Behaviour in the hand predicts male natal dispersal distances in an establishing reintroduced hihi (*Notiomystis cincta*) population.

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Abstract

Natal dispersal is a complex behaviour influenced by multiple factors that are often sex-specific and density-dependent. Reintroduced populations are typically low density in the initial years of establishment; hence understanding natal dispersal patterns in this context is a critical component of reintroduction biology. Natal dispersal is a key behaviour that both influences the probability of recruitment, and simultaneously dictates the spatial configuration of the reintroduced population as it establishes. Here, we examine natal dispersal in a reintroduced population of an endangered New Zealand forest passerine, the hihi (*Notiomystis cincta*), in the first three years after reintroduction to a large, mature forest reserve. We examined a) differences between the sexes, and b) the relationship between temperament and natal dispersal distances in locally-bred hihi over this time period. We found natal dispersal distances varied widely in both sexes, with mean natal dispersal distances significantly higher in males than females. There was a sex-specific effect of temperament, with males that distress-called during handling dispersing further than those that did not. Our results show that while clusters of individuals have established across the reserve due to conspecific attraction, there is movement between these clusters, primarily a consequence of dispersal of males of a distinct temperament. Continuing to monitor natal dispersal patterns as populations establish will provide further insights into the role of dispersal in shaping establishment patterns in reintroduced populations.

Introduction

Natal dispersal is defined as the movement from the site of birth (or hatching) to the first

breeding site (Matthysen, 2012). It is the primary mechanism by which gene flow occurs, and

variation in this dispersal behaviour has consequences at the individual, population,

metapopulation and species level. The drivers of natal dispersal in reintroduced populations, and

the effects of any behavioural variation, are less well understood, despite studies that have

emphasised the potential for dispersal to play a strong role in reintroduction success, in both the

early stages of population establishment (Mihoub, Le Gouar and Sarrazin, 2009, Mihoub,

Robert, Le Gouar *et al.*, 2011) and longer-term persistence (Richardson, Doerr, Ebrahimi *et al.*,

2015).

In reintroduced populations, density will typically be low in the early years of population

establishment, and maximising recruitment of offspring into the new population is critical. Natal

dispersal is a key behaviour that both influences the probability of recruitment, and

simultaneously dictates the spatial configuration of the reintroduced population as it establishes.

Natal dispersal can therefore either facilitate or limit spatial expansion of the population, both

within the intended release area, and outside of it. Such expansion can have both positive and

negative effects, depending on the goals of the reintroduction and the survival probability of

individuals in the wider landscape (Richardson, Doerr, Ebrahimi *et al.*, 2015). For these reasons,

understanding dispersal movements of the offspring of reintroduced animals is an important

component of reintroduction success.

Natal dispersal is driven by complex interactions of multiple factors, which are often sex-specific

or density-dependent (Clobert, Baguette, Benton *et al.*, 2012, Clobert, Le Galliard, Cote *et al.*, 2009). These are generally considered in two broad categories, those related to the external environment, and those related to the internal state of the individual (Matthysen, 2012). With regard to the latter, the role of animal personality or temperament has been given particular attention in recent years (Cote, Clobert, Brodin *et al.*, 2010). Multiple studies have shown links between natal dispersal propensity and personality type, with individuals at the "proactive" end of the personality spectrum (generally those characterised as "bold", "fast", or "aggressive"; Cockrem, 2007, Groothuis and Carere, 2005) typically being the most dispersive individuals (e.g. Dingemanse, Both, van Noordwijk *et al.*, 2003, Duckworth and Badyaev, 2007) although this can be scale- and state-dependent (Quinn, Cole, Patrick *et al.*, 2011).

It has not yet been examined if natal dispersal in low-density, reintroduced populations is personality-dependent. Variation in personality types is known to facilitate range expansion in established populations (Duckworth and Badyaev, 2007), and also plays a critical role in the invasion process (Carere and Gherardi, 2013, Chapple, Simmonds and Wong, 2012), with the most dispersive personality type leading the invasion or range expansion front. Given there are some similarities between establishing reintroduced populations, and colonisation events of expanding or invasive species, it could be expected that personality, or temperament, plays an important role in reintroduced populations. Despite repeated calls to integrate studies of personality into conservation science (Anthony and Blumstein, 2000, Smith and Blumstein, 2013, Swaisgood, 2010), few have yet done so, particularly in the case of reintroduction biology (but see Bremner-Harrison, Prodohl and Elwood, 2004, Sinn, Cawthen, Jones *et al.*, 2014).

Here, we examine natal dispersal patterns in an establishing reintroduced population of an endangered passerine, the hihi (stitchbird, *Notiomystis cincta*), and the role of animal temperament in the dispersal process. Previous research in natal dispersal patterns of this species have been conducted in a closed island population (Tiritiri Matangi Island, 36°36'S, 174°53'E, 220 ha), where breeding individuals utilise artificial nest boxes. This earlier study found sex-specific density effects as the population established (Richardson, Armstrong, Hauber *et al.*, 2010), with males the more dispersive sex in the first two years after initial release, and thereafter females. Here, we first expand on this earlier study by examining natal dispersal distances (NDD), and differences between the sexes, in the first three years after reintroduction at a mature forest reserve more than 15 times the size of Tiritiri Matangi Island (Maungatautari Ecological Island, henceforth 'Maungatautari', 38°03′08″S 175°33′58″E, ~3400 ha), where breeding takes place in natural nest cavities and hence dispersal opportunities are not constrained by artificial nest box placement. Second, we examine the relationship between temperament (measured by scoring behaviour in the hand during capture and handling) and natal dispersal distances in the Maungatautari population.

Methods

Study species

The hihi is an endangered New Zealand passerine (Vulnerable on the IUCN Red List; IUCN, 2013) that has been subject to multiple reintroduction attempts (Ewen, Renwick, Adams *et al.*, 2013). Reduced to a sole island population by the 1880s (Te Hauturu o Toi/Little Barrier Island), hihi now persist at additional reintroduction sites including two islands (Tiritiri Matangi and

Kapiti), and three mainland reserves (Karori Wildlife Sanctuary, Maungatautari Ecological Island and Bushy Park). All reintroduced populations are reliant on management, including maintenance of an environment free from mammalian predators (all populations), as well as provision of supplementary food (all reintroduced populations; Chauvenet, Ewen, Armstrong *et al.*, 2012) and artificial nest boxes (all reintroduced populations except Maungatautari and Kapiti). Hihi are typically socially monogamous, but have high frequencies of extra-pair paternity (Brekke, Cassey, Ariani *et al.*, 2013, Castro, Minot, Fordham *et al.*, 1996, Ewen, Armstrong and Lambert, 1999), and breed from September to March each year. Juveniles reach independence within 1-2 weeks of fledging and the majority of individuals breed at one year of age (Higgins, Peter and Steele, 2001).

Study site

Maungatautari is a volcanic cone (797 m a.s.l.; Fig. 1) in the Waikato region of the North Island of New Zealand. It is covered primarily in mixed podocarp/broadleaf forest, largely surrounded by pasture, (McQueen, Smuts-Kennedy, Collier *et al.*, 2004). A predator-exclusion fence was completed around the forest edge in 2006 and all invasive mammals except mice (*Mus musculus*) and very low numbers of rabbits (*Oryctolagus cuniculus*) and hares (*Lepus europaeus*) have now been eradicated. A total of 11 endemic species have been reintroduced (Smuts-Kennedy and Parker, 2013), of which seven are listed as Endangered or Vulnerable on the IUCN Red List (IUCN, 2013).

Hihi reintroductions to Maungatautari 2009-2011

Hihi were first released at Maungatautari in March 2009, when 79 birds were translocated from

Tiritiri Matangi Island and Te Hauturu o Toi/Little Barrier Island (Table 1) (Ewen, Parker,

Richardson *et al.*, 2011). A mark-recapture survey in early 2010, in combination with later field

research, suggested that 26-41 (33-52%) of these survived to the first breeding season (October

2009, seven months post-release) (Ewen *et al.*, 2011). Two further releases of juvenile hihi

occurred from Tiritiri Matangi Island in 2010 (37 birds) and 2011 (39 birds) (Table 1).

Subsequent monitoring indicated a minimum of 17 hihi from the 2010 translocation survived to

their first breeding season (46%), and a minimum of 15 hihi from the 2011 translocation (38%)

(Richardson, 2015). By the 2011/12 breeding season approximately 71 adult hihi were present at

the site, comprising a mix of the original translocated hihi (38) and locally-bred birds (33), with

an estimated annual population growth rate of 1.2 (Richardson, 2015). Six supplementary feeders

are provided, all within 150 m of the release site (Fig. 1), and these are utilised by some, but not

all, of the birds present. All 155 translocated individuals were colour banded and genotyped prior

to translocation.

Post-release monitoring and location of breeding territories

Intensive breeding monitoring and colour-banding of locally-bred birds was carried out between

October 2010 and December 2012 (Richardson and Ewen, 2016). Breeding territories were

located by comprehensive searches of the reserve using the existing monitoring line network

(Fig. 1) established for detecting mammalian pest presence, as well as following up reported hihi

sightings from pest monitoring staff and local volunteers. These monitoring lines are distributed

evenly across the release area and designed to be no more than 200 m apart, although there are some larger gaps. We therefore consider the release area was searched thoroughly and evenly across habitat types. The majority of territories were located in late September through to mid-November when hihi males are most vocal and hihi females are most detectable. Most lines were walked at least once during this peak calling time by experienced personnel, and all were covered by staff or volunteers during this time. We considered male hihi to be resident to a location if they were identified at least three times there during the breeding season, and female hihi to be resident if they were observed engaged in breeding behaviour (e.g. nest building, incubating, or feeding chicks), or otherwise observed at the same location at least twice during the breeding season. Breeding locations were found up to 80 m away from monitoring lines by listening for hihi calls during searches, and using playback of male calls. However, about 500 ha of the 3400 ha reserve fell more than 80 m from a monitoring line (Fig. 1). Therefore in 2011/12 and 2012/13 these areas were searched using the same methods but no resident hihi found.

The majority of locally-bred recruits from the 2009/10 (Year 1) to 2011/12 (Year 3) breeding seasons were captured, either by mistnetting (49 birds) or in cages at supplementary feeder stations (27 birds). All birds were colour banded, and genotyped to assign parentage (see below, Table 2). Male hihi can be aged in the hand up until the second year of age using plumage characteristics, but ageing female hihi is more problematic. The majority of females were captured as juveniles at the end of the breeding season and were easily differentiated from adult females (a combination of plumage condition and behavioural characteristics). For females captured at other times of year we either aged them by inference from parentage (e.g. two females were caught in 2011 and sired by a male that was not translocated until 2010, and one

female could not be aged so was excluded from further analyses).

At the time of capture we recorded the behaviour of the bird in the hand as a measure of temperament (Pascual and Senar, 2014). Individuals that did not struggle (i.e. exhibited behaviour such as wing-flapping, leg movements, or other attempts to escape that involved movement) or distress-call were assigned a handling score of '0', individuals that struggled but did not distress-call were recorded as '1', and individuals that both struggled and distress-called were recorded as '2'. No bird distress-called without struggling.

Assignment of parentage and calculation of natal dispersal distances
We colour banded 76 locally bred hihi from 2009/10 until the end of 2012. Two of these were excluded from this analysis: one male from 2009/10 who was not blood sampled, and a female caught in early 2012 of unknown age (see above).

All individuals were genotyped at 19 highly polymorphic autosomal microsatellite loci (see Brekke, Dawson, Horsburgh *et al.*, 2009 for extraction and amplification details). To reduce genotyping errors (null or false alleles, allelic dropout and stutter), samples were amplified twice, or, if not consistent, these were amplified until they were considered consistent, or were excluded. Genotyping errors were estimated using Microchecker 2.2.3 (Van Oosterhout, Hutchinson, Wills *et al.*, 2004). We then attempted to assign parentage to 74 birds using the maximum-likelihood software Colony 2.0 (Wang and Santure, 2009). Both sexes were defined as polygamous, and allele frequencies and genotyping error rates were provided. In 2009/10, parent

candidate lists included all translocated individuals from 2009; in 2010/11 all translocated individuals from 2009 and 2010, and locally-bred birds from 2009/10; and in 2011/12 all translocated individuals from 2009, 2010 and 2011, and locally-bred birds from 2009/10 and 2010/11. The probability of the true parents being in the candidate lists was set at 0.99 for individuals from 2009/10, and 0.75-0.8 for 2010/11 and 2011/12. The lower probability in later years reflected our knowledge that unsampled (unbanded) resident putative parents were in the population during these seasons.

We were able to assign maternity to 64 of the 74 offspring analysed (from 19 individual mothers, 16 of known territory location), and paternity to 69 (from 30 individual fathers), with > 95% confidence. Where we could not assign parentage, this was likely attributable to parentage by unbanded birds in the population. In 2010/11, we could not assign maternity to eight offspring, and Colony output suggested these offspring were from four individual females from the 2009/10 cohort (prior to the start of intensive banding efforts) that had not been genotyped and therefore were not in our candidate list. In 2011/12, we could not assign maternity to two individuals, both of which were captured in an area where two unbanded adult females were known to be present.

Of the 64 offspring for which it was possible to assign maternity, 39 were recruited into the breeding population, and then located at their first breeding territory. Natal dispersal distances were calculated by measuring the distance from the natal site (inferred by the breeding location of the bird's mother) to the first breeding site of each individual.

Data analysis

We fitted generalised linear mixed models with an exponential distribution and log-link function in WinBUGS 1.4 (Lunn, Thomas, Best *et al.*, 2000) to examine the effect of covariates on natal dispersal distances. We began by running a constant model, and then introduced sex as a fixed effect, and a random effect of mother. We then considered fixed effects of cohort and handling score one at a time, and tested for interactions with sex. For each model we obtained 100,000 samples after a burn-in of 10,000 samples. Where there were missing values, we imputed them by sampling from either a normal or Poisson distribution as appropriate (Nakagawa and Freckleton, 2008). Alternative models were compared using DIC (Deviance Information Criteria; Spiegelhalter, Best, Carlin *et al.*, 2002). As models imputing missing values from a Poisson distribution could not generate DIC values, we also divided the mean dispersal distance estimated under the highest covariate score by the mean dispersal distance estimated under the lowest covariate score to generate comparable effect sizes between models.

Results

We found variation in natal dispersal patterns between individuals that differed by sex and temperament. Mean NDD was 1749 m for male hihi (range 0-5170 m) and 876 m for female hihi (range 0-3425 m) (Figs 2, 3), and including sex as a covariate lowered DIC in comparison to the constant model (ΔDIC=0.21; Table 3). There was a significant interaction between sex and handling score, with the generalised linear mixed model estimating a mean NDD of 3472 m for males that distress-called in the hand, 1912 m for those that struggled in the hand but did not distress-call, and 1141 m for those that neither struggled or distress-called (Table 3; Fig. 4).

Handling score did not influence female NDD, and there was no significant effect of cohort on NDD (Table 3).

Discussion

We found a relationship between temperament and male NDD, in an establishing reintroduced hihi population. Birds that distress-call during handling have been shown to be at the proactive end of the personality spectrum in a study of another species (Pascual and Senar, 2014), and this behaviour has been shown to be highly consistent and heritable in another (Koenig, Stanback, Hooge *et al.*, 1991). Here, we find male distress-callers to be those with greater NDD in a low density reintroduced population.

This result provides some support to studies that have shown a link between personality and natal dispersal patterns (Cote and Clobert, 2007, Cote et al., 2010, Dingemanse et al., 2003, Duckworth and Badyaev, 2007), with proactive individuals having greater dispersal tendencies. Duckworth and Badyaev (2007) found more aggressive male western bluebirds (*Sialia mexicana*) had greater dispersal propensity than their less aggressive counterparts, and therefore tended to be the individuals colonising new habitat and leading the range expansion of this species in North America. Our finding with hihi provides preliminary evidence that a similar mechanism may exist in reintroduced populations, with population expansion being facilitated by individuals of a particular temperament.

Natal dispersal in an establishing hihi population

There was considerable variation between individuals of both sexes, with a small number of both males and females remaining at their natal site, and the maximum dispersal distance 5.2 km. Natal dispersal patterns of hihi at Maungatautari bear both similarities and differences to natal dispersal patterns in Tiritiri Matangi as previously investigated. Unsurprisingly, mean NDD was higher at Maungatautari than at the much smaller Tiritiri Matangi. Given that Maungatautari is constrained by the forest boundary and the greatest possible distance from known natal sites was ~6 km, it is likely that maximum NDD would be higher in unconstrained habitat. Sex-specific differences were apparent at Maungatautari in the first three years of population establishment, with males having higher mean NDD than females. On Tiritiri Matangi, this was also the case for the first two years, but as population density increased female NDD also increased, and male NDD decreased.

Implications for reintroduction success

Our result suggests that the spatial expansion of reintroduced populations may be facilitated by specific personality or temperament types, in a similar manner to colonisation patterns in species extending their range, or invading new environments (Chapple et al., 2012, Duckworth and Badyaev, 2007, Fogarty, Cote and Sih, 2011). In reintroduced populations, this variation could have both positive and negative consequences for reintroduction success both in terms of initial establishment and long-term persistence. These consequences will be largely dependent on the outcomes for dispersers in the wider landscape. Where dispersers have high mortality (or become geographically lost to the population) this will lead to immediate behavioural selection and therefore reduced phenotypic diversity in the founding population. This can occur both through natal and post-release dispersal behaviour. Another aspect of our study examined the effects of

temperament on immediate post-release dispersal and exploration in the first few weeks after translocation, and found a similar effect to what we report here for natal dispersal (male distress-callers dispersing further in the first week post-release, and distress-callers of both sexes exhibiting greater exploratory movements in the first four weeks post-release; KM Richardson, JG Ewen, LK Walker, P Brekke, KA Parker, IC Castro, DP Armstrong, unpubl. data). Hence, it appears that there are multiple mechanisms by which individual variation in dispersal propensity can reduce phenotypic diversity in reintroduced populations across multiple phases.

In our study, the release area is surrounded by non-forested habitat, thereby restricting opportunities for dispersal outside of the protected area – therefore even those individuals that dispersed the farthest still recruited into the population eventually. In contrast, at a release area where dispersal is not restricted, individuals with higher NDD are likely to have lower recruitment probabilities. For example, an earlier hihi reintroduction attempt to a protected forest reserve (1300 ha) was located within a larger area of continuous forest (13,000 ha) (Richardson, Castro, Brunton et al., 2015), where the greatest possible dispersal distance was >20 km, but only ~4 km within the protected area. At that site, assuming similar NDD to Maungatautari, at least 10% of potential recruits, and probably more, would have dispersed outside of the reserve, where survival probabilities were likely significantly lower due to an absence of predator control.

However, behavioural variation in natal dispersal may have positive effects in reintroduced populations in the long-term. Reintroductions to large areas may result in fragmented clusters of individuals establishing that are geographically isolated from one another, with potential for this to lead to genetic bottlenecks and demographic issues. Long-distance natal dispersers can link

such clusters, creating metapopulations and enabling further spatial expansion of populations. The Maungatautari hihi population showed clusters establishing across the release area in the first three years after reintroduction, with the results of another study showing these clusters were maintained by conspecific attraction (Richardson and Ewen, 2016). Our findings here show that temperament-mediated natal dispersal of males enabled linkage of these clusters, by ensuring movement of individuals between them, and therefore providing potential for gene flow.

Ultimately, the influence of natal dispersal on reintroduction success will be determined by characteristics of the wider landscape, and whether dispersal of individuals away from the intended release area influences the probability of recruitment of such individuals. Careful consideration of potential release areas is therefore critical to reintroduction planning (see Richardson, Doerr, Ebrahimi *et al.*, 2015 for a more detailed discussion of this issue). In addition, understanding the relationship between temperament and other life history traits such as survival and reproductive success may also be significant (we were not able to examine this with our data).

Overall, we suggest our findings highlight the importance of maintaining a wide range of phenotypic diversity in new populations, to facilitate the occurrence of the full spectrum of possible behaviours - both for dispersal, as well as other important behaviours. As with the invasion process, the reintroduction process can act as a "selective filter" (Carere and Gherardi, 2013, Chapple et al., 2012) for behavioural types, and an awareness of this can enhance selection of appropriate release sites and strategies during reintroduction planning. A high diversity of

behavioural types is linked to population persistence and stability (Wolf and Weissing, 2012), and in invading populations this diversity is predicted to increase the probability of species establishment (Fogarty et al., 2011). We suggest this would also be the case in reintroduced populations, and that diversity in natal dispersal behaviour is one mechanism that can contribute to reintroduction success.

Acknowledgements

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Table 1. Hihi released at Maungatautari, 2009-2011

Year (Source)	Adults	Juvenile males	Juvenile females	Total
2009 (Tiritiri Matangi Island)	0	31	28	59
2009 (Te Hauturu o Toi/Little Barrier Island)	9	7	4	20
2010 (Tiritiri Matangi Island)	0	18	19	37
2011 (Tiritiri Matangi Island)	0	20	19	39

Table 2. Number of hihi banded, maternity assigned, and available natal dispersal distance (NDD) data, by cohort at Maungatautari.

	Males			Females			Total NDD
Cohort	Banded	Maternity assigned	NDD available	Banded	Maternity assigned	NDD available	
2009/10	10	10	8	2	2	2	10
2010/11	17	13	8	11	7	5	13
2011/12	18	18	8	16	14	8	16
Total	45	41	24	29	23	15	39

Table 3. Results from generalised linear mixed models assessing effects of individual covariates on natal dispersal distances of hihi at Maungatautari. Best model is in bold.

	pD[a]	DIC[b]	ΔDIC[c]	Effect size[d]
sex (re.m[e])	3.57	645.60	0	2.06
Constant	1.00	645.81	0.21	NA
sex (re.m) + cohort	4.49	647.30	1.70	1.27
sex (re.m) + cohort + cohort*sex	5.51	649.27	3.67	1.25 (females) 1.07 (males)
sex (re.m) + HS[f]	NA	NA	NA	2.7
sex (re.m) + HS + HS*sex	**NA**	**NA**	**NA**	**1.2 (females) 1.77 (males)**

[a] pD = Effective number of parameters (mean of posterior deviance minus mean of posterior distribution.

[b] DIC = Deviance information criterion, where lower DIC means higher predictive value.

[c] ΔDIC = Difference in DIC from that of best model.

[d] Effect size = Mean dispersal distance estimated under highest covariate score divided by mean dispersal distance estimated under lowest covariate score.

[e] re.m = Random effect of mother.

[f] HS = Handling score/behaviour in the hand at time of capture.

Fig. 1. Map of Maungatautari Ecological Island (release area) showing monitoring lines with 80 m buffer either side, and release site for translocation of hihi between 2009 and 2011. Hihi were detectable at least 80 m from a monitoring line; hence grey areas show areas well covered during searches (approx. 85% of the release area).

Fig. 2. Natal dispersal distances of hihi at Maungatautari from 2009/10 (first breeding season after translocation) to 2011/12 (third breeding season after translocation).

Fig. 3. Map showing natal dispersal patterns at Maungatautari for juvenile a) males and b) females from 2009/10 to 2011/12 (first three breeding seasons after translocation).

Fig. 4. Mean natal dispersal distances estimated from generalised linear mixed model for male and female hihi with handling scores of 0) quiet, no struggle, 1) quiet, struggled, and 2) distress-called and struggled.
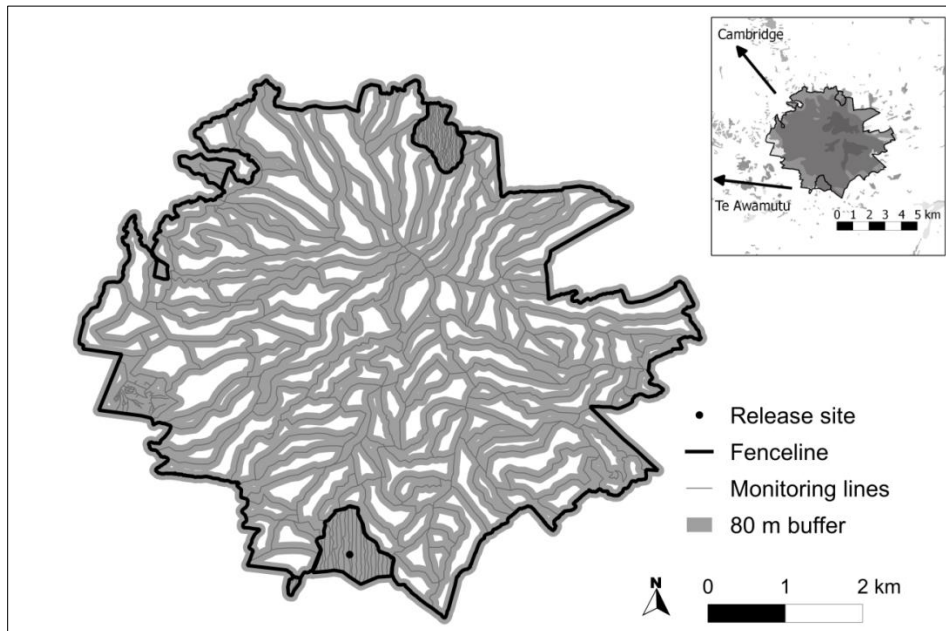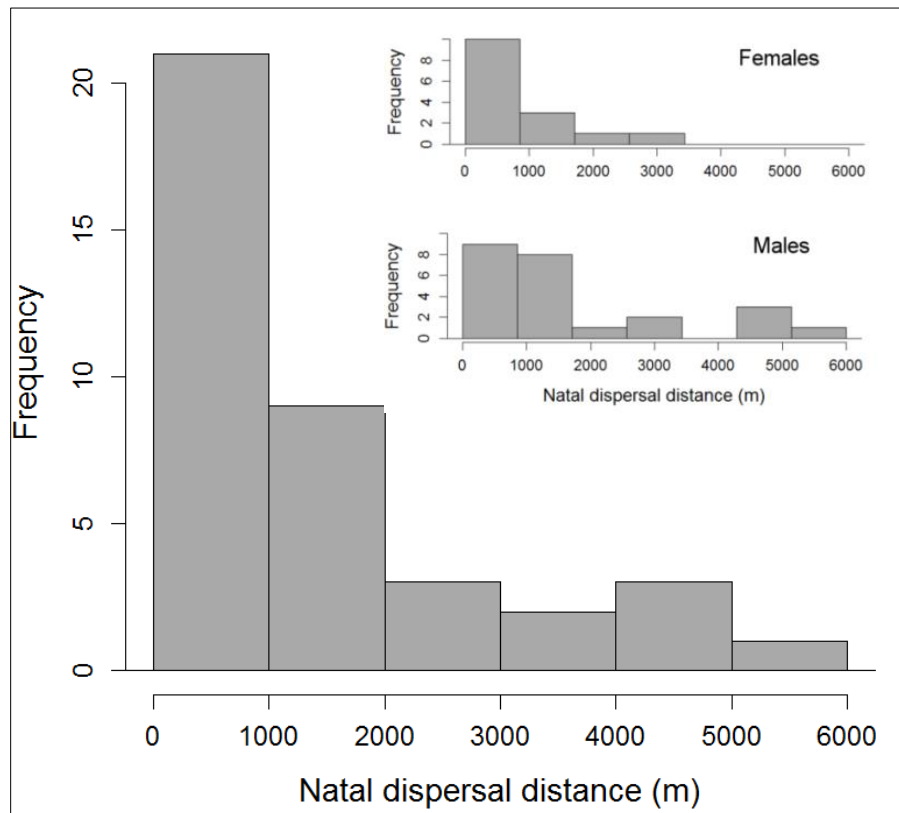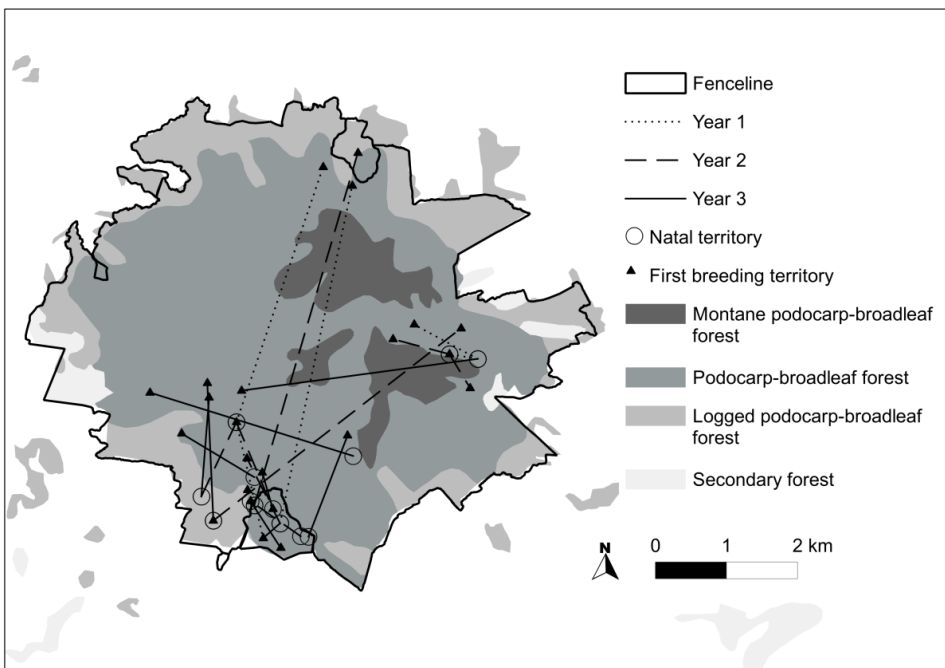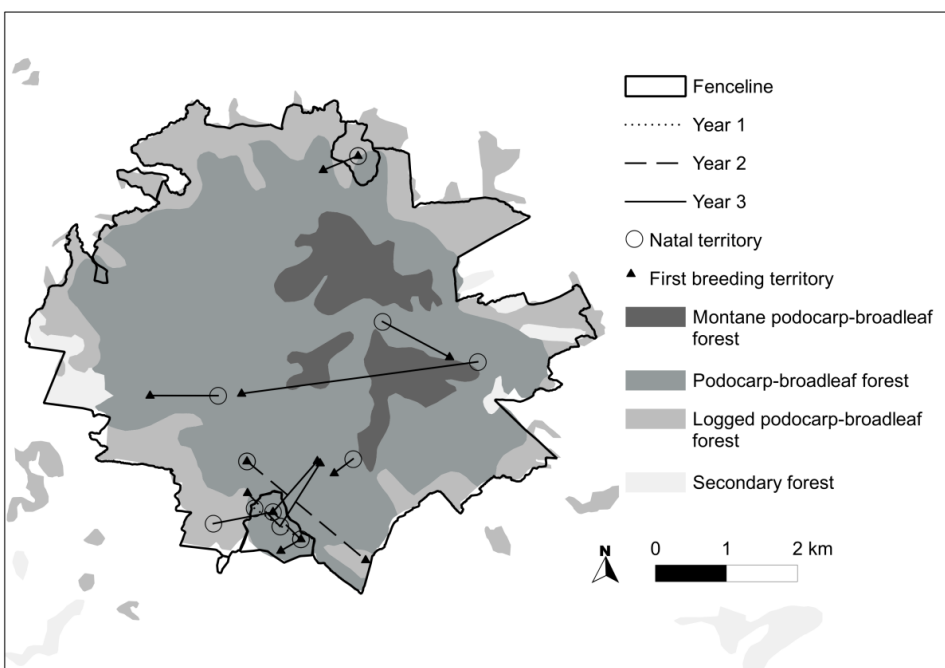
Fig. 1

Fig. 2

Fig. 3

a)

b)

Fig. 4