.09
~ PS_i + heterospecifics	1300.37	1.12	0.06
~ 1 + heterospecifics	1300.54	1.29	0.06
~ PS_i ∗ sex + tarsus + heterospecifics	1300.60	1.35	0.05
~ PS_i ∗ age + tarsus + heterospecifics	1300.70	1.44	0.05
~ PS_i ∗ tarsus + age + heterospecifics	1300.77	1.52	0.05
~ PS_i + age + heterospecifics	1300.85	1.59	0.05
~ PS_i + sex + tarsus + heterospecifics	1300.89	1.64	0.05
~ PS_i ∗ tarsus + heterospecifics	1300.89	1.64	0.05
~ PS_i ∗ sex + heterospecifics	1301.15	1.90	0.04
~ age ∗ tarsus + PS_i + heterospecifics	1301.23	1.98	0.04
~ PS_i + sex + heterospecifics	1301.74	2.48	0.03
~ PS_i ∗ age + heterospecifics	1302.11	2.85	0.03
~ PS_i ∗ age + PS_i ∗ tarsus + heterospecifics	1302.21	2.95	0.02
~ PS_i ∗ sex + age + heterospecifics	1302.22	2.96	0.02
~ PS_i ∗ sex + PS_i ∗ tarsus + heterospecifics	1302.23	2.98	0.02
~ PS_i ∗ tarsus + sex + heterospecifics	1302.30	3.04	0.02
~ PS_i ∗ sex + sex ∗ tarsus + heterospecifics	1302.43	3.18	0.02
~ sex ∗ tarsus + PS_i + heterospecifics	1302.64	3.38	0.02
~ PS_i ∗ age + age ∗ tarsus + heterospecifics	1302.64	3.39	0.02
~ PS_i ∗ tarsus + age ∗ tarsus + heterospecifics	1302.69	3.43	0.02
~ PS_i + sex + age + heterospecifics	1302.73	3.48	0.02
~ PS_i ∗ tarsus + sex ∗ tarsus + heterospecifics	1303.93	4.67	0.01
~ PS_i ∗ sex + PS_i ∗ tarsus + sex ∗ tarsus + heterospecifics	1303.97	4.72	0.01
~ PS_i ∗ age + sex + heterospecifics	1304.02	4.76	0.01
~ PS_i ∗ age + PS_i ∗ tarsus + age ∗ tarsus + heterospecifics	1304.07	4.81	0.01
~ PS_i ∗ sex + PS_i ∗ age + heterospecifics	1304.19	4.94	0.01
~ PS_i ∗ sex ∗ tarsus + heterospecifics	1305.86	6.60	<0.01
~ PS_i ∗ age ∗ tarsus + heterospecifics	1306.01	6.75	<0.01

Supplementary Table 3.8. Results of an AIC_c model selection explaining the number of heterospecifics present inside the feeder at the time an individual entered. All models included year as a covariate.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**
~ PS_i + age + sex	4113.98	0.00	0.17
~ PS_i + sex	4114.45	0.47	0.14
~ 1	4114.59	0.62	0.13
~ $PS_i *$ sex + age	4115.39	1.41	0.09
~ $PS_i *$ age + sex	4115.88	1.91	0.07
~ $PS_i *$ sex	4115.99	2.01	0.06
~ PS_i + sex + tarsus	4116.42	2.44	0.05
~ PS_i	4116.59	2.62	0.05
~ $PS_i *$ tarsus + sex	4117.41	3.44	0.03
~ $PS_i *$ sex + $PS_i *$ age	4117.42	3.45	0.03
~ $PS_i *$ sex + tarsus	4117.98	4.01	0.02
~ $PS_i *$ sex $*$ tarsus	4118.08	4.11	0.02
~ PS_i + age	4118.15	4.17	0.02
~ sex $*$ tarsus + PS_i	4118.44	4.47	0.02
~ PS_i + tarsus	4118.59	4.62	0.02
~ $PS_i *$ sex + $PS_i *$ tarsus	4118.79	4.81	0.02
~ $PS_i *$ tarsus + sex $*$ tarsus	4119.45	5.47	0.01
~ $PS_i *$ tarsus	4119.98	6.00	0.01
~ $PS_i *$ age	4120.01	6.03	0.01
~ $PS_i *$ sex + sex $*$ tarsus	4120.01	6.04	0.01
~ PS_i + age + tarsus	4120.17	6.20	0.01
~ $PS_i *$ sex + $PS_i *$ tarsus + sex $*$ tarsus	4120.82	6.84	0.01
~ $PS_i *$ tarsus + age	4121.68	7.70	<0.01
~ $PS_i *$ age + tarsus	4122.04	8.07	<0.01
~ age $*$ tarsus + PS_i	4122.15	8.17	<0.01
~ $PS_i *$ age + $PS_i *$ tarsus	4123.58	9.60	<0.01
~ $PS_i *$ tarsus + age $*$ tarsus	4123.58	9.61	<0.01
~ $PS_i *$ age + age $*$ tarsus	4124.04	10.07	<0.01
~ $PS_i *$ age + $PS_i *$ tarsus + age $*$ tarsus	4125.52	11.54	<0.01
~ $PS_i *$ age $*$ tarsus	4126.02	12.04	<0.01

Supplementary Table 3.9. Results of an AIC_c model selection explaining an individual's network degree, which reflects both the number and strength of its associations with conspecifics in a social network derived from feeder entrance data. All models included year as a covariate.

Model	**AIC_c**	**$\triangle AIC_c$**	**AIC_c Weight**
~ 1	76.88	0.00	0.52
~ PS_i	79.07	2.19	0.17
~ PS_i + sex	80.85	3.97	0.07
~ PS_i + tarsus	81.01	4.14	0.07
~ PS_i + age	81.51	4.63	0.05
~ PS_i + sex + tarsus	82.92	6.04	0.03
~ PS_i ∗ sex	83.10	6.22	0.02
~ PS_i + sex + age	83.13	6.25	0.02
~ PS_i ∗ tarsus	83.43	6.55	0.02
~ PS_i + age + tarsus	83.60	6.72	0.02
~ PS_i ∗ age	83.86	6.98	0.02

A1.3 CHAPTER 4 SUPPLEMENT

Supplementary Materials 4.1: Supplemental Methods

To evaluate the ecological similarity of the three study sites, we conducted habitat assessments. Each site was divided into four equal quadrants, with four points randomly selected in each to designate 16 habitat plots. On each plot, we created five 20 m transects radiating from a central point, with one sampling point located every 4 m along the transect. At each sampling point, we conducted the following assessments. First, the canopy height was estimated, which we averaged across all points in the plot to assign an average canopy height. Next, we counted and identified (to species level) every mature plant intersecting an imaginary cylinder of 1 m radius and 2 m height. We summed these counts across all 25 sampling points and divided by the total sampling area (25π m^2) to estimate the understory density of the plot. We also calculated a Shannon diversity index (Shannon 1948) as:

$$-\sum_{i=1}^{R} p_i ln p_i,$$

where R is the total number of unique species present and p_i is the proportion of plants belonging to species i. This provided a measure of species abundance and evenness. Lastly, we completed a vertical habitat assessment (adapted from Scott 1965; Makan et al. 2014) by extending an imaginary cylinder of 10 cm radius to the canopy. In each height bracket beginning from the ground to 30 cm, 30 cm to 2 m, and continuing in 2 m increments thereafter, we counted the number of unique species with intersecting foliage. Summing these counts across all height brackets and all points on the plot provided a proxy of canopy density. Combined with the understory assessments, these vertical assessments were also used to produce a count of the total number of unique species on the plot.

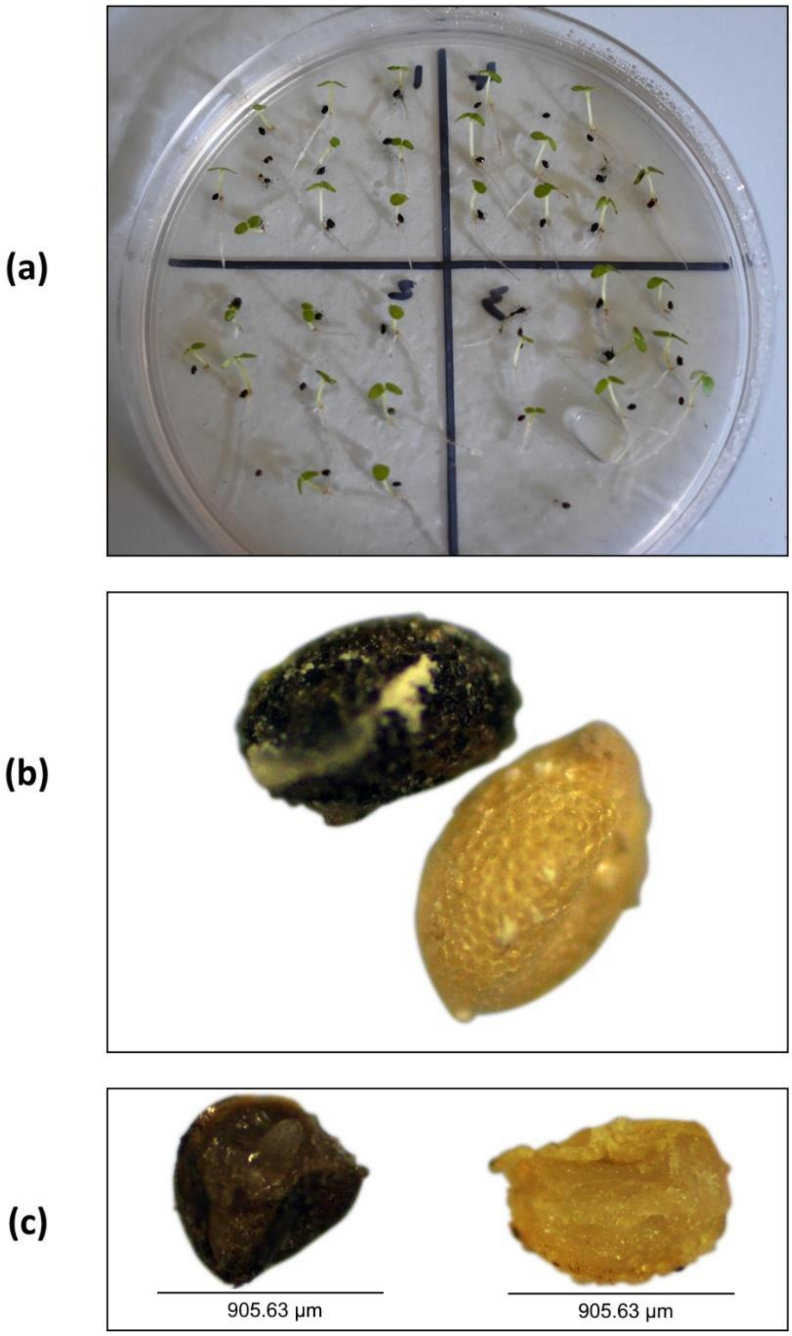
We then conducted a Principal Component Analysis (PCA) to quantify the ecological similarity of the three study sites. Data from each habitat plot were pooled across sites and standardized prior to analysis to account for the variables' different scales. The minimum number of components needed to explain at least 70% of the variance (Supplementary Table 4.1.1) were visually examined using biplots (Figure 4.3d), with convex hulls drawn around all datapoints (habitat plots) belonging to each site. Using the vegan package (Oksanen et al. 2019), site differences were then tested quantitatively with a permutational multivariate analysis of variance using Euclidean distance matrices (M. Anderson 2001). As this indicated significant differences among sites (R^2 = 0.22, P = 0.001), post-hoc pairwise comparisons between sites were performed using a pairwise permutation MANOVA (PERMANOVA) with 1,000 permutations (RVAideMemoire package: Hervé 2020). Because we predicted that the Source

Site would differ significantly from the two Release Sites, we applied a Bonferroni correction to the resulting *P*-values to avoid increasing the likelihood of Type I errors.

Supplementary Table 4.1.1. Results of the Principal Component Analysis (PCA) of variables measured on each habitat plot. The first two components explained a cumulative 75% of variance among plots, while the three remaining components (PC4 and PC5 not presented) explained only 25% of variance. Variables with the strongest loadings on each component are indicated in bold.

	PC1	PC2	PC3
Total species	**−0.47**	**0.44**	−0.13
Understory density	−0.10	**0.65**	**0.49**
Shannon diversity	**−0.51**	0.08	**−0.69**
Canopy density	**−0.60**	−0.14	**0.44**
Canopy height	−0.39	**−0.60**	0.25
Eigenvalue	2.15	1.60	0.69
Proportion of variance explained	0.43	0.32	0.14

A1.4 CHAPTER 6 SUPPLEMENT



Supplementary Figure 6.1. Germination and seed viability tests were performed on seeds collected from a subset of plants in the pollinator exclusion experiment. (a) Seeds plated on an agar petri dish for the germination test, close to the date that germination was assessed (at least four weeks after plating). (b) Undissected viable seed (left) and unviable seed (right). (c) Cross-section of a dissected viable seed (left) and unviable seed (right). Photo credit: Karin van der Walt.

Supplementary Table 6.1. Number of replicates tested by site and pollination condition for (a) the seed viability and germination probability of all seeds tests and (b) the germination of viable seeds test. Values in parentheses indicate the number of unique plants from which the replicates were derived. In some cases, values are lower for (b) than (a) because germination of viable seeds could not be assessed for replicates containing no viable seeds.

		Auckland		**Wellington**	
		Hihi+	**Hihi−**	**Hihi+**	**Hihi−**
(a)	**Insect**	53 (8)	49 (7)	78 (10)	41 (6)
	Insect+Bird	58 (9)	80 (11)	68 (11)	60 (8)
(b)	**Insect**	49 (7)	49 (7)	75 (10)	41 (6)
	Insect+Bird	58 (9)	80 (11)	68 (9)	60 (8)

A1.5 PERMITS

All observational work on Tiritiri Matangi Island was carried out under:

- Wildlife Act Authority Authorization Number 44300-FAU issued by the Department of Conservation (New Zealand)

All pollination studies were carried out under:

- Tiritiri Matangi: Plants, Soil, Rocks, Historic Material Authorization Number 61071-RES issued by the Department of Conservation (New Zealand)
- Tāwharanui Regional Park: Auckland Council Permit to Undertake Research NS384
- Zealandia Ecosanctuary: Admission to the Valley to Undertake Research
- Belmont Regional Park: Greater Wellington Regional Council Low Impact Collecting Permit