

**Female Scarcity and Natal Dispersal Differences Between Sexes Among
Bellbirds (*Anthornis melanura*)**

By

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Abstract

Sex ratio imbalances in wild bird populations have been a challenge for wildlife managers for decades. Differences between sexes during natal dispersal has long been thought to promote sex ratio imbalances. Natal dispersal distances may differ between sexes because of competition for food and space, or intrasexual competition and aggression. I investigated natal dispersal and intrasexual competition as mechanisms for a sex ratio imbalance in a small, translocated population of a New Zealand honeyeater, the bellbird (*Anthornis melanura*) in the Karori Wildlife Sanctuary- Zealandia, Wellington, New Zealand. I analysed long term records of population size and structure to document annual variation in sex ratios since the reintroduction of bellbirds to Zealandia. Radio telemetry was used to track the 2008/2009 cohort of bellbirds for five months after fledging to observe movements and distances travelled from their hatching location. Observations at a supplemental food source that was used by both adults and fledglings, were used to study intrasexual competition and aggression. Dispersal distances did not differ between the sexes for any of the measurement types used. Males did however significantly dominate the use of a supplemental food source and were significantly more aggressive around this food source, which is most likely responsible for the lower feeding rate among females. Therefore, I conclude that the sex ratio imbalance in the bellbird population in Zealandia may not result from a difference in natal dispersal, but from males dominating a supplemental food source, raising their population and fitness over that of females.

Chapter One

General Introduction

After New Zealand became isolated from other landmasses nearly 85 million years ago (Ericson *et al.* 2002), the flora and fauna evolved into some of the planet's most unusual species. New Zealand became dominated by birds, filling niches occupied by mammals in other parts of the world. Modern New Zealand harbors 1,865 endemic plants and 136 vertebrate species, 68 of which are birds (Myers *et al.* 2000). Because of this high number of endemic species, New Zealand is now considered one of the planet's biodiversity hot spots (Myers *et al.* 2000) and the focus of many conservation efforts. In the absence of mammalian predators, New Zealand birds lack evolutionary adaptations to avoid predation by mammals, and many have lost the ability to fly, including the kakapo, kiwi, and the extinct moa. Humans and rats, the first mammalian predators, arrived between 700 and 1000 years ago (Diamond *et al.* 1989; Duncan *et al.* 2002; Duncan & Blackburn 2004). People hunted many of the larger birds for food, often led to their extinction (Duncan *et al.* 2002). With the arrival of Europeans, other species greatly decreased in numbers due to habitat destruction and the introduction of additional mammalian predators, such as cats, possums and mustelids.

Bellbirds (*Anthornis melanura*) were extirpated from Wellington in the past century. However, have been reintroduced into the Karori Wildlife Sanctuary- Zealandia in Wellington, which is an area of native habitat protected by a predator proof fence.

Bellbird numbers in Zealandia have fluctuated since their first translocation to Zealandia, in 2001. Female numbers are thought to have consistently decreased, giving rise to a male biased sex ratio in the population. A male biased population can hinder conservation efforts for many reasons. For example, male biased sex ratios in the common lizard (*Lacerta vivipara*) has led to reduced female fecundity and increased female mortality (Le Galliard *et al.* 2005). Males can have a large effect on a population through harassment of females by heightened aggression, out competing females for resources, even increasing female mortality, leading to an increasingly male biased population (Rankin & Kokko 2007). Although aggression by males can cause biased sex ratios, it may not be the only cause. Mechanisms causing skewed sex ratios can include resource availability (Martínez-Padilla & Fargallo 2007), parental condition (Daan *et al.* 1996) or differences in dispersal (Whitfield *et al.* 2009).

A sex ratio bias during natal dispersal could occur adaptively, to avoid inbreeding, competition for resources, or competition for mates (Lambin *et al.* 2001; Hanski & Selonen 2009). In a large, undisturbed habitat this is unlikely to have any detrimental effects on a population. However, habitat suitable to bellbirds on the mainland of New Zealand is now highly fragmented, which can negatively affect small avian populations, like the Zealandia bellbirds. Fragmentation can increase isolation between populations, increase contact with predators, and increase the risk of not finding suitable habitat or mates (Dale 2001). Isolation in turn often leads to smaller populations and can increase the risk of extinction through decreased genetic diversity (Westemeier *et al.* 1998; Purvis *et al.* 2000; Dale 2001). Loss of genetic diversity can also decrease individual

fitness due to Allee effects, which can also increase the risk of extinction in small populations (Courchamp *et al.* 1999).

The apparent male biased sex ratio in the Zealandia population of bellbirds may be a consequence of differential natal dispersal between males and females. Even though natal dispersal is an important part of an animal's ecology it has been understudied (White & Faaborg 2008), especially in birds. Natal dispersal, the dispersal from place of birth to breeding grounds, facilitates range expansion, competition avoidance, location of food sources and finding mates (Liu & Zhang 2008). However, natal dispersal may also skew population sex ratios and increase the risk of predation and failure to find suitable habitat (Greenwood 1980; Greenwood & Harvey 1982). The body of knowledge concerning dispersal of non-migratory birds is scarce and little is known about the mechanisms behind sex-biased dispersal strategies (Wolff & Plissner 1998). Natal dispersal in birds is often female biased (Greenwood 1980; Clarke *et al.* 1997). For example in the stripe-backed wren (*Campylorhynchus nuchalis*) population in Venezuela females were found to disperse further than males (Yáber & Rabenold 2002).

Differences in dispersal distances between sexes can be exacerbated by sexual conflict. Conflict between the sexes is a common occurrence in nature, but its general ecological importance requires further study (Tregenza *et al.* 2006). Sexual conflict is often manifested in aggressive, territorial behaviour in males. Aggressive behaviour as a result of territoriality is defined as a repeated act of aggression in and around the same

area, which results in a second individual acting submissively. The subordinate individual can be member of the same or different species (Pyke *et al.* 1996). Aggression and territoriality are found in many avian populations and have been well documented (Wolf 1978), especially in honeyeaters (Meliphagidae), to which the bellbird belongs. Previous work indicates that bellbirds can be aggressive towards conspecifics, and other species, and defend their territory aggressively (Craig *et al.* 1981; Craig 1984; Craig 1985; Craig & Douglas 1984a; Sagar 1985; Bartle & Sagar 1987; Rasch & Craig 1988; Higgings *et al.* 2006). This is consistent with other honeyeater species, such as the Australian red wattlebird (*Anthochaera carunculata*), regent honeyeater (*Xanthomyza phrygia*), and the tui (*Prothemadera novaeseelandiae*), observed acting highly territorial and aggressive around food sources (Wolf 1978; Ford 1981; Armstrong 1992a; McFarland 1996; Pyke *et al.* 1996; Oliver 1998; Male & Roberts 2001). Heightened levels of testosterone in response to social or environmental stimuli, such as length of day, pheromones, or the need to defend a territory or mate, is thought to be the main cause of aggression (Wingfield *et al.* 1987). Wingfield *et al.* (1987) concluded that different mating systems may affect the longevity of heightened testosterone and aggressiveness, with more promiscuous species defending mates and territories for longer than monogamous species. Bellbirds are thought to have a monogamous mating system (Higgings *et at.* 2006) but they have also been shown to exhibit polygynandry and even polygyny and polyandry (Cope 2007). Aggression associated with the acquisition and maintenance of territories and food sources, as defined by Pyke *et al.* (1996), applies to bellbirds and could promote male biased sex ratios.

Since aggression frequently occurs around food sources (McFarland 1996) it is likely that competitively subordinate individuals will be excluded from, or have limited access to defended food resources. This exclusion may lead to an increase in mortality or dispersal distances. Nectar is an important food source to honeyeaters (Ford & Paton 1976). Given these circumstances it would seem that if food were more available, dispersal would be reduced (Arcese 1989). Zealandia installed artificial nectar feeders within the predator-proof-fence because honeyeaters remain in an area by providing a constant food supply (van Riper 1984). The feeders are often near or at the center of bellbird territories, and are actively defended by the dominant male in that territory. Male bellbirds have been observed being aggressive towards females and excluding them from these feeders (Zealandia, unpublished data). It is possible that this male behaviour leads to increased female dispersal and is responsible for the skewed sex ratio and female scarcity. This study will use radio telemetry and detailed feeder observations to investigate the mechanisms behind natal dispersal and female scarcity.

Chapter Two
Female Scarcity and Post Fledging Dispersal
Differences Between Sexes in Bellbirds (*Anthornis melanura*)

Introduction

Many New Zealand birds have gone extinct or declined in number since the arrival of man due to hunting, introduced mammalian predators, and the loss of habitat (Stead 1932). However, the populations of many rare New Zealand birds have recently recovered with predator control, habitat restoration and preservation (Miskelly *et al.* 2005). Conservation efforts in the Wellington region have proved to be successful for the tui (*Prothemadera novaeseelandiae*), while abundant today, was rare before management efforts. Bellbirds (*Anthornis melanura*) were extirpated in Wellington prior to their reintroduction to The Karori Wildlife Sanctuary- Zealandia. Wildlife managers and conservationists struggled to maintain bellbird numbers in Zealandia and an increased understanding of their behaviour and ecology will undoubtedly improve conservation efforts.

Zealandia is an “island” of restored habitat surrounded by urban, suburban, and rural areas in the Wellington region, which is surrounded by a predator-proof-fence. This excludes a wide variety of mammalian predators, including cats, rats, and possums. Natural immigration of bellbirds into Zealandia is uncommon and any long distance dispersers are essentially lost to the breeding population (Dale 2001). Therefore, for Zealandia to be effective in conserving native New Zealand birds, endangered birds need to be translocated into the reserve to initiate new populations.

Reintroductions and translocations of an extirpated species to its previous range can be a useful tool for wildlife managers (Deredec & Courchamp 2007). While reintroductions can be successful they can also sometimes fail for a number of reasons. Several variables could determine whether or not the reintroduction is successful or not, such as number of individuals being translocated, the state of the habitat they are being moved into, the diet of the species, and the species resilience to changes around them during being moved (Wolf *et al.* 1996; Deredec & Courchamp 2007). Wolf *et al.* (1996) found between 67-63% of avian reintroductions were successful. A successful reintroduction is one that a self sustaining breeding populations is established (Wolf *et al.* 1996). There have been many successful reintroductions of birds to previous ranges, such as in a the Aldabra rail (Wanless *et al.* 2002). This success was attributed to making sure the birds were well acclimatised to their new surroundings and in very good physical condition prior to release, ensuring plenty of energy reserves (Wanless *et al.* 2002). There have also been many successful reintroductions of New Zealand species, such as, reintroduction of saddlebacks (*Philesturnus carunculatus*) and robins (*Petroica australis*) to islands (Taylor *et al.* 2005).

Sex ratio imbalances can threaten small populations and present a challenge for conservation managers. In avian populations these imbalances can arise from differential survival and/or differential sex allocation at birth. Sex ratio imbalances can develop at either the primary, secondary, or tertiary life stages (Mayr 1939). Primary sex

allocation arise before females lay eggs (Sheldon 1998; Pike & Petrie 2003). Secondary sex allocation occurs at the time of hatching (Mayr 1939). Tertiary sex ratio refers to the sub-adult or adult life history stages, where a sex ratio imbalance may develop from differences in dispersal distances or from intersexual competition (Waser 1985; Liu & Zhang 2008).

Females in good condition in a high quality habitat, or those that have access to a high quality food resources, can produce more males at birth (Bradbury & Blakey 1998; Stauss *et al.* 2005; Dowling & Mulder 2006). Under benign environmental conditions, male offspring, often have a greater lifetime fecundity than females (Hamilton 1967; Trivers & Willard 1973). Therefore, male biases sex ratios can arise at primary and secondary life history stages.

Sex biases in natal dispersal are known to occur in birds and mammals (Greenwood 1980; Arlt & Pärt 2008), and may result from inbreeding avoidance, competition for resources, or competition for mates (Hanski & Selonen 2009). Dispersal, can be defined in a variety of different ways. For example, Liu & Zhang (2008) define dispersal as the movement away from others in a population, at any stage of ontogeny. Alternatively, dispersal can also refer specifically to movement from birthplace to first breeding site (Greenwood 1980; Runciman *et al.* 1995). This project focuses on the latter definition of dispersal in an effort to determine whether dispersal away from the natal area results in a tertiary sex ratio imbalance.

In some species of birds where males actively defend their mates, younger males tend to be the more likely to disperse (Greenwood 1980). Yet dispersal is not well understood (Donald 2007) and it is not clear whether male-biased dispersal is more common than female-biased dispersal. Dispersal can help an animal find new food sources, new mates, and avoid competition (Liu & Zhang 2008). However, dispersing from place of birth can increase the risk of mortality due to increase exposure to predators, or a lack of suitable habitat or food. In mammals, males have a propensity to disperse further (Liberg & VonSchantz 1985). In birds females are more likely to disperse further (Greenwood 1980; Clarke *et al.* 1997). Mating systems can also influence which sex disperses further, for example in monogamous systems females tend to disperse further, however in polygynous systems there should be no differences between sexes in dispersal distances (Liberg & VonSchantz 1985). In most mating systems, the tendency for juvenile females, which are often competitively subordinate, to disperse further increases (Greenwood 1980; Liberg & VonSchantz 1985; Clarke *et al.* 1997; Hanski & Selonen 2009). In some mating systems males have more incentive to remain near their natal areas to defend territories and resources (Arlt & Pärt 2008), while females must search for areas away from fathers or brothers to avoid inbreeding (Greenwood 1980; Wolff & Plissner 1998; Sutherland *et al.* 2000). However, Liberg & VonSchantz (1985) suggest it may benefit both sexes by leaving the natal area. For almost all mating systems there are conflicting examples of both sexes dispersing further, for both birds and mammals. Questions such as how far and where the species disperse often remain

unanswered; but knowing the new areas dispersed to and distances travelled can have long lasting benefits on population management.

An understanding of sexually dimorphic dispersal patterns may be crucial for effective species management. Female-biased natal dispersal can detrimentally affect a small, spatially isolated population further impacting its long term viability and increasing its risk of extinction (Dale 2001). Management of such populations would benefit from a detailed understanding of movement patterns during this vulnerable life stage. Managers must also be cognizant of the interplay between dispersal differences and other factors driving the probability of extinction, such as isolation, high predator abundances, and lack of resources or space.

This thesis will focus on the tertiary life stage where sex ratio imbalances can develop during natal or fledgling dispersal. Differences in fledgling or natal dispersal between sexes has been identified as a possible mechanism for sex ratio imbalances in other bird species (Greenwood 1980; Donald 2007).

Study Species

Bellbirds are a medium-sized non-migratory passerine, that is endemic to New Zealand. They are in the family Meliphagidae which comprise the honeyeaters. The only other bird in New Zealand undisputedly in that family is the tui. However, the hihi is often

considered part of this family because of similar behaviour and feeding habits (Ewen *et al.* 2006; Driskell *et al.* 2007). Bellbirds are sexually dimorphic. Females are generally smaller than males by about 13% (Craig *et al.* 1982), males weigh 32.5g on average with a body length of ~19-20cm; females weight about 25.2g on average with a body length of ~17-18cm (Higgings *et al.* 2006). They can live up to eight years and are known to continue to use and defend the same territory year after year (Heather & Robertson 1996). The bellbird diet consists of mainly nectar and they are important pollinators for many plant species (Murphy & Kelly 2001), but they will supplement their diet with insects and berries (Stead 1932; Craig *et al.* 1981; Rasch & Craig 1988). The males are highly territorial (Pyke *et al.* 1996), aggressive and will actively defend food sources (Craig & Douglas 1984a). Male bellbirds are only subordinate to the tui, but dominate over female bellbirds and hihi (Craig 1984; Craig 1985).

In 2001 and 2003 a total of 92 bellbirds were translocated to Zealandia for reintroduction, 47 males and 45 females (Zealandia unpublished data). However, population numbers have fluctuated since the first translocation for unknown reasons. Knowing that by increasing nectar supplies honeyeaters will be more likely to remain in an area (van Riper 1984) managers at Zealandia installed sixteen feeders supplying either sugar water or wombaroo, which is a high protein supplement for birds, and these feeders are extensively monitored by Zealandia staff and volunteers. The food source is surrounded by a cage which is designed for bellbirds and hihi (*Notiomystis cincta*) to enter but to exclude the larger tui, which are known to be very aggressive towards the

smaller bellbird and hihi. The sixteen feeders are located throughout the sanctuary, mostly close to the entrance and along trails, to allow for public viewing (Figure 1).

The bellbird population in Zealandia has had a suspected biased sex ratio, which is skewed towards males. A sex ratio imbalance can have severe negative impacts on conservation efforts. The sex ratio imbalance has not been confirmed but has been highly suspected based on detailed field observations. The objective of this study is to confirm a sex ratio imbalance then explore the underlying mechanisms responsible for the sex ratio imbalance. The post fledgling dispersal difference between male and female bellbirds is thought to be female-biased resulting in a male-biased population. This imbalance is suspected to have occurred each year since the first translocation in 2001 and seems to persist despite repeated translocations of females. Evidence from banding of nestlings and fledglings may provide some indication a skewed sex ratio at hatching which can be the leading cause of a skewed adult sex ratio. It remains unclear as to whether sex-biased natal dispersal patterns are the sole underlying mechanism accounting for the imbalanced sex ratios or if other factors also play a role. If juvenile females are dispersing farther it is unclear why this is occurring, where they go, what they are feeding on, and their ultimate fate. Birds outside Zealandia may be predated on and, even if they survive, they are ultimately removed from the breeding population within Zealandia since they do not appear to return. Predation risk and competition for suitable habitat, mates, and resources make dispersal dangerous for individuals leaving their natal ranges. Bellbirds in other regions of New Zealand have been shown to be prolific and active dispersers. In Craig & Douglas (1984a) and the more recent account

in Brunton *et al.* (2008) found bellbirds dispersing about 25km in a few months. It is likely the same situation is occurring in and around Zealandia, however unchecked predator populations and lack of reliable food sources remain a threat.

Objectives

The goal of this thesis is to document the sex ratio imbalance in the Zealandia population of bellbirds and identify the processes responsible for this imbalance. Even though females are recruiting into the population through hatching and repeated translocations, their adult numbers still appear to be declining. This paper will document potential sex ratio imbalances and how they have developed through time. It will also test two hypotheses that can potentially explain the sex ratio imbalance:

1. The sex ratio imbalance results from greater natal dispersal distances in females.
2. Intersexual competition with socially dominant males limits female access to an artificial food source, reducing female survivorship.

Methods

Study Area

All observations were conducted within Zealandia and surrounding neighbourhoods in Wellington (41° 18'S, 174° 44'E), (Figure 2). The entire 252 ha area of the sanctuary is surrounded by an 8.6km long, 6m high predator-proof fence and the sanctuary has been predator free since 2000 (www.sanctuary.org 2008). Both the fence and the predator free status on the mainland are world first accomplishments, and have facilitated the reintroduction of many New Zealand species to the mainland for conservation, education, and human enjoyment. Several native bird species have been translocated to Zealandia such as: whiteheads (*Mohoua albicilla*), hihi, tui, North Island robin (*Petroica australis longipes*), North Island saddleback (*Philesturnus carunculatus rufusater*), kaka (*Nestor meridionalis septentrionalis*), or naturally colonized into Zealandia including: fantails (*Rhipidura fuliginosa*), grey warbler (*Gerygone igata*), silver eye (*Zosterops lateralis*), kererū (*Hemiphaga novaeseelandiae*), and morepork (*Ninox novaeseelandiae*).

The Zealandia forest is composed primarily of hardwoods and many native tree species including: kowhai (*Sophora microphylla*), rangiora (*Brachyglottis repanda*), northern rata (*Metrosideros robusta*), kohekohe (*Dysoxylum spectabile*), tutu (*Coriaria arborea*), pigeonwood (*Hedycarya arborea*), rewarewa (*Knightia excelsa*), ngaio (*Myoporum laetum*), five finger (*Pseudopanax arboreus*), fuchsia (*Fuchsia excorticata*), hangehange

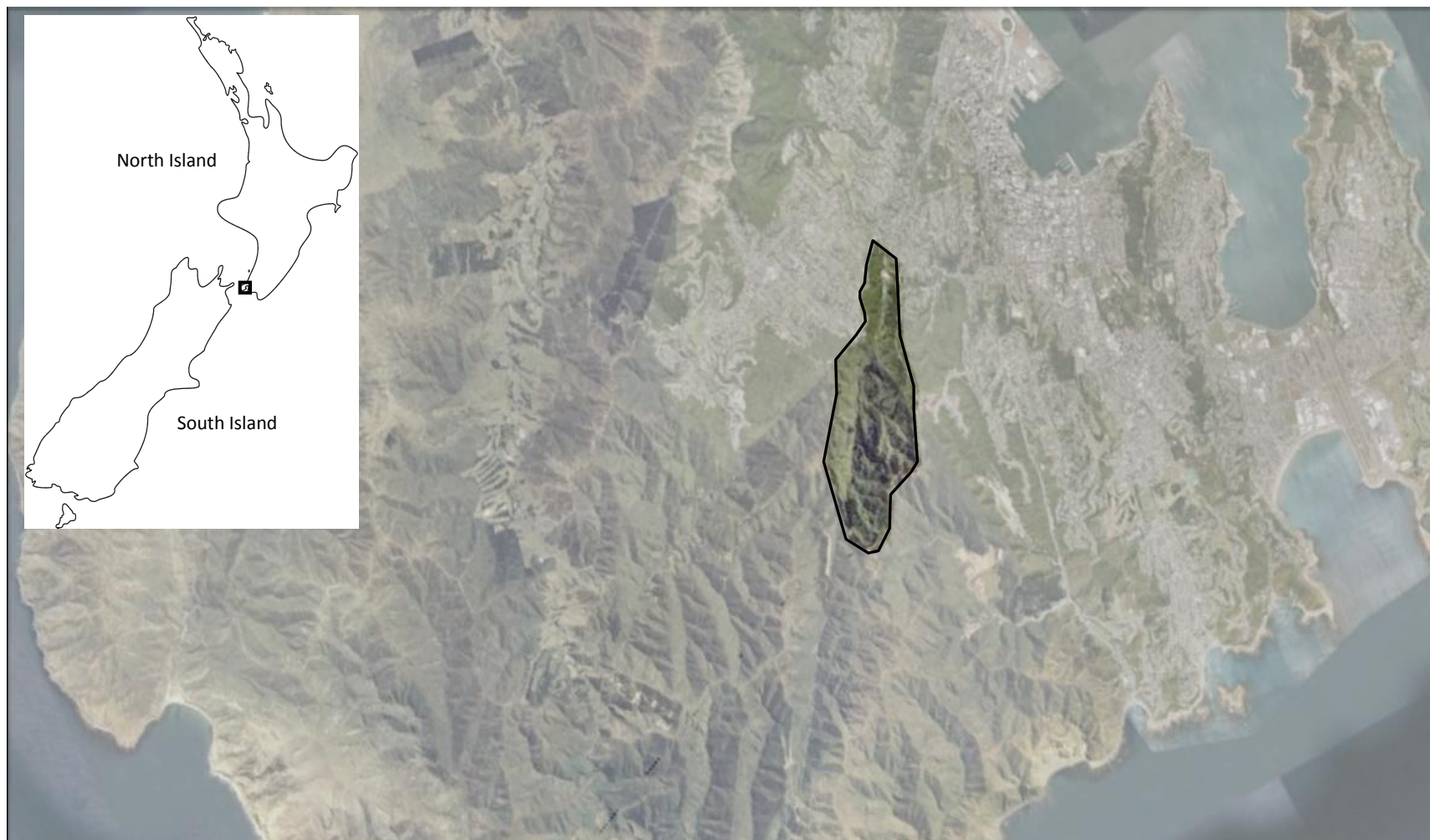


Figure 1 Map of study area, Zealandia (highlighted) and surrounding areas with map of New Zealand (inset) as reference. Map taken from Google Earth accessed on 14 January 2010.

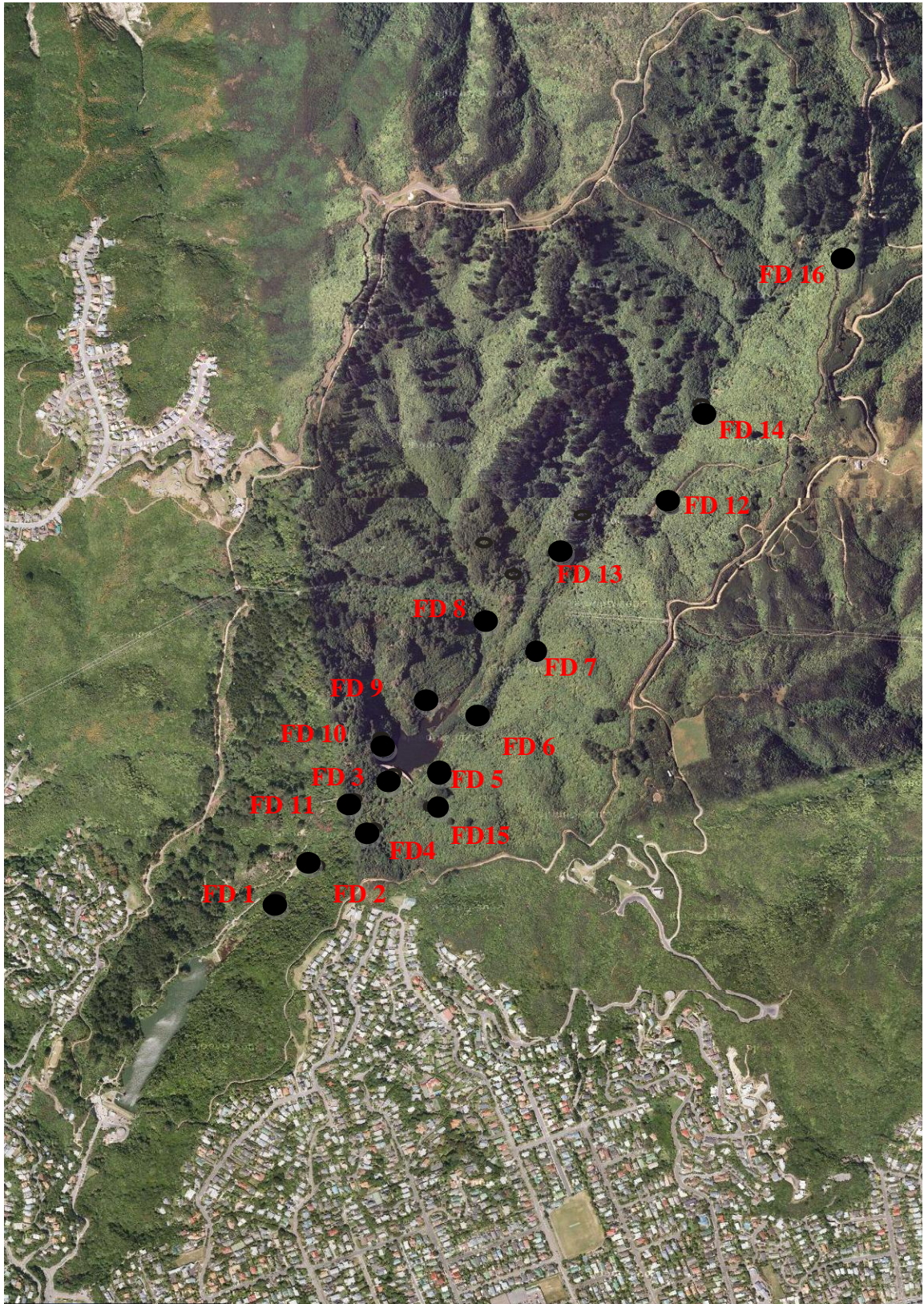


Figure 2 Areal image of Zealandia with feeder locations and feeder identification numbers. FD- feeder, ● - feeder location on ground.

(*Geniostoma rupestre*), kawakawa (*Macropiper excelsum*), lemonwood (*Pittosporum eugenioides*), bush lawyer (*Rubus cissoides*), supplejack (*Ripogonum scandens*), and many species of ferns. Average canopy height is about 10-15m. There are also two small lakes separated by a dam which now harbour four species of shags and various native and non-native ducks. Early European settlers throughout the 1800s extensively used the valley surrounding the dam and water catchment for grazing, farming, logging, and gold mining. Therefore, the forest is still under going succession.

Population Size Estimates

The entire bellbird population in Zealandia is monitored continuously throughout the year. Monitoring began immediately following translocation and has continued every year since. A team of experienced ornithologists search the entirety of Zealandia for signs of bellbird breeding activity. At the start of the breeding season, in early September, the population was censused thoroughly by searching Zealandia for breeding pairs and their nests. Throughout the year the feeders within Zealandia are monitored, by staff, volunteers, and myself during this study, all birds using feeders were individually identified from uniquely coloured leg bands. All bellbirds hatched in Zealandia are colour banded in the nest or soon after fledging. Each year's, or nesting season's, cohort received a unique combination of three colour bands, along with one metal band for further identification. All birds that were subsequently translocated to Zealandia are also banded in the same manner, therefore the whole population of bellbirds within Zealandia can be identified individually. This allows for easy observation of new recruits and existing members

of the population. Non-feeder sightings of birds by volunteers or staff were also noted. All observations are recorded by hand then transferred to a database for analysis and historical reference. Data from these feeder observations, mainly between January 2009 and June 2009, and nesting observations since first translocation, were used to quantify temporal changes in population size for this study.

Radio-tracking

Radio telemetry and detailed observations of non-radio tagged birds were used to determine natal dispersal distance of male and female bellbirds. I was able to track movements of bellbirds for five months post fledging. Time constraints placed on this project from a limited number of transmitters and the limited battery life of those transmitters did not allow for observing the 2008/09 hatched birds into their subsequent breeding stage. Tracking sessions ran from January 22 to June 17, 2009 in and around Zealandia (Figure 2). The study period encompassed hatching, fledging, independent foraging, and dispersal. Twelve individuals (nine females and three males) had transmitters attached between January 23 and April 28, 2009 (Table 1). Approximate locations of these birds were attempted to be found every other day. In addition to birds with transmitters, movements and locations of non-transmitted juvenile bellbirds were noted by myself and a team of staff and volunteers at Zealandia on a daily basis. To supplement the data for each measurement and analysis, movements of five additional non radio-tagged juvenile males were used in analysis in addition to the three males with radio transmitters. At least seven separate sightings of non-radio tagged birds over the five months were needed to be

confident of home range and movements. More specific information on birds with radio transmitters is in Table 1.

Table 1 Identification, sex, and transmitter histories of the 12 birds tracked at Zealandia during the 2009 study period, table adapted from Runciman *et al.* (1995).

I.D.	Sex	Date banded soon after hatched	Date of transmitter attachment	No. of days monitored	Expected transmitter life (days)	Furthest distance moved (Km)	Actual life of transmitter
		all 2009					
FPY-PGM	F	5 Jan. '09	23 Jan.	25	57	0.66	57
PGM-PUPG	F	4 Feb. '09 29 Dec.	17 Feb.	19	60	0.66	51
GK-PGM	F	'08	18 Feb.	20	60	1.14	51
PGM-PUB	F	3 Feb. '09 29 Dec.	3 Mar.	15	60	3.03	16
GPG-PGM	F	'08	9 Mar.	19	60	3.01	54
WPU-PGM	F	NA	17 Mar.	17	60	2.12	44
PGM-FPPU	F	2 Jan. '09	19 Mar.	12	60	0.83	Ukn, lost track of soon after tx attached Bird died after 35 days of carrying tx Tx lasted about 31 days, fell off bird after 44 days
PGM-FPK	F	20 Oct. '08	19 Mar.	11	60	3.45	
PGM-PBW	F	26 Jan. '09	20 Mar.	19	60	2.15	
WFP-PGM	M	19 Oct. '08	26 Feb.	23	60	0.74	34
PGM-PUPB	M	3 Feb. '09	2 Mar.	21	60	1.02	49
PGM-FPG	M	4 Jan. '09	2 Mar.	23	60	3.37	57

Tx- Transmitter

Each bird intended to be fitted with a transmitter was captured in a small cage baited with sugar water by Zealandia staff. Birds were fitted with radio transmitters

weighing about 0.82g (Holohil Systems Ltd., Carp, Ontario, Canada). Transmitter weight never exceeded 3% of the bird's body weight. The transmitters were attached using the "harness" method after a trial run of this method, preformed by Zealandia staff, on non-breeding males did not seem to negatively affect the birds. The trial birds did not lose a significant amount of weight nor were their movements or social interactions affected. The transmitter was attached to two pieces of string that fit around the upper parts of the bird's legs. This method allowed the transmitter to rest on the lower back of the bird (Raim 1978) without glue or other attachments and was similar to Rappole & Tipton's (1991) (Figure 2). The string was designed to degrade and fall off if the bird was not caught again. All work was conducted under approval of both scientific staff at Zealandia and Victoria University of Wellington Animal Ethics Committee (2008R9).

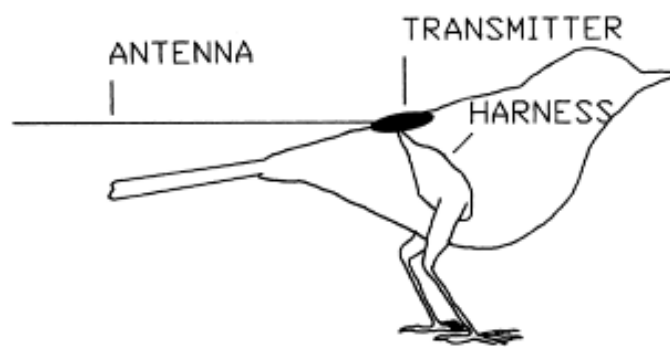


Figure 2 Showing radio transmitter attachment method adapted for this study from Rappole & Tipton (1991).

The transmitters emitted frequency signals at 2 Pulses/Minute for an average of 55-75 days. During this time birds were located within or outside the sanctuary, usually getting within at least 5-10m of the bird, if not visual sightings. Each bird's unique

frequency was picked up using a 148-174 MHZ telemetry receiver (Communications Specialist, Inc., Orange, California) and a three element folding yagi antenna (Sirtrack, Wildlife Tracking Solutions, New Zealand). If the bird's signal was not found within Zealandia, then searching by foot in surrounding neighbourhoods or wooded areas was conducted. If this did not lead to any findings, then an extended search by vehicle was done to additional possible sites. As in Anders *et al.* (1998), if a bird's transmitter signal was not detected and the bird was not seen within Zealandia, it was considered to have dispersed outside of Zealandia, lost its transmitter, or its transmitter died, until further evidence was collected, which were practices used in Kennedy & Ward (2003) and Anders *et al.* (1998).

Spot-Mapping

Spot mapping is a simple, popular method for estimating bird densities (Witham & Kimball 1996). I used a modified spot mapping method to document dispersal distances of individual bellbirds in conjunction with the program ImageJ, 1.42 (2009). I estimated the spatial position of each bird located in the field on printed maps, which were then transferred into digital form using ImageJ. I imported maps of Zealandia and surrounding areas obtained from Google Maps into ImageJ, which I then used to quantify dispersal distances. Using the drawing tool in ImageJ the locations where the bird was seen or was known to have been were marked. This was done separately for each individual bird, for known transmitter locations and for feeder locations separately, and then for both observation methods together (see appendix).

Statistical Analysis

Testing for abundance differences between sexes

Generalized linear models (GLM) were used to test for differences between the number of males and females present in Zealandia through time. Bellbird numbers were estimated two different times of the year, at the time of banding immediately after hatching and at the start of each breeding season. One GLM assumed the dependent variable followed the Poisson distribution was used to test for differences between sexes at time of hatching and included all juveniles and adults. The second GLM also assumed the Poisson distribution and tested for differences at the start of the breeding season when the population was composed only of adults. In both models sex was treated as a fixed factor, year was treated as a second fixed factor and their interaction was also assessed. Birds banded in the nest or soon after fledging were counted as juveniles, and birds found at the start of the breeding season were counted as adults.

Dispersal differences

Two types of measurements were made to characterize natal dispersal cumulative total distance moved among all observations for each bird and the total area circumscribed by birds observed three or more times (White & Faaborg 2008). Each variable was calculated for: 1) feeder and non-transmitter observational data only (Zealandia, unpublished data), 2) transmitter data only, 3) both data sets combined. Cumulative total distance moved was determined by measuring the distance from hatch site to first location at which the bird was found, this distance was then added to the distance from the first to the second location found, and so on following

Stapleton & Robertson (2006) and White & Faaborg (2008). Area covered was determined by calculating the area between the first three locations then using two of those locations to form a triangle between that and the third site, this was then repeated for all locations the birds was seen (Figure 3). Distances and area covered were added cumulatively and averages for each observation of all females and all males were quantified. The maximum final distance or area for each final observation was plotted on a scatter plot.

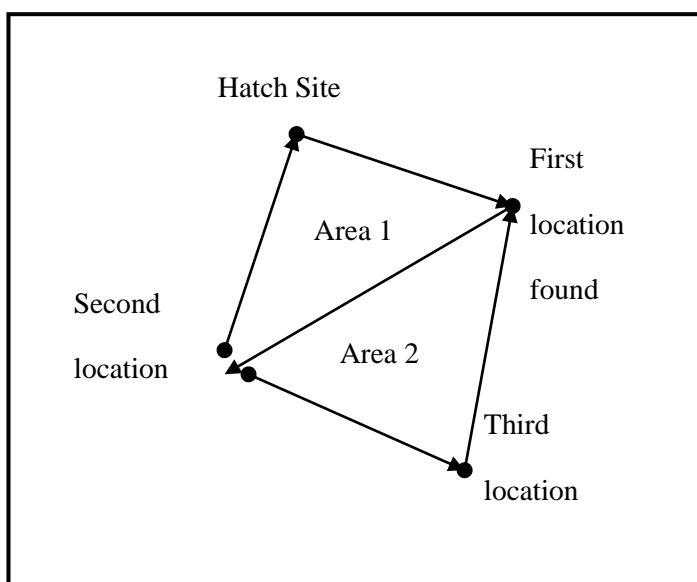


Figure 3 Method used to calculate total area covered by dispersing bellbirds in Zealandia.

Some birds were observed many times and have many measurements associated with them, while others were observed on fewer occasions. Differences in sampling effort may confound estimates of dispersal distances if estimates of dispersal distances increase passively with each observation obtained. Line graphs were created to illustrate the cumulative average for each observation for all females and all males

and to inspect how estimates of dispersal distances must increase with number of observations.

General linear models were used to test for differences in dispersal distances between the sexes. Separate analyses were conducted for each dependant variable. Sex was considered a fixed factor and the number of observations was included as a covariate to correct for sampling effort. All statistical analyses were conducted in SPSS Inc. 16.0.

Feeder use

To test for evidence of intersexual competition for food resources, differences in visitation rates between the sexes to artificial nectar feeders were observed. Behavioural interactions, including chases and aggressive displays, were also recorded. Feeder observations spanned 116 days, between the hours of 9:00 to 16:00, from January to May 2009.

A generalized linear model with Poisson distribution was used to test for differences in feeder use. The dependant variable was the total number of visits to all feeders under observation. Sex and cohort, or the year an individual was hatched, were considered fixed-factors and the independent effects of each factor and their interaction was assessed. Cohort was included in the model to test if age or amount of time the bird was in Zealandia affected feeder visitation rates. Males may have higher visitation rates in Zealandia simply because they survive for longer periods and therefore have longer periods to visit feeders, not necessarily because they defend feeders. Including cohort in the model accounts for this effect and facilitates an unbiased comparison between the sexes.

Aggression

Utilizing feeder observations, the number of times male and female bellbirds behaved aggressively towards one another was quantified. Aggressive displays were quantified specifically as when one bird displaced another at a feeder, either by chasing a bird from its previous location or prohibiting a bird from approaching the feeder (Pyke *et al.* 1996). A binomial test was used to test that male bellbirds displace females from feeders at a higher rate than females displace males. To test aggressive interactions between male and female bellbirds the total number of aggressive displays made by either a male or female bellbird towards either the same or the other sex were quantified. The number of times males displaced females was compared to the number of times females displace males in the test.

Results

Abundance differences between sexes

The first generalized linear model (GLM) to test for differences in the abundance of male and female bellbirds at time of hatching in Zealandia showed there was a significant difference between male and female numbers ($F_{(1,1)} = 13.62$; $P < 0.001$). there was also a significant difference for year ($F_{(1,7)} = 88.45$; $P < 0.001$). There was no significant difference in the relationship between sex and year ($F_{(1,6)} = 8.76$; $P=0.187$) indicating that regardless of sex, bellbird numbers increased through time. Figure 4b shows the abundance of males and females being banded soon after hatching increases at a similar rate through time and no difference in slope

The second GLM with Poisson to test differences in abundance of adult sexes at the beginning of the breeding season showed a significant difference for sex ($F_{(1,1)} = 21.0$; $P < 0.001$). There was also a significant difference in year ($F_{(1,7)} = 30.76$; $P < 0.001$). The interaction between year and sex was not significant ($F_{(1,7)} = 4.07$; $P = 0.772$). Figure 4c shows the number of adult males at the beginning of the breeding season consistently increases at a higher rate than adult female numbers over the years since the first translocation. These changes occur even with repeated translocations of females (Figure 4a).

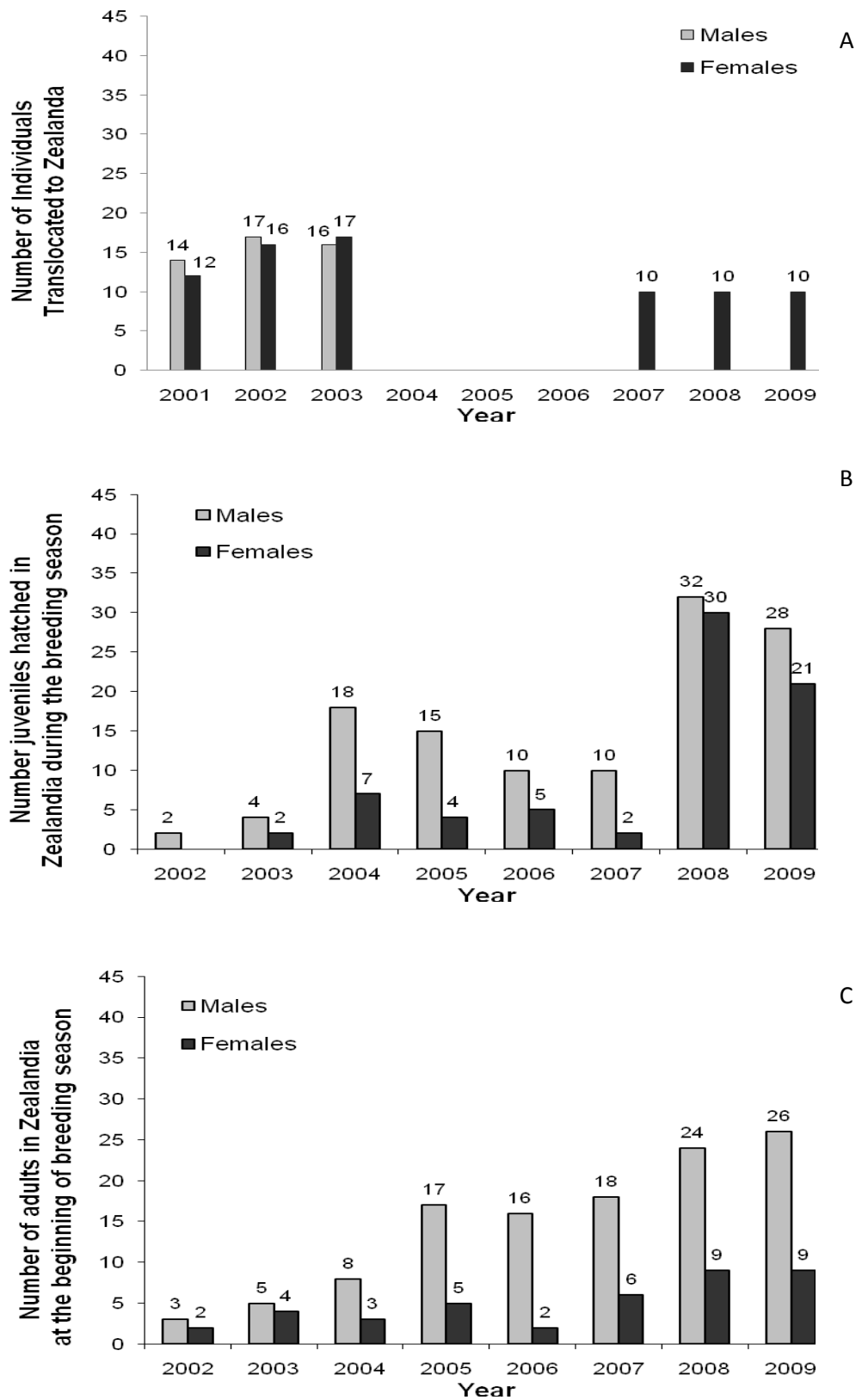


Figure 4 Number of individual bellbirds (*Anthornis melanura*) A) translocated, B) banded at hatching, and C) known to be alive in September, since the first translocation to Zealandia 2001.

Dispersal Differences

Cumulative total distance moved

When testing for differences between sexes in total distance moved, ANCOVA results for the covariate, number of observations, were significant when transmitter and feeder data were combined ($F_{(1,15)} = 18.8, P = 0.001$). Results for the covariate when just transmitter data were used the difference was not significant ($F_{(1,8)} = 2.3, P = 0.182$), and were again significant when just feeder data were used ($F_{(1,12)} = 8.3, P = 0.016$). ANCOVA revealed the relationship between the sex and number of observations was not significant for any measurement method used: transmitter and feeder data- $F_{(1,15)} = 0.92, P = 0.354, P \geq 0.05$; just transmitter data- $F_{(1,8)} = 0.27, P = 0.625$; just feeder data- $F_{(1,12)} = 0.93, P = 0.358$. While females did have a higher final distance than males, results for differences between sexes, the fixed factor, were also not significant for any measurement method used: transmitter and feeder data- $F_{(1,15)} = 0.55, P = 0.472$; just transmitter data- $F_{(1,8)} = 0.39, P = 0.557$; just feeder data- $F_{(1,12)} = 0.9, P = 0.365$. Figure 5, 7, and 9 show averages for each observation of cumulative total distance moved for both sexes for each type of measurement used. Figure 6, 8, and 10 show maximum final distance plotted against final observations for all birds used in analysis and for each type of measurement used.

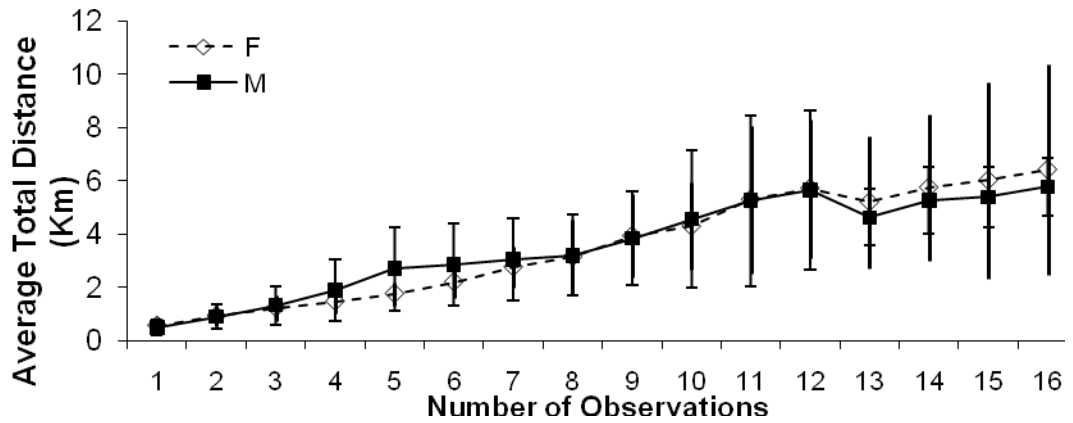


Figure 5 Average cumulative total distance moved for males and females using transmitter and feeder data. Error bars indicate 95% confidence intervals, male bars capped.

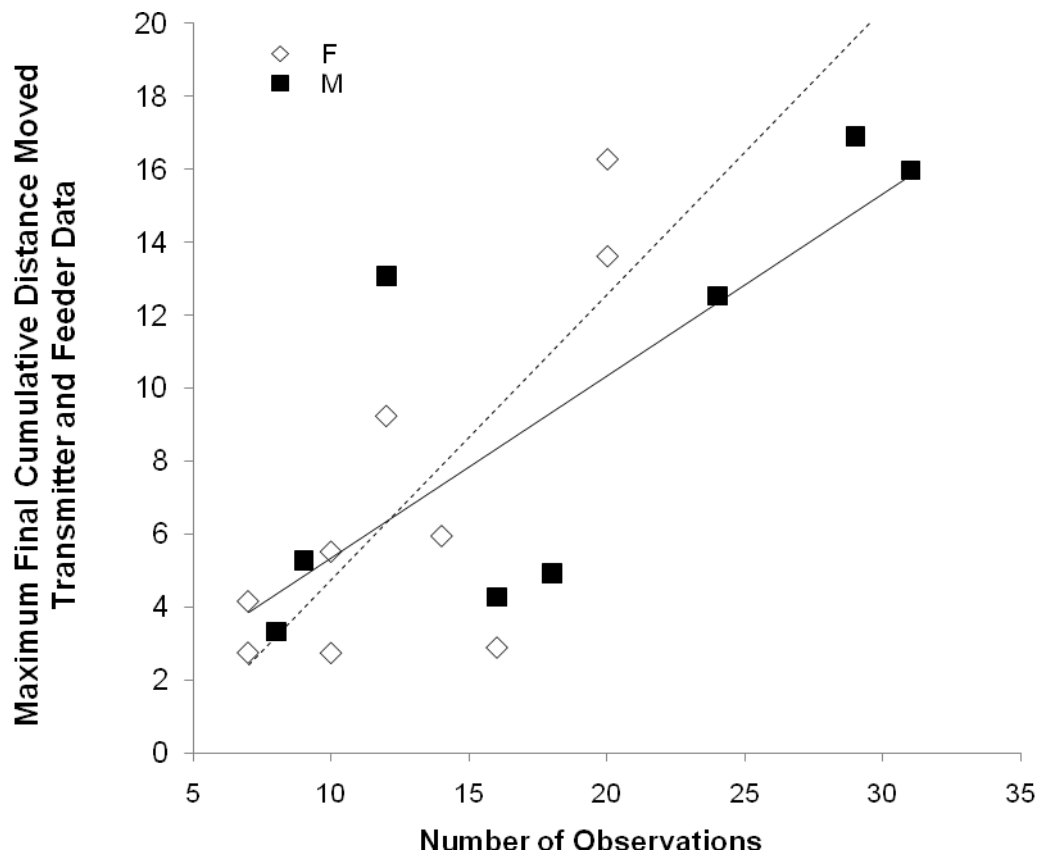


Figure 6 Scatter plot with best fit lines for both sexes. Symbols represent maximum final cumulative total distance for each individual bird used in analysis.

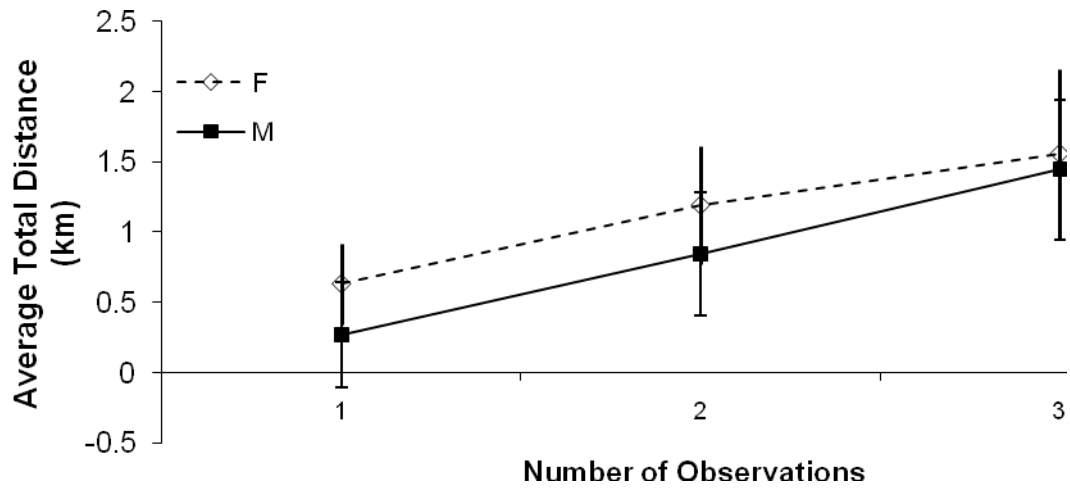


Figure 7 Average cumulative total distance moved for males and females using just transmitter data. Error bars indicate 95% confidence intervals, male bars capped.

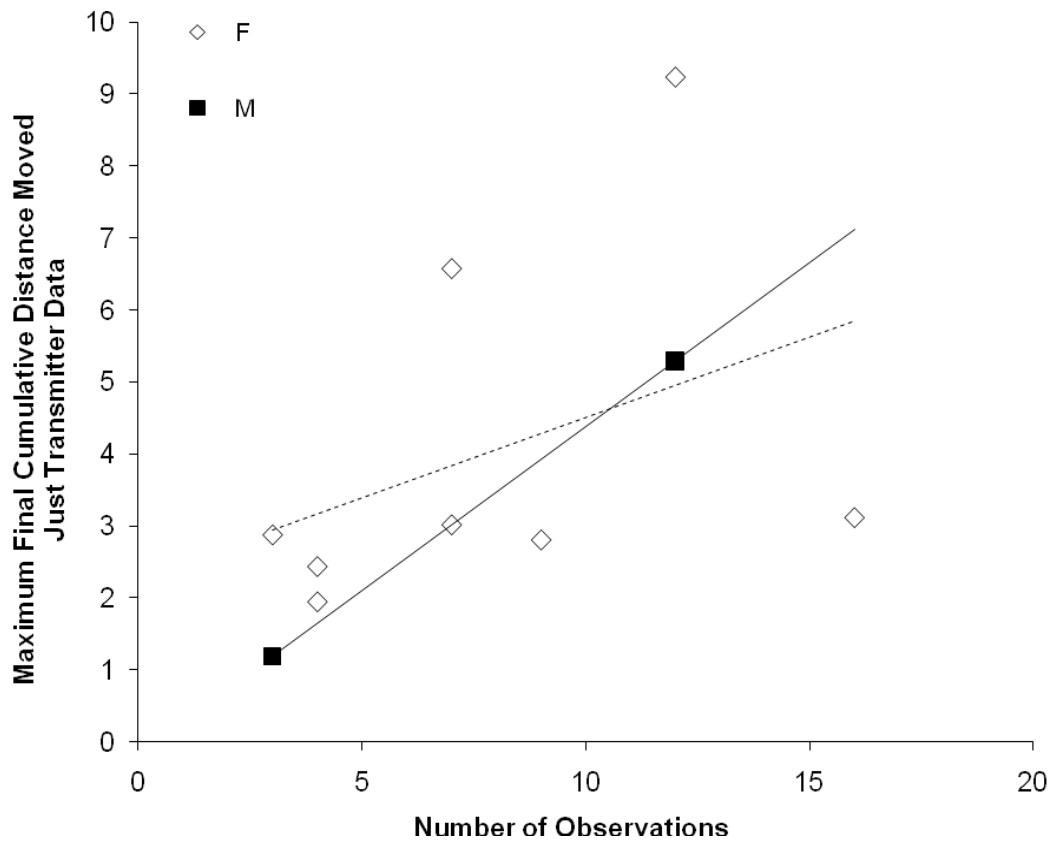


Figure 8 Scatter plot with best fit lines for both sexes. Symbols represent maximum final cumulative total distance for each individual bird used in analysis.

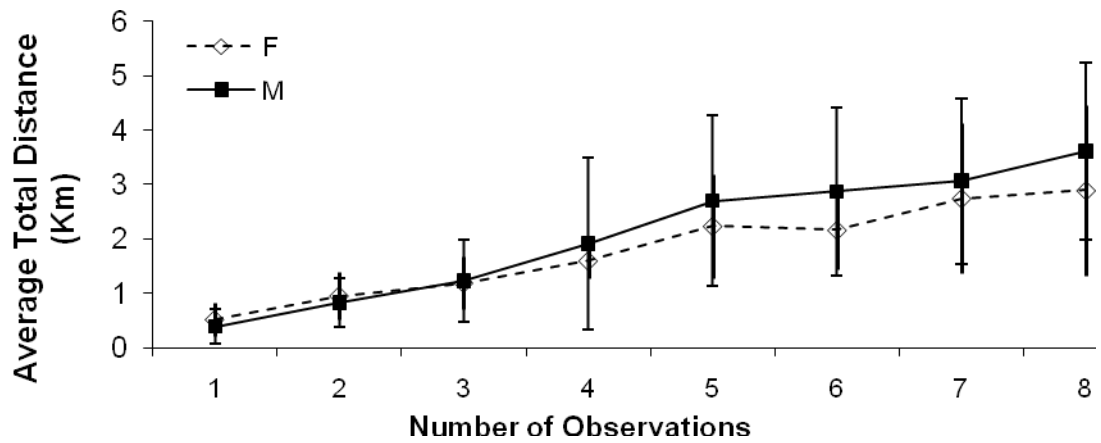


Figure 9 Average cumulative total distance moved for males and females using just feeder data. Error bars indicate 95% confidence intervals, male bars capped.

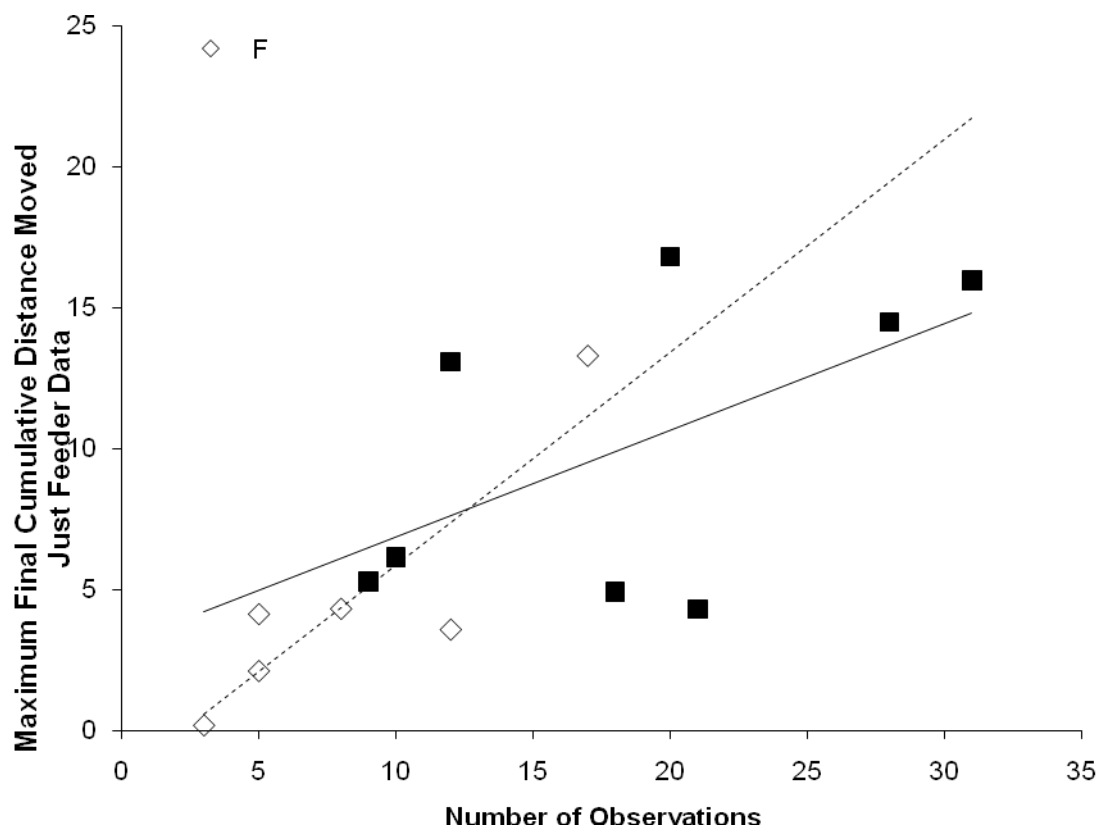


Figure 10 Scatter plot with best fit lines for both sexes. Symbols represent maximum final cumulative total distance for each individual bird used in analysis.

Cumulative total area

When testing for differences in area covered between sexes ANCOVA results for the covariate, number of observations, were significant when transmitter and feeder data were combined and when just feeder data were used ($F_{(1,15)} = 5.6, P = 0.034$; $F_{(1,13)} = 9.6, P = 0.010$). When just transmitter data were used the results for the covariate were not significant ($F_{(1,9)} = 0.08, P = 0.784$). ANCOVA revealed the relationship between the sex and number of observations was not significant for any measurement method used: transmitter and feeder data- $F_{(1,15)} = 1.9, P = 0.193$; just transmitter data- $F_{(1,9)} = 0.134, P = 0.725$; just feeder data- $F_{(1,13)} = 4.1, P = 0.069$. While females did have a higher final cumulative area covered than males, results for differences between sexes, the fixed factor, were also not significant for any measurement method used: transmitter and feeder data- $F_{(1,15)} = 1.5, P = 0.235$; just transmitter data- $F_{(1,9)} = 0.34, P = 0.580$; just feeder data- $F_{(1,13)} = 1.6, P = 0.231$. Figure 17, 19, and 21 show averages for each observation of cumulative area covered for both sexes and for each type of measurement used. Figure 18, 20, and 22 show maximum final area plotted against final observations for all birds used in analysis and for each type of measurement used.

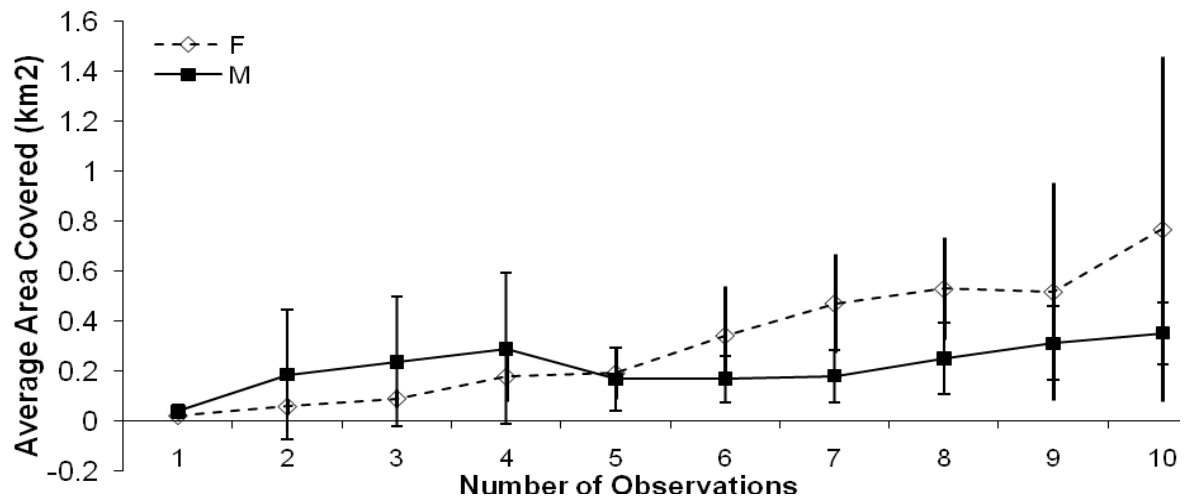


Figure 17 Average cumulative area covered for males and females using transmitter and feeder data. Error bars indicate 95% confidence intervals, male bars capped.

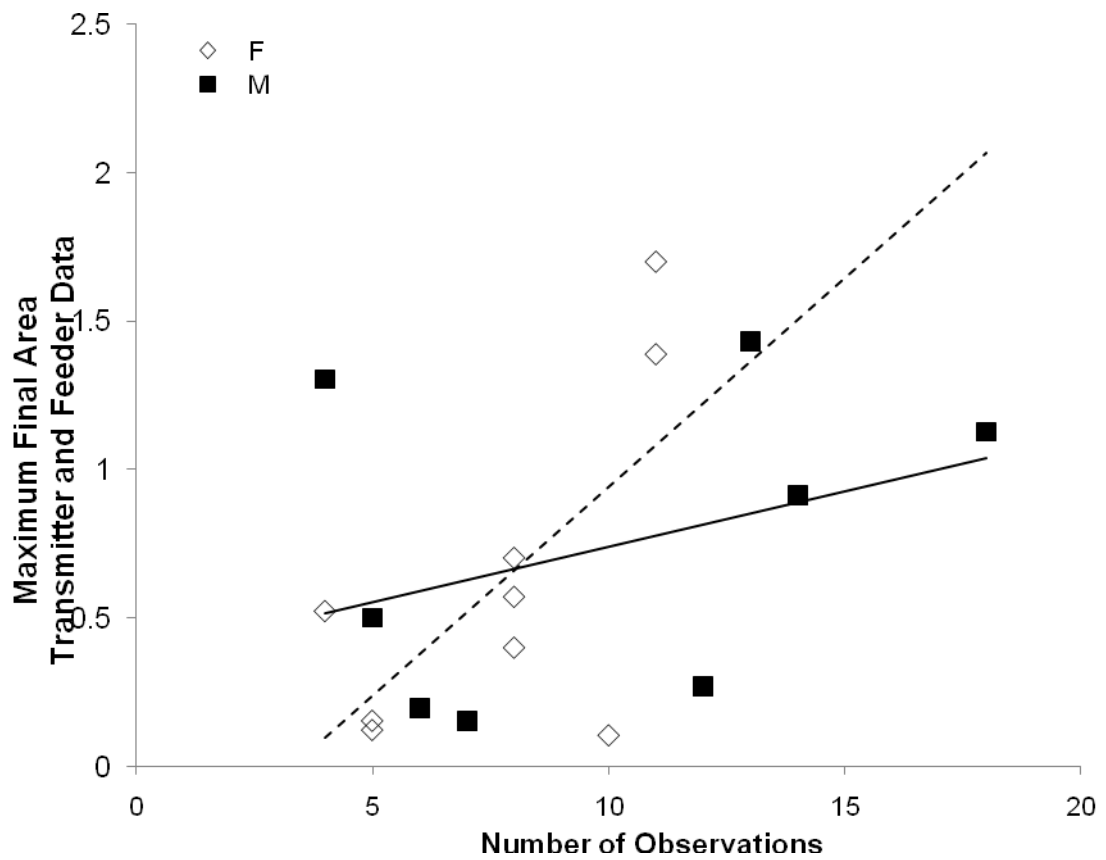


Figure 18 Scatter plot with best fit lines for both sexes. Symbols represent maximum final cumulative area for each individual bird used in analysis.

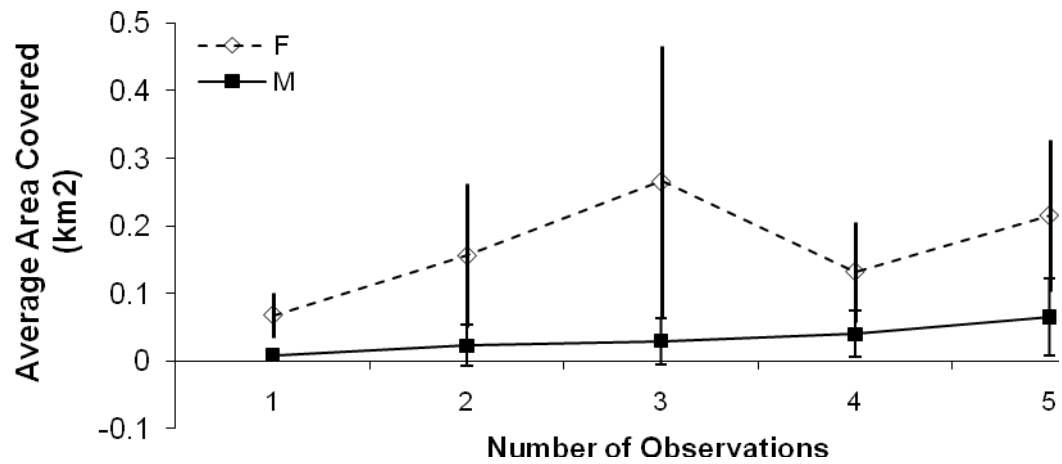


Figure 19 Average cumulative area covered for males and females using just transmitter. Error bars indicate 95% confidence intervals, male bars capped.

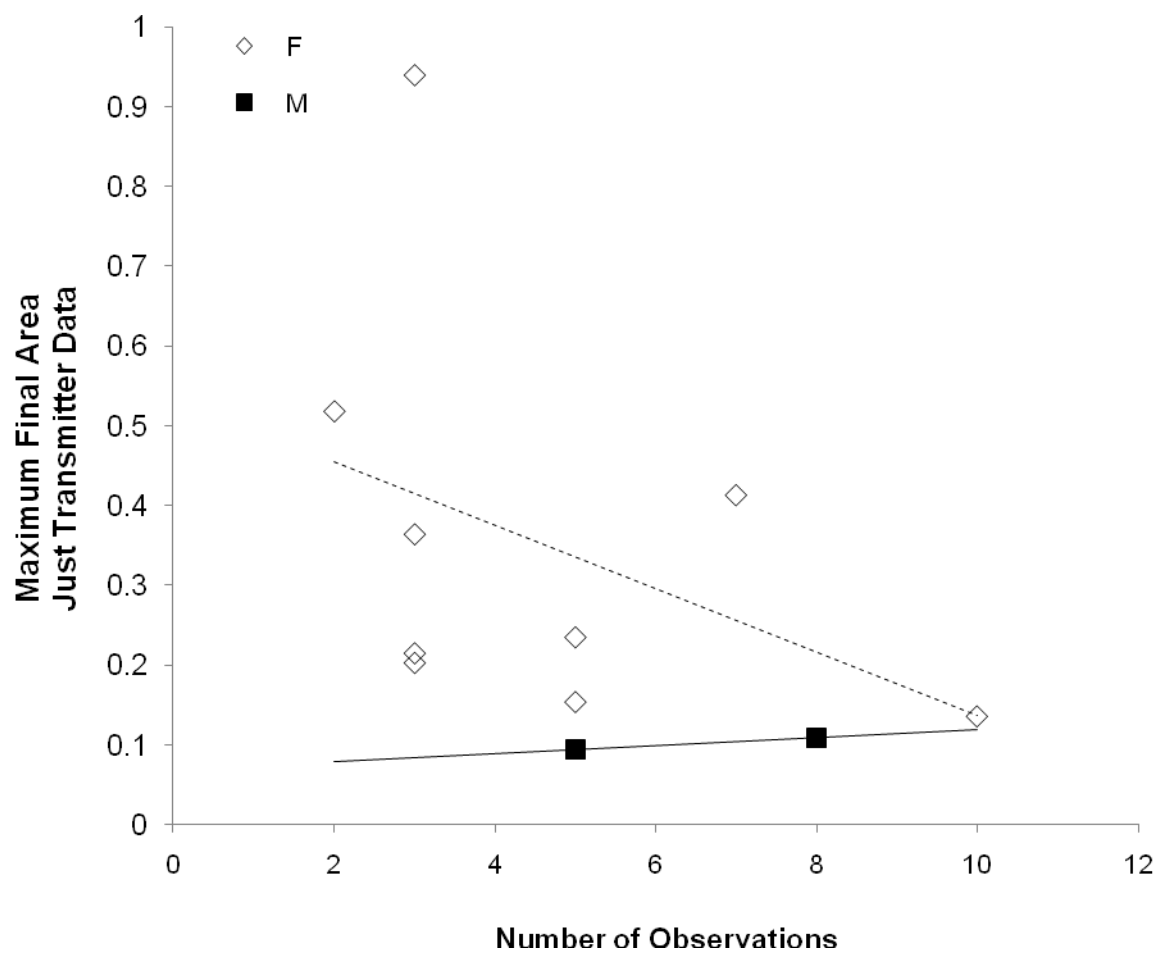


Figure 20 Scatter plot with best fit lines for both sexes. Symbols represent maximum final cumulative area for each individual bird used in analysis.

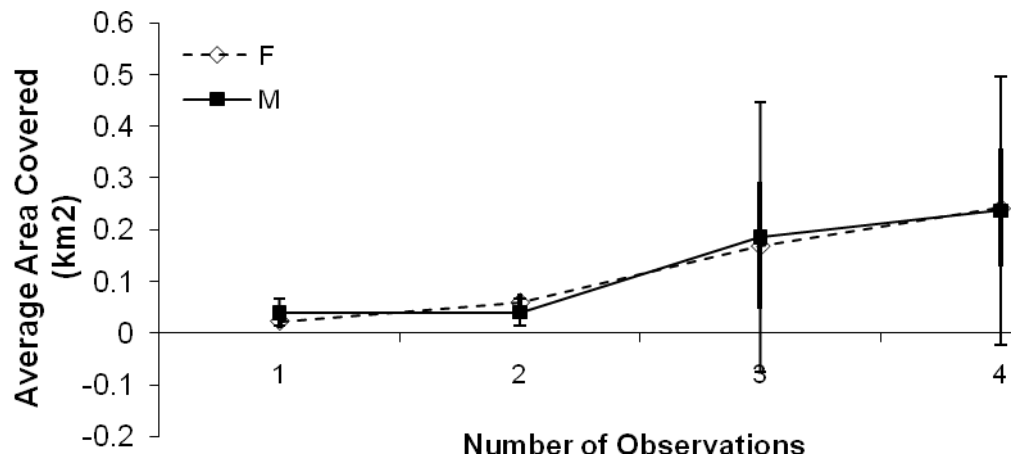


Figure 21 Average cumulative area covered for males and females using just feeder data. Error bars indicate 95% confidence intervals, male bars capped.

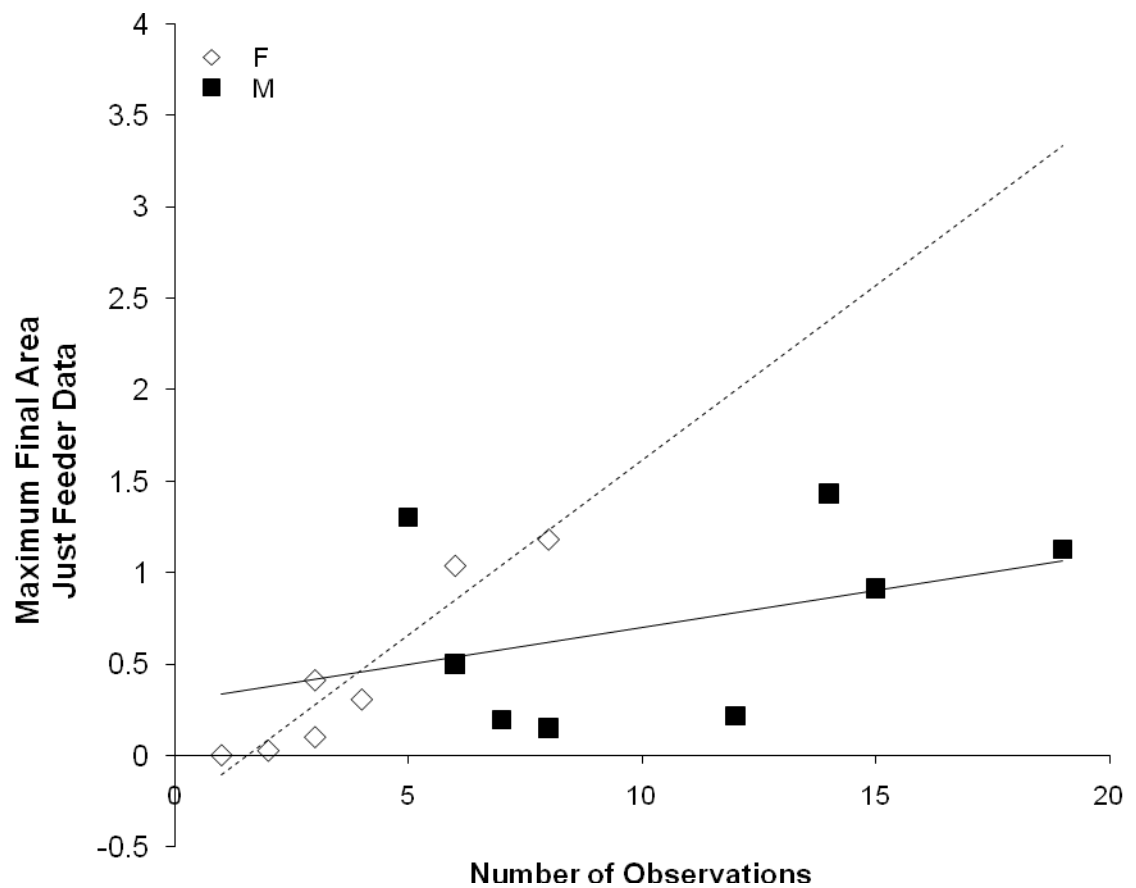


Figure 22 Scatter plot with best fit lines for both sexes. Symbols represent maximum final cumulative area for each individual bird used in analysis.

Birds with transmitters were tracked for an average of 18.7 days and battery life averaged 44 days (Table 1). Twelve non-transmitted birds were observed ~3km southeast outside of Zealandia in the suburb of South Karori. Four of these birds were juvenile females, six were juvenile males, one was an adult female, and one was an adult male. One banded juvenile male was seen by a member of the public in another location about ~3.6 km from where it was hatched within Zealandia. Two females, one adult and one juvenile, were also seen by members of the public in Otari Wilton's Bush, about 2.5 km away. There did not seem to be any strong sex bias dispersal from these non-transmitted birds, however, statistical analysis was not possible since they were not seen a significant amount within Zealandia or elsewhere that season, but the information is worth noting.

Only one possible predation of a tagged female (PGM-FPK) was discovered outside of the predator-proof-fence of Zealandia in the suburb of South Karori. Unfortunately, no body was found, only a few feathers and the transmitter. The exact cause of death was undetermined. Only three 2008/09 juvenile females, one previously radio-tagged, reappeared the next breeding season (2009/10). Two of the three females had confirmed nests, one within the Zealandia and one at South Karori.

Feeder Use Between Sexes

Of the 1152 documented feeder visits over five months. The 47 males visited the feeders 79.34 percent of the time and the 20 females 20.66 percent. Figure 23 shows more males visiting feeders and more often than females. Figure 24 shows a higher distribution of visitation for males to feeders than for females.

A generalized linear model (GLM) with Poisson was used to test for differences between bellbird male and female feeder use, with the dependant variable as the number of visits, and sex and cohort, or the year an individual was hatched, as main effects separately, then fitted into the model to determine the interaction between them. There was a significant difference between sex and feeder visits ($F_{(1,1)} = 28.58$; $P=0.000$) and was significant for cohort ($F_{(1,6)} = 215.66$; $P = 0.00$). There was also a significant difference for the sex and cohort interaction ($F_{(1,4)} = 18.89$; $P=0.001$).

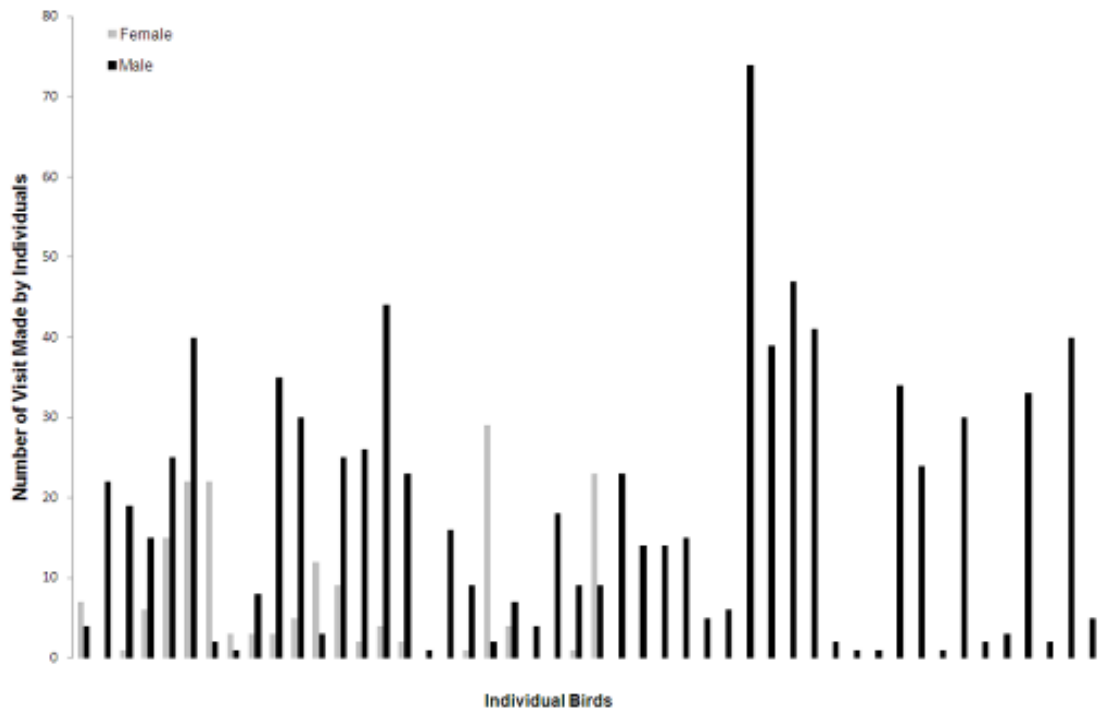


Figure 23 Visits made to feeders in Zealandia by individual bellbirds over a five month period between January and May. Each line represents an individual bird and the number of times they were seen at a feeder.

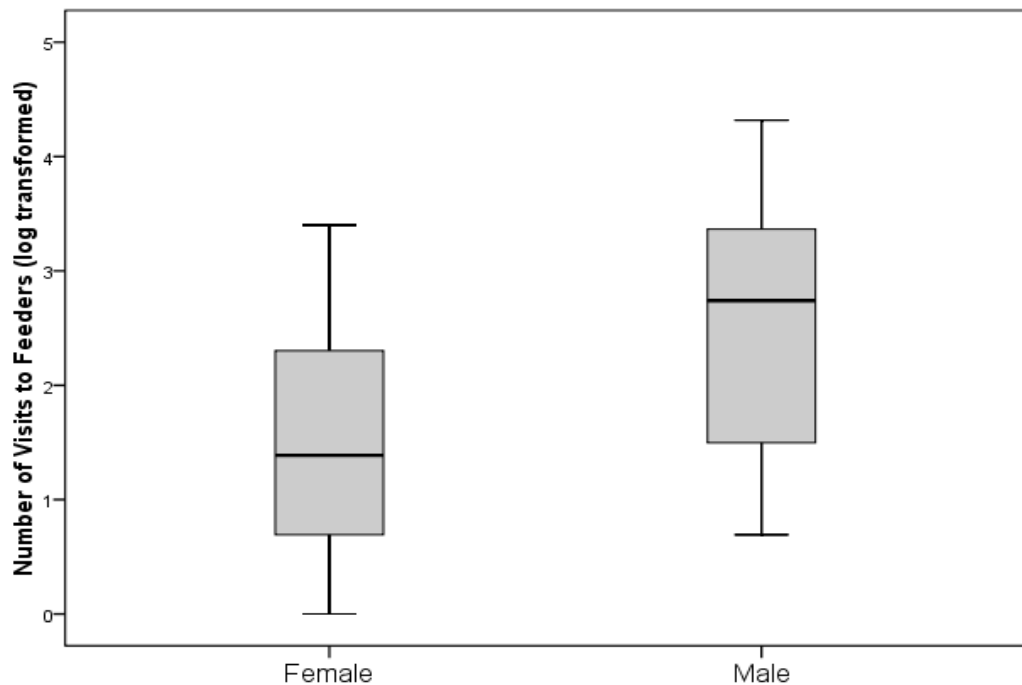


Figure 24 Box plot showing a higher distribution of male feeder visitation rates than females within Zealandia. Male median=2.74; n=47. Female median=1.39; n=25.

Aggression Shown at Feeders

The binomial test revealed a significant deviation from an expected even ratio of aggressive displays between males and females ($P = 0.0003$). There were 20 female bellbirds and 48 male bellbirds seen using feeders in Zealandia over 116 days. Out of 124 observations of aggressive behaviour in and around feeders which includes male and female bellbirds, as well as male and female hihi, male bellbirds were seen to be aggressive 103 times. Male bellbirds were observed being dominant over female bellbirds 16 times. While female bellbirds were not seen to be dominant over males at all during the observation period. Therefore, the ratio is highly skewed towards bellbird males as being the disproportionably aggressive part of the population of birds using feeders in Zealandia. This is consistent with the hypothesis that males are socially dominant over females.

Discussion

The ratio of male to female bellbirds slowly increased since the first translocation to Zealandia in 2001, despite repeated translocations of additional females. The abundance of males and females in Zealandia was significantly different at time of hatching and at the start of the breeding season. Female bellbirds were found to move slightly further than males from hatch site when overall averages for all females were taken for same number of observations as males for almost all measurement types used. However, when maximum final distances were analysed for both sexes the difference between them was not statistically significant. When averages were taken for all observations of cumulative distance moved for each bird, then averaged separately for males and females, males moved slightly further (average 0.53 km) than females (average 0.52 km). There is only a difference of 0.08 km between the furthest distance a male travelled and the furthest distance a female travelled from hatch site (Table 1). Males were found to use feeders at a higher rate than females and were found to be more aggressive around those feeders

Dispersal

There were consistently more observations of males, providing more opportunities to measure their movements. While there were only two males with transmitters they were observed on a greater number of occasions. Because of males' conspicuous nature they appear to be more mobile than females, when this may not be true. This is congruent with some past observations of bellbird activity. Craig & Douglas

(1984b) found that male bellbirds move more and that female bellbirds were less likely to move far distances unless pressured by competition from males. Craig & Douglas (1984a) also stated that males are more likely to move over water in a study in Northland, New Zealand, but females much less likely to do so. This is corroborated by Heather & Robertson (1996) where they state that females would seldom move to the mainland from islands, while males were seen to do this. Brunton *et al.* 2008 also showed males and females dispersing from islands to the mainland, this paper shows stresses that bellbirds have dispersed into areas of low predator levels. However, overall the literature for other bird species suggests female birds move further than males especially if there is strong competition for resources (Greenwood 1980; Greenwood & Harvey 1982; Sutherland *et al.* 2000; Liu & Zhang 2008). The tendency for Zealandia bellbirds to move to the South Karori location is congruent with these previous findings, however the lack of predator control being done there may prevent a viable population settling in South Karori. Nectar is an important source of food for bellbirds and can sometimes influence survivorship, but its availability can also greatly effect movement (van Riper 1984). In a study by Rasch & Craig (1988), male bellbirds were thought to be more likely to move long distances in search of food, while the females would remain behind and feed on lower quality food. This does not follow other studies that theorised that the more subordinate sex or individual is more likely to disperse so that the more dominant individual has better access to close, high quality resources (Arcese 1989; Belthoff & Ritchison 1989). Competition between the sexes is thought to cause more subordinate individuals to move further and more often than dominant individuals (Arcese 1989). Males which also spend a lot of time defending territories are less likely to disperse because they benefit more by knowing the habitat and area

better (Arlt & Pärt 2008; Wilson & Arcese 2008). Sharing space and resources with other species and conspecifics may cause conflict which may lead to increased dispersal in the more subordinate sex in that population (Waser 1985). A study conducted by Kennedy & Ward (2003) concluded that better food availability in an area encouraged juvenile goshawks (*Accipiter gentiles atricapillus*) to stay in or return to natal areas within the first year, but recognised the need for more long term studies.

The findings in Arcese (1989), Belthoff & Ritchison (1989), and Rasch & Craig (1998) along with the findings in this study, suggest that a male-biased sex ratio is not primarily caused by natal dispersal related in bellbirds; despite the substantial research in favor of females moving further than males in other avian populations. Such as the helmeted honeyeater (*Lichenostomus melanops cassidix*) in Victoria, Australia, where a radio tracking study proved that natal dispersal was skewed towards females (Runciman *et al.* 1995). Without knowing the breeding location of the radio tracked birds, it cannot be known from this study whether or not movements were for the purpose of finding breeding sites, which has been suggested as a reason to disperse (Greenwood & Harvey 1982; Arlt & Pärt 2008). Other possible mechanisms that could encourage dispersal are population density, carrying capacity, or searching for optimal habitat. Mortality tends to be higher in young, which could lead to confusing a low recovery of fledglings with dispersal, leading to false conclusions (Greenwood & Harvey 1982). Juveniles may not be dispersing far, but are being predated upon, or simply dying over winter months due to lack of resources.

Limitations

Sources of Bias

The data on how many bellbirds hatched in Zealandia and how many are there at the beginning of the breeding season is autocorrelated data. The information on bellbirds in Zealandia in successive years is built on and related to the year previously. Autocorrelated data can effect the outcome of the statistical test used and lead to false outcomes and conclusions (Bjørnstad & Falck 2001; Keitt *et al.* 2002). The additional translocations of females in addition to females being hatched in Zealandia could have also biased results of abundance of bellbirds at time of hatching.

There is a bias between the number of times male bellbirds with a transmitter and male bellbirds without were seen. Birds with a transmitter were concentrated on and had more locations found in more days than birds with no transmitters that were also used in analysis. This could have also effected some conclusions.

Sources of Error

While radio-tracking animals can lead to some valuable, otherwise unattainable conclusions, some error in estimated location is to be expected (Lloyd 1988). Not every location of a bird was confirmed with a visual sighting in this study. With the mobility of these birds being so high, the estimated locations can be considered accurate, as they were very likely to be in and around the finalized location for that day a similar practice was found in Runciman *et al.* (1995). It has also been found

that having two or more bearings on a moving or stationary animal simultaneously greatly increases accuracy (Lloyd 1988; Schmutz & White 1990), which was not possible every tracking day of this study. Lloyd (1988) and Kenward (2001) also discuss the problems in and around radio tracking animals in forested or rugged, hilly terrain, resulting in lower levels of accuracy of locations, as opposed to tracking on flat terrain, which was a concern in this study. To try and alleviate this effect during this study, tracking would begin by getting the first bearing on the highest point possible. However, if the bird in question was directly below the aerial, signals would come from conflicting locations. Once a general area was determined, it was likely to be in a wooded and hilly area, thus confounding the possible error in location. The mobility of these birds could have also accounted for some error in signal detection. As a bird moves the signal given off by the tag changes, especially when the bird moves behind an object, such as a tree (Kenward 2001) and this would add difficulties during tracking.

Feeder Use and Aggression

Male visitation rates to supplemental feeders in Zealandia were significantly higher than female visitation rates. The significance of cohort, or year the bird was hatched in, on visitation rates suggests that the age of the bird or time spent in Zealandia does increase its chances of visiting a feeder. More specifically Craig & Douglas (1984a) found that only males and no females used a supplementary feeder on Little Barrier Island, New Zealand, although they also found females to be much more inconspicuous. Aggressive behaviours shown by bellbird males and females were also significantly different, with males dominating females as well as, other males.

However, conclusions should be made cautiously because of the small amount of female aggressive acts. Total aggressive acts including all bellbirds and all hihi using feeders were counted at 124, while 103 came from male bellbirds and female bellbirds showed only four aggressive acts in 116 days of observation, which is disproportionate to the ratio of males and female bellbirds in the population. These findings are in agreement with previous studies and observations of male bellbirds being aggressive towards other males, females, or individuals of other species (Taylor 1969; Craig 1981; Craig *et al.* 1981; Craig 1984; Craig & Douglas 1984b; Sagar 1985; Higgings *et al.* 2006).

Because males dominated the use of a high quality food source, this could cause the body condition of subordinate females to be lower (Rasch & Craig 1988). This in turn will continuously cause the more dominant male to maintain a high level of body condition through regular access to a high quality food source (Craig & Douglas 1984b). When nectar reserves and rewards were lower females had a chance to feed (see Craig & Douglas 1984b). Van Riper (1984) found that birds will begin to actively defend territories only when the food resource levels allow them to expend the energy required to do so. However, as within Zealandia the rewards stay constant and high, males will not give females a chance to feed. The likelihood of male bellbirds allowing females access to food sources in their territories during non-breeding times does not always increase with an increase in food supply (Craig & Douglas 1984b; Sagar 1985; Pyke *et al.* 1996; Higgings *et al.* 2006). This can greatly impede a female's chance of survival during these times. Female mortality is already considered to be higher than males in birds (Donald 2007), and less access to high quality food may intensify this.

Competition and aggression may lessen if resources are so abundant that there is no need to defend a territory (Armstrong 1992a). Feeder placement and number of feeders may be encouraging only a few territories, which will always be defended by a male and may always be excluding subordinate individuals, younger males or females. The purpose of the feeders is to keep the birds inside the Zealandia fence but, it may also be encouraging bellbird males to be aggressive and harming females either by forcing them to disperse in search of food, or by simply excluding them from a high quality food source they may need to get through winter. Adding new feeders within Zealandia outside of current bellbird territories may lessen the need to defend territories and feeders so aggressively, as was concluded by Carpenter (1987). If food is abundant then long term defence may expend more energy than necessary (Carpenter 1987), however this may not always be the case. In Armstrong's (1992b) study, an increase in nectar supply in the form of supplemental feeders outside of natural food sources and outside of territories did not decrease aggressive acts in Australian honeyeaters.

Aggression can also be detrimental to a species as shown in Wolf (1978); a highly aggressive male may mate less often than a less aggressive male. Kvarnemo & Ahnesjö (1996) have modelled that as the sex ratio of a population becomes more skewed towards either sex the potential for finding mates reduces, therefore competition for mates increases. For male bellbirds within Zealandia a rise in competition may also mean a rise in aggression, which may further exacerbate the sex ratio bias in Zealandia. As the number of female bellbirds decreases each year competition and therefore, aggressiveness, in males may increase.

While this study shows male bellbirds actively defend territories and food sources from females, they will also do so from other species such as the hihi (Bartle & Sagar 1987). Even though hihi are a slightly larger species they lack wing slots that aid in dominance displays of the bellbird (Craig 1984). So male bellbirds may be affecting the fitness of not only female conspecifics but also another species.

Limitations

Sources of Error

Much of the feeding data and behaviour observations were centred around artificial food sources. Females may be actively avoiding feeders because of male aggression. Not enough visuals of males or females using natural food sources were available during the time of this study to rule out that they are not utilising natural sources. This means there needs to be more attempts made to get visuals of birds feeding on other sources available within Zealandia and outside. Behavioural observations around these food sources and whether more male or more female bellbirds are using them, need to be determined.

In summary, sex ratio imbalances can be detrimental to a population and have been shown to be a challenge for bellbirds being established at Zealandia. By understanding bellbird natal dispersal behaviour and behaviour in and around nectar sources, more appropriate management actions can be put in place to try and increase female numbers. However, further studies will need to take place before this can be done effectively. These studies should include more males with transmitters to be able to properly compare differences. More emphasis on how much natural food sources are used by male and female bellbirds and their behaviour around those resources should also be made in future studies.

Chapter Three

General Discussion

Summary of results

This thesis contributes to the understanding of sex ratio imbalance in bellbirds by studying juvenile dispersal, an important stage in a bird's life and an important part of ecology in general. Results from chapter two, based on one season of data collection, conclude that female bellbirds do not move significantly further than males. When all observations were analysed for both sexes, males were shown to move further due to increased observational opportunities because males exhibit more conspicuous behaviour than females. When maximum cumulative final distance or area occupied was analysed for both sexes, there were no significant differences between the two. These findings suggest inconsistencies between results in this study and in the literature which states that females consistently move further. (Greenwood 1980; Clarke *et al.* 1997; Dale 2001). More studies incorporating multi-year telemetry would greatly improve the body of knowledge in this field.

Based on the non-statistically significant results from the natal dispersal study, the aggressive nature of male bellbirds may be a more likely mechanism for causing female scarcity. Male dominance over a high quality food source leads to female exclusion of the resource. Males were shown to use feeders at a significantly higher rate than females. Females may feel pressure to leave the protection of Zealandia because of this competition over feeders. Females dispersing outside the bounds of Zealandia likely face higher rates of predation and lower quality resources. Females

may simply retreat to further reaches of Zealandia, resulting in female miscounts in regular censuses and their possible deaths from exclusion of the high quality food.

Conservation implications and management recommendations

Dispersal is a major conservation issue because it affects individuals' ability to find mates, food, or colonize new areas. Habitat connectivity and quality both play an important role in dispersal patterns. Before effective management decisions can be made further information on habitat and resource preferences, demographics, intra and interspecies interactions, and effects of density are needed (Bowler & Benton 2005). A better understanding of these possible dispersal mechanisms and how each affects the sexes would require more study. The ability to predict animal movement, directions, and distances would be beneficial to wildlife managers. Future development of additional models pertaining to different processes and mechanisms of dispersal may aid in conservation efforts (Macdonald & Johnson 2001).

Products of this research can allow conservation actions to be put in place to aid in species management even though mechanisms behind sex ratio imbalances are not fully understood. Habitat management within Zealandia and its surrounding areas include: removing invasive plants and planting high-producing nectar trees. These measures would alleviate some of the competitive pressure caused by the feeders. Competition may lessen, allowing females to feed within Zealandia. Bellbirds in Zealandia choose to create and defend territories close to feeders and a male will only allow one female to use that feeder during the breeding season. Perhaps placing new feeders in other suitable habitat around Zealandia would encourage more

territories and therefore, more males encouraging more females to stay and breed. Males may still defend the newly planted trees and extra feeders but with more potential territories, more pairs would form which should help to increase the female numbers. Encouraging the public to plant nectar producing trees may help to improve bellbird survival rates outside Zealandia. Increasing habitat connectivity between nesting areas and areas of suitable habitat (e.g. Otari Wiltons Bush, Wellington) will also increase survival rates.

On-going predator control outside Zealandia would also increase the chances of survival when birds disperse out of Zealandia. The possibility of bellbirds establishing new populations would increase. With fewer predators, the likelihood of a bellbird returning to Zealandia to breed may also improve. Involving the public in predator control, such as keeping cats indoors at least during the day when birds are more active, could reduce predation on native birds.

If all of Zealandia's 252 ha were suitable bellbird nesting and feeding habitat, there could be potentially 1,040 territories, using the estimation of resident male territory size for bellbirds from Higgings *et al.* (2006). However, this number would be substantially reduced due to two main limiting factors. The first is that other resident birds in Zealandia may not allow overlapping territories with bellbirds. The second factor is that much of the habitat in Zealandia is still not ideal for bellbird feeding or breeding, which, combined with the small number of females, contributes to the limited breeding potential. While the territory estimate is speculative and

overestimated, this could be a number to aim for. By continuing to improve habitat within Zealandia and surrounding areas bellbird numbers could increase.

Recommendations for future research

Based on the findings in this thesis, I recommend the following future research avenues. Studying sex ratios at time of hatching would gain much insight into adult sex ratios. This can be done with multi-year studies determining the sex of unhatched eggs and any chicks that die, if they can be found. Since bellbirds are sexually dimorphic, the costs of producing sons over daughters or vice versa could determine sex ratio imbalances (Weatherhead & Montgomerie 1995). Further studies concerning food quality and quantity for the female before laying, nestlings and fledglings in relation to sex ratios are also needed (Trivers & Willard 1973; Tella 2001; Stauss *et al.* 2005; Kekkonen *et al.* 2008). Effects of habitat quality should also be considered as an indicator of sex ratios (Stauss *et al.* 2005).

The overall consensus in the literature is that natal dispersal tends to be female biased in birds (Greenwood 1980). However, in this study, there were no strong statistical conclusions that dispersal is either male or female biased. Data collection for this study only spanned one nesting season and more data needs to be collected. In order to reach any strong conclusions, additional attempts should be made to track the animals more frequently and over a longer period. However, time, human resources, and monetary constraints may prevent this.

Radio tracking is limited by the equipment used. A longer battery life, stronger signals, lighter transmitters, and utilizing GPS and GIS would all improve future tracking studies by allowing a longer tracking period and more accurate results. A new potential breeding site with banded bellbirds was discovered because of radio telemetry used in this study. Additional radio-tracking in other seasons would be beneficial to locate other new foraging or breeding sites. It is also my recommendation that an equal number of males and females be tagged to better compare movements. Staggering the radio tag attachment to different clutches and following some to the next breeding season would add new and useful information. It is clear from the literature that there are still conflicting conclusions on mechanisms behind juvenile dispersal and field work on more species over a longer time period would greatly improve the body of knowledge. Other areas that need exploration to increase the body of knowledge of natal dispersal are inbreeding avoidance, competition for space, competition for resources, searching for more attractive resources, carrying capacity of the habitat and area, and population density (Greenword & Harvey 1982; Matthysen 2005).

Suggestions are already in place for having a year-round nectar supply from trees that produce abundant nectar for honeyeaters' use. Trees such as pohutukawa (*Metrosideros excelsa*), puriri (*Vitex lucens*), kohekohe (*Dysoxylum spectabile*), haekaro (*Pittosporum umbellatum*), rewarewa (*Knightia excelsa*), maire taike (*Mida salicifolia*), Native Jasmine (*Parsonsia heterophylla*), and manuka (*Leptospermum scoparium*) and some Australian trees from the genera of *Banksia*, *Grevillea*, *Eucalyptus*, or *Melaleuca* are already known to be of high priority for bellbirds and other honeyeaters (Craig *et al.* 1981; Craig 1985; Rasch & Craig 1988). When

possible, diversifying the amount and type of microhabitats available by having trees of different heights would allow for more individuals to feed. By increasing Zealandia's resources, through feeders or increased nectar producing trees, and comparing annual rates of survival in Zealandia with previous years, we will then better understand the cause of female decline (Pyke *et al.* 1996).

There have been cases of bird species, where females disperse further, as in the Seychelles warbler (Eikenaar *et al.* 2008) and of mammal species, where males disperse further, such as the Belding's ground squirrel and the olive baboons (Dobson & Jones 1985) because of competition (Greenwood 1980). To establish how this relates to the Zealandia bellbird population multi-year studies will be necessary to show a strong natal dispersal pattern. By improving both the resources within Zealandia and the surrounding areas, the bellbird population is more likely to increase both male and female numbers.

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Appendix

Six examples of the maps scanned into ImageJ and used to make measurements. Often birds were seen in and around the same area multiple days in a row, while these counted as multiple observations used it will appear as though there are not many observations (yellow or red dots) for that bird. The bird's sex and leg band combination are written in blue at the top of the map. Yellow dots are transmitter observations and red for feeder observations. Red dots on maps in Figure 2, 3, and 4 are observations from both transmitter and feeder data. Figure 1 is observations just using feeder data, as that bird did not have a transmitter attached.

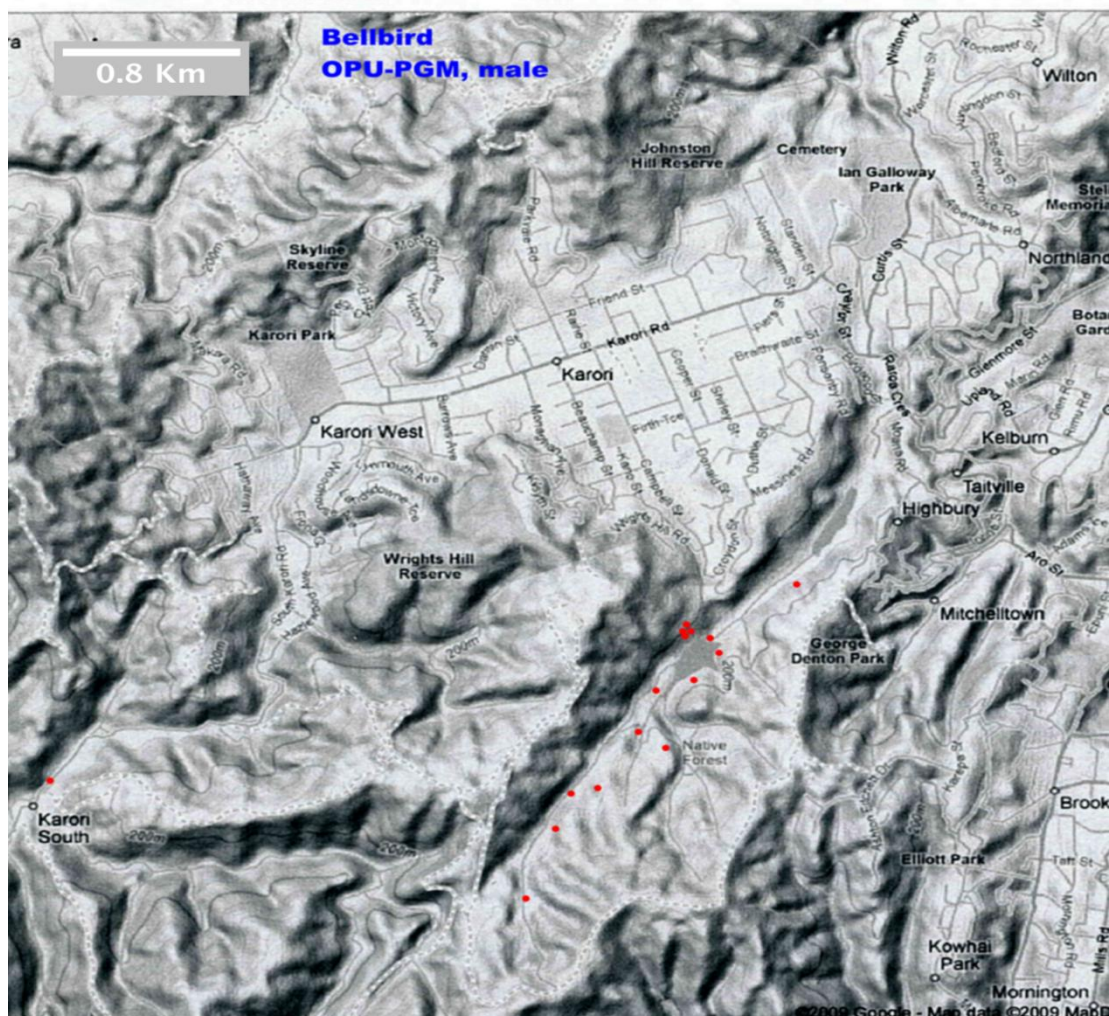


Figure 1 ImageJ map for OPU-PGM, male bellbird. Red dots indicate areas in and around Zealandia where the bird was located using feeder data.

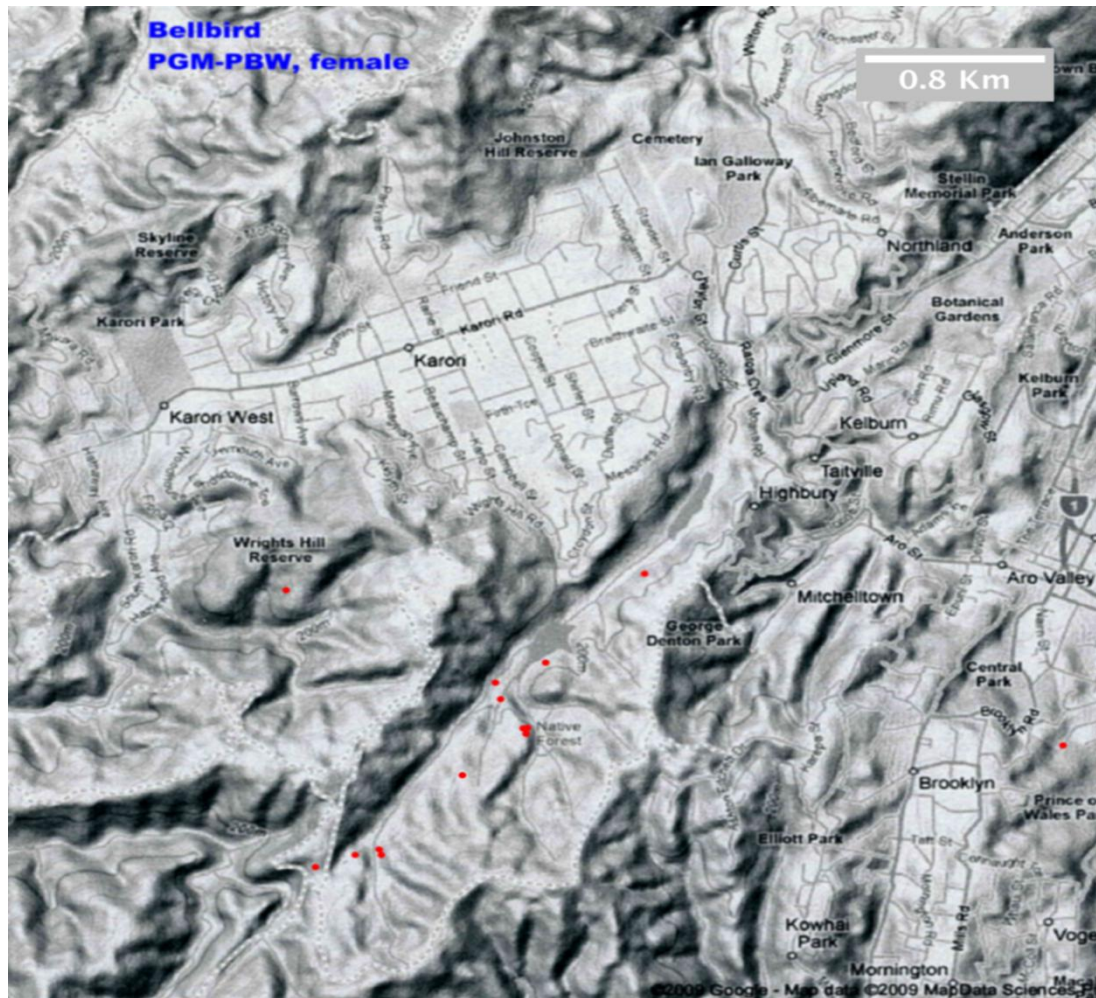


Figure 2 ImageJ map for PGM-PBW, female bellbird. Red dots indicate areas in and around Zealandia where the bird was located using feeder and transmitter data.

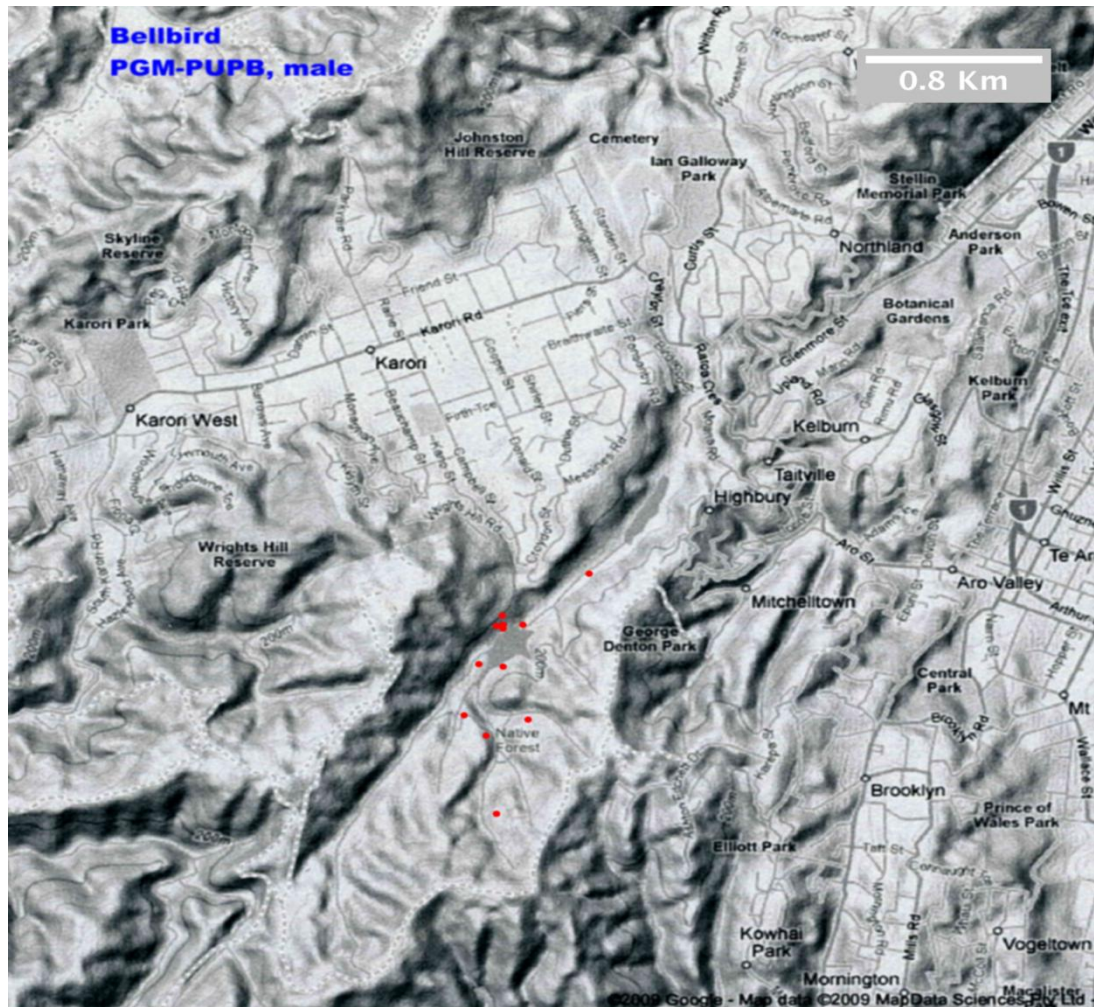


Figure 3 ImageJ map for PGM-PUPB, male bellbird. Red dots indicate areas in Zealandia where the bird was located using feeder and transmitter data.

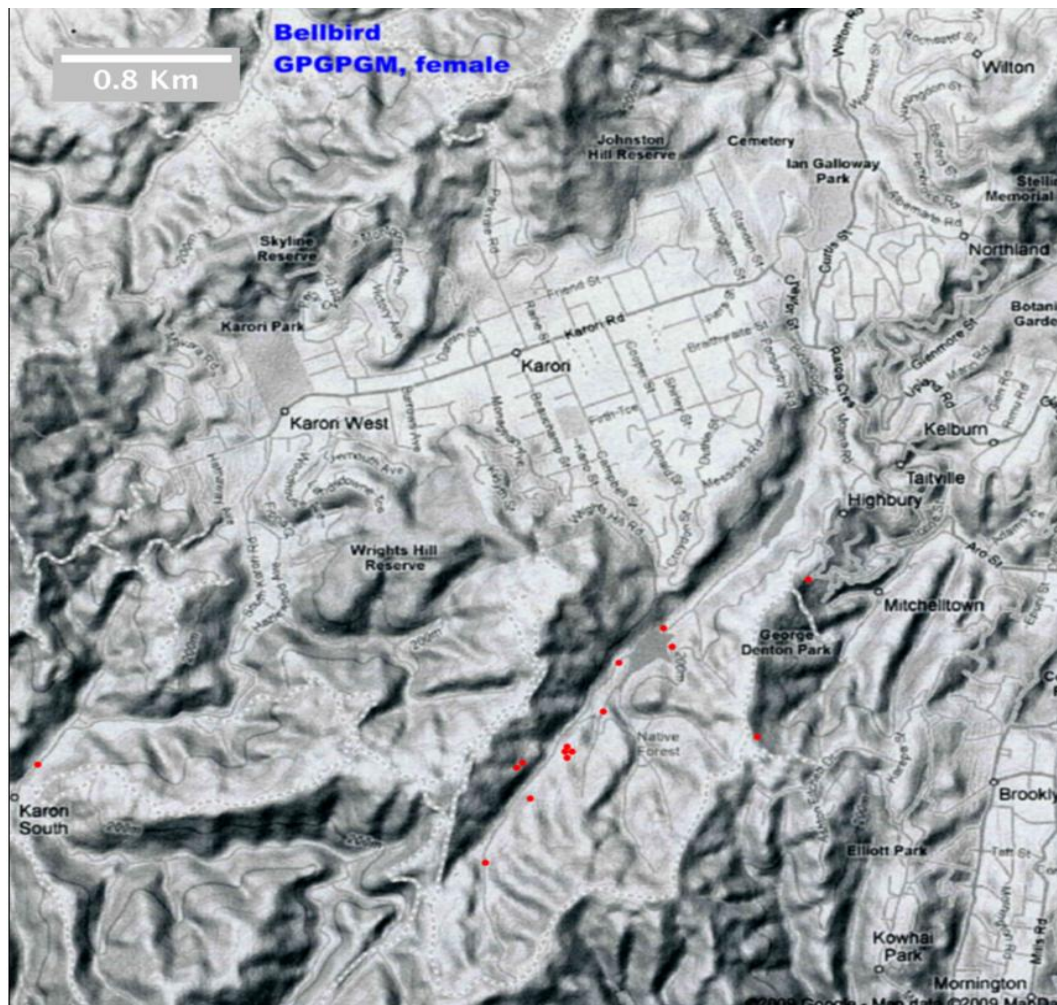
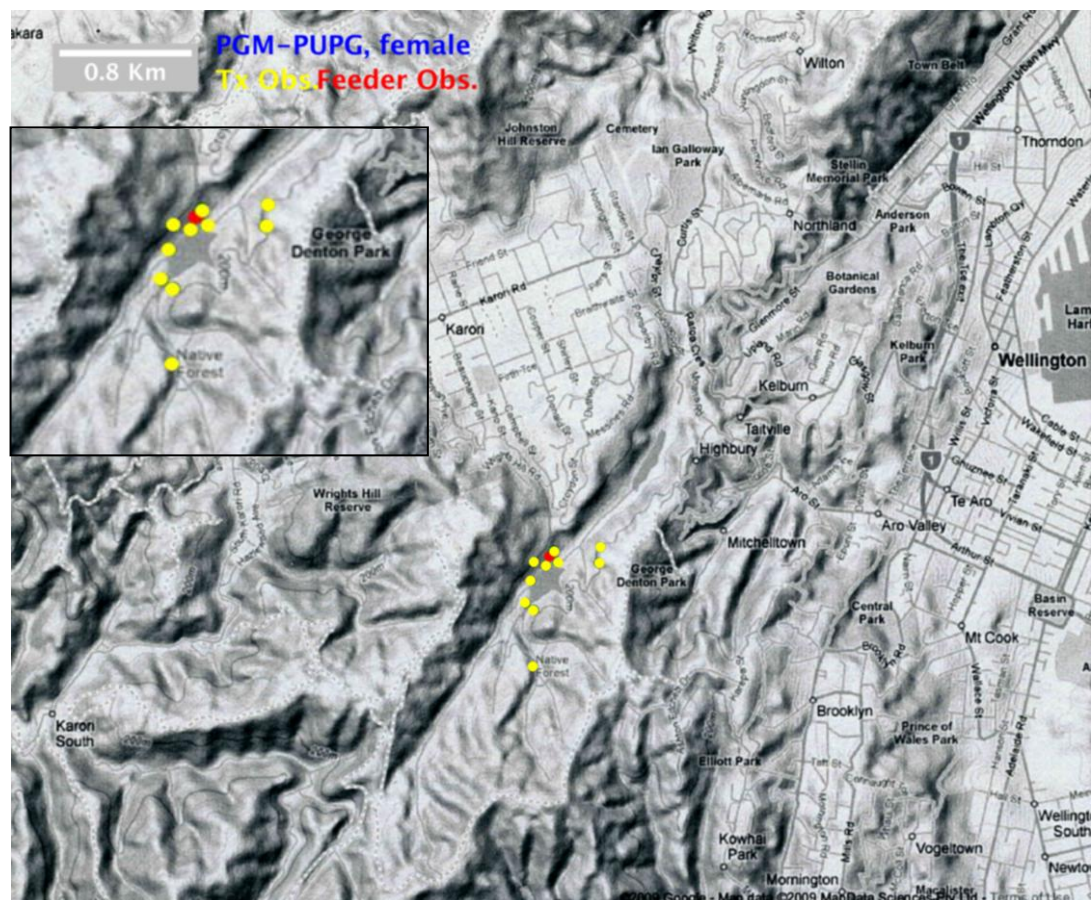


Figure 4 ImageJ map for GPG-GPM, female bellbird. Red dots indicate areas in and around Zealandia where the bird was located using feeder and transmitter data.



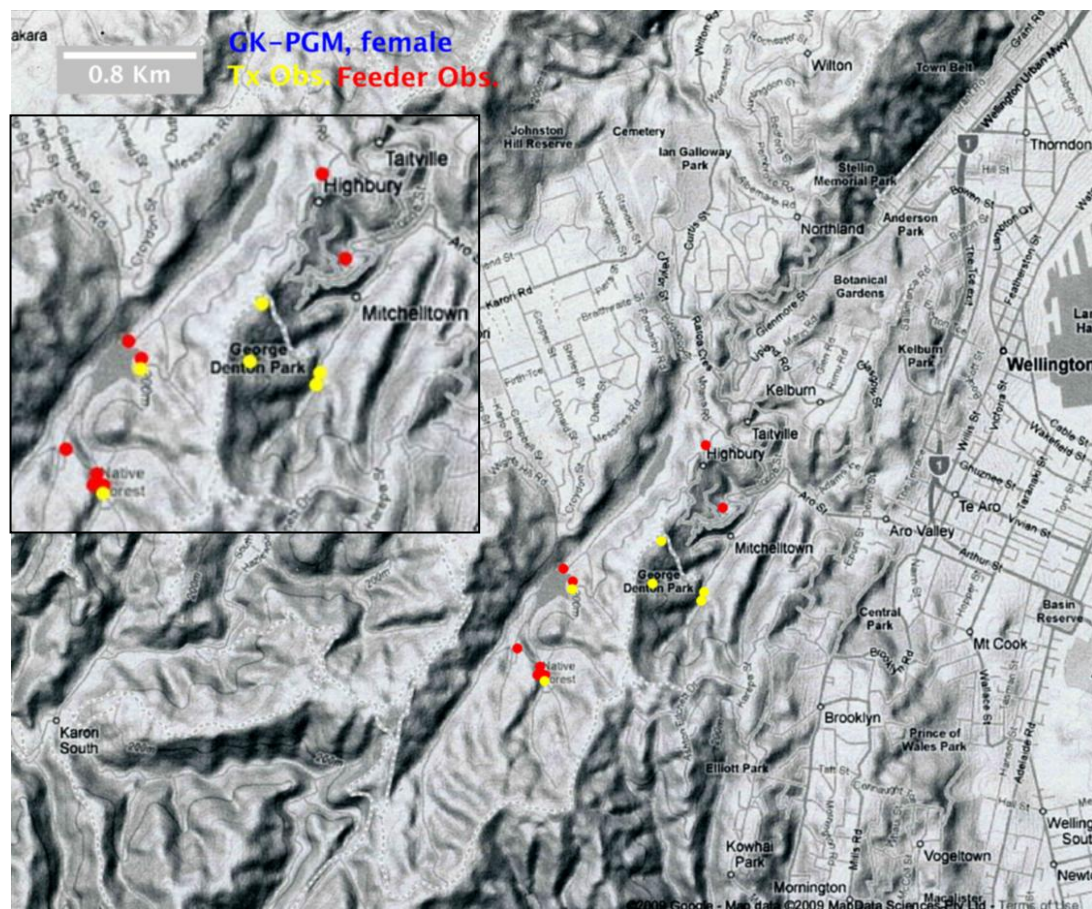


Figure 6 ImageJ map for GK-PGM, female bellbird. Red dots indicate areas in and around Zealandia where the bird was located using feeder data. Yellow dots represent areas the bird was found using transmitter data. Area with concentration of sightings is enlarged.