Habitat selection in a reintroduced population: social effects differ between natal and post-release dispersal

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Abstract

Understanding the factors driving dispersal behaviour and habitat selection in reintroduced populations can be critical to reintroduction success. Social factors in particular can influence habitat selection, for example through conspecific attraction, and this can have both positive and negative effects on reintroduction success, particularly where multiple releases occur. In addition, little is known about how habitat selection differs between natal and post-release dispersal within species. Often it is assumed that information from a species’ natal dispersal preferences and patterns can act as a guide for predicting post-release dispersal behaviour, but no studies to date have examined this. We examine the factors influencing habitat selection during both natal and post-release dispersal in a reintroduced hihi (stitchbird, Notiomystis cincta) population using species distribution models. We demonstrate a strong social effect in habitat selection of natal dispersers bred at the release area (largely the offspring of founders), yet find no social effect in habitat selection of juveniles translocated 2 years after the first releases occurred. In addition, we establish that environmental variables are important in habitat selection in both groups. We suggest (1) that consideration of social effects and conspecific attraction should play a role in planning reintroduction release strategies, especially if reinforcement releases are considered necessary, and (2) that it may not always be appropriate to assume post-release dispersal in reintroduced populations will be driven by the same factors that influence natal dispersal.

Introduction

The importance of understanding dispersal behaviour in reintroduction biology is well recognized (reviewed in Le Gouar, Mihoub & Sarrazin, 2012). Habitat selection is an important component of dispersal, with dispersing individuals expected to respond to features of the habitat and demonstrate active selection of certain areas over others (Matthysen, 2012). Definitions of what comprises ‘habitat’ have varied widely in the literature (Hall, Krausman & Morrison, 1997; Armstrong & Seddon, 2008), with some authors limiting habitat to the physical characteristics of the environment (e.g. Jones, 2001), and others including biological factors such as interspecific and intra-specific competition, and interactions with predators and parasites. Here, we use the latter, and consider habitat as defined by Osborne & Seddon (2012): ‘a species-specific complex of interacting physical and biotic components, including other species’.

Social factors can be an important influence on post-release habitat selection behaviour and dispersal, and can inform on decisions around release methodology, particularly with regard to multiple releases. The presence of conspecifics can act as a cue for habitat quality, providing a guide to enable dispersers to select optimal habitat (Serrano et al., 2003; Parejo et al., 2007; Martin et al., 2008; Harrison, Green & Krannitz, 2009). Conspecific attraction can lead to negative density-dependent relationships to dispersal propensity (Matthysen, 2012), and can limit expansion of reintroduced populations, or result in clusters of individuals. In cases where residents are present in sub-optimal habitat, conspecific attraction can act as an ecological trap to translocated individuals and prevent expansion into more optimal habitat (Mihoub, Le Gouar & Sarrazin, 2009). In meta-populations, conspecific attraction can increase the probability that empty, but otherwise suitable, patches will not become occupied (Muller et al., 1997; Mihoub et al., 2011). Conversely, conspecific repulsion can increase dispersal of newly reintroduced individuals, resulting in geographical isolation from the intended release area (e.g. Dunham, 2000).

It is important to carefully consider the objectives behind multiple releases (or reinforcements) to ensure the potential effects of conspecific attraction or repulsion are considered at the planning stage. For example, many reintroductions are undertaken as a series of releases over time – often because of logistical constraints in releasing the appropriate number of individuals simultaneously, because of limiting factors in
the numbers available for reintroduction, or because of concerns over impacts of harvesting from source populations (Griffith et al., 1989; Armstrong & Seddon, 2008; Tracy et al., 2011). Frequently, it is assumed that survival and dispersal probabilities will remain constant between releases. However, evidence to date suggests that this is not always the case (Suin, Pitaqano & Moe, 2009; Le Gouar et al., 2012), and quantifying the changes in these probabilities between subsequent releases can have important ramifications for planning of release strategies. Additionally, reinforcements can sometimes occur for purposes other than bolstering numbers, such as attempting to introduce new genetic material to the population (Tracy et al., 2011; Weiser, Grueber & Jamieson, 2013; Weeks et al., 2015). Successful integration of these later released individuals into the population can be undermined by density-dependent (Armstrong & Jamieson, 2013; Weeks et al., 2015) or other behavioural (Mihoub et al., 2009, 2011; Parker et al., 2012) barriers due to the presence of conspecífics.

Here, we examine the habitat selection behaviour of dispersing juvenile hihi Notiomystis cincta, during the initial years after release of an establishing population in a large reserve free of introduced mammalian predators. Reintroduction is the primary conservation action used in hihi recovery, yet we remain uncertain about habitat requirements and preferences of hihi, basing our knowledge predominantly on habitat comparisons to the one remnant island population (Ewen et al., 2013). Generally speaking, some increasing level of habitat complexity (particularly vegetation structure and diversity) is linked with improved site suitability (Makan et al., 2014), hence recent reintroductions have looked to the mainland where such habitat is more commonly found. In contrast to islands targeted for early hihi reintroductions, mainland attempts are vulnerable to individuals dispersing from the release site, and the first mainland reintroduction of hihi to a large, mature forest site failed at least partially for this reason (Richardson, 2009). We have little information about the role of conspecífic attraction in hihi, either in dispersing juveniles as populations establish or after release during reinforcement translocations. Reinforcement translocations are frequently undertaken with hihi, hence understanding the effect of already established conspecífics is of importance to assess the effectiveness of these translocation strategies.

In this study, we first examine which, if any, physical characteristics of the environment can predict preferred habitat for juvenile hihi at our mature forest release area, and second, compare the additional effects of conspecífic presence on habitat selection of resident juveniles (those bred at the release area by founder individuals; hereafter ‘natal dispersers’) and the juveniles released in reinforcement translocations (hereafter ‘post-release dispersers’).

**Materials and 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 et al., 2013). Reduced to a sole island population by the 1880s (Hauturu/Little Barrier Island), hihi currently 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 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 et al., 2012) and artificial nest boxes (all reintroduced populations except Kapiti and Maungatautari). Hihi are typically socially monogamous, but have high frequencies of extra-pair paternity (Castro et al., 1996; Ewen, Armstrong & Lambert, 1999; Brekke et al., 2013), and breed from September to March each year. The majority of individuals breed at 1 year of age, and show strong breeding site fidelity between breeding seasons. Natal dispersal distances vary between populations, with a mean of 455 m (Richardson et al., 2010) on Tiritiri Matangi Island (220 ha), cf. 1.3 km at Maungatautari Ecological Island (~3400 ha) (Richardson, 2015).

**Study site**

Maungatautari Ecological Island (henceforth ‘Maungatautari’, Fig. 1) is a reserve in the Waikato region of New Zealand’s North Island (38°03′08″S 175°33′58″E). Maungatautari is a volcanic cone (797 m) covered primarily in mixed podocarp/broadleaf forest, largely surrounded by pasture, creating a ‘mainland island’ effect (McQueen 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 now been reintroduced (Smuts-Kennedy & Parker, 2013), of which seven are listed as endangered or vulnerable on the IUCN Red List.

**Hihi reintroductions to Maungatautari, 2009–2011**

A total of 155 hihi were released at Maungatautari between 2009 and 2011 (Table 1), all of which were colour banded and genotyped prior to translocation. In 2009, the released birds consisted of 59 juveniles from Tiritiri Matangi Island and 20 (a mix of adults and juveniles) from Hauturu/Little Barrier Island (Ewen et al., 2011). A mark-recapture survey in early 2010, in combination with later field research, suggested 26–41 (33-52%) of these survived to the first breeding season (October 2009, 7 months post-release) (Ewen et al., 2011; Richardson, 2015).

Two further releases of juvenile hihi occurred from Tiritiri Matangi Island in 2010 (37 birds) and 2011 (39 birds). Subsequent monitoring indicated a minimum of 17 from the 2010 translocation survived to their first breeding season (46%), and a minimum of 15 from the 2011 translocation (38%). By the 2011/2012 breeding season, c. 71 adult hihi were present at the site, comprising a mix of the original
translocated hihi (38) and locally bred birds (33) (Richardson, 2015). Six supplementary feeders are provided, all within 150 m of the release site, and these are utilized by some, but not all, of the birds present.

**Post-release monitoring and location of breeding territories**

The majority of locally bred recruits between 2009/2010 and 2011/2012 were captured by a combination of mist netting (49 birds) and catching at supplementary feeder stations (27 birds). All were colour banded as well as being genotyped to assign parentage (Richardson, 2015).

To answer our first question, testing whether physical characteristics could be used to predict preferred breeding habitat, we used data for all active hihi breeding territory locations between 2010/2011 and 2012/2013. Breeding sites were located by comprehensive searches of the reserve using the existing monitoring line network (Fig. 1c) established for detecting invasive mammal presence, as well as following up reported hihi sightings from invasive mammal monitoring staff and local volunteers. These monitoring lines are distributed evenly across the reserve and designed to be no more than 200 m apart, although there are some larger gaps. We therefore consider that the reserve was searched evenly across habitat types.

Monitoring was carried out from October 2010 to February 2011 (one full-time field worker and additional volunteers), September 2011 to March 2012 (two full-time field workers and additional volunteers) and September to December 2012 (two full-time field workers and additional volunteers). The majority of territories were located in late September through to mid-November when male hihi are most vocal and female hihi 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 in the same location during the breeding season, and female hihi 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. 1c). Therefore, in 2011/2012 and 2012/2013...
2013 these areas were searched, but no resident hihi were found. This methodology resulted in active breeding sites being identified in 34 different locations, some of which were utilized over multiple seasons and others only once.

For our second question, determining if there is a social effect in habitat selection behaviour during natal and post-release dispersal, we used data from the 2011/2012 season only, specifically looking at differences in breeding territory selection between natal dispersers bred at the site in 2010/2011, and post-release dispersers that had been translocated that year (April 2011). Thirty-four natal dispersers were known to be present at the beginning of the breeding season (October 2011), and 25 of these were identified at a territory during the season (Table 2; Fig. 1c). The remaining nine individuals were either floater males that remained unpaired (Brekke et al., 2015) or never identified at a territory. Of the 25 identified at a territory, 15 were natal dispersers from the 2010/2011 cohort and 10 were post-release dispersers recently translocated to the reserve in April 2011. In addition to these first year birds, a further 29 adults in their second or third season were identified at 19 territories that had also been occupied the previous season. The locations of these 19 territories were used to calculate distance to conspecific territory for use in the modelling below (Fig. S1f).

**Species distribution modelling**

We applied species distribution modelling (SDM) methods (Guisan & Thuiller, 2005) to examine the effect of both environmental and social factors on breeding location selection for reintroduced hihi at Maungatautari. We used maximum entropy models (MaxEnt, see Phillips, Anderson & Schapire, 2006; Merow, Smith & Silander, 2013) as our data were presence-only, and it is possible that some areas explored did contain breeding hihi that were not identified, although we believe this number to be very low (<5 per season, based on sightings of birds at supplementary feeders and subsequent genotyping of juveniles; Richardson, 2015). All analyses were carried out using the ‘dismo’ package in R v. 3.01 (R Development Core Team, 2013). We built four different models (referred to as m1–m4 in the text, Table 3), and for each model, used 10 000 randomly selected background points (Barbet-Massin et al., 2012), set aside 20% of the sample as test data, and used the remainder as training data for the model. Model predictive performance was assessed using the ‘evaluate’ function in the dismo package, including area under curve (AUC), kappa scores, omission rates, and sensitivity and specificity thresholds. AUC was >0.7 for all models, and >0.8 for all models other than m4.

To investigate whether physical characteristics could be used to predict breeding location, we treated the 34 territory locations found during the study period (2010/2011–2012/2013) as our presence data, and first used the following environmental variables as possible predictors (m1; see Table 3): vegetation class (four classes: podocarp–broadleaf forest, montane podocarp–broadleaf forest, logged podocarp–broadleaf forest and secondary forest), aspect (0–359°), primary productivity [PP, using mean Normalized Difference Vegetation Index values derived from Landsat 7 and 8 data across the site during the study period] (Pettorelli et al., 2005) and distance to nearest stream (metres) (Fig. S1a–d). We did not include altitude as there was strong collinearity between this variable and vegetation class. We then re-ran the same analysis but this time included distance to release site/supplementary feeders (Fig. S1e) as an additional environmental variable (m2), as we suspected that both of these factors could influence breeding site selection. As the supplementary feeders are within close proximity of the release site, it was not possible to distinguish between the effects of release site versus effect of supplementary feeder location.

To investigate the effect of conspecific presence in breeding site selection for natal and post-release dispersers, we used the same environmental variables as in the first analyses (including distance to release site), but included an additional social variable, distance to conspecific territory (Fig. S1f, as described above). We generated two models, one using the first breeding location of natal dispersers as presence data

| Model | Presence data (n) | Environmental variables | Social variables |
|-------|------------------|-------------------------|-----------------|
| m1    | All hii breeding territory locations 2010/2011–2012/2013 (34) | Vegetation class, aspect, primary productivity | None |
| m2    | All hii breeding territory locations 2010/2011–2012/2013 (34) | Vegetation class, aspect, primary productivity | None |
| m3    | Natal dispersers (2010/2011 cohort) – first breeding territories 2011/2012 (15) | Vegetation class, aspect, primary productivity | Distance to conspecific territory (based on 19 territory locations) |
| m4    | Post-release dispersers (2011 release) – first breeding territories 2011/2012 (10) | Vegetation class, aspect, primary productivity | Distance to conspecific territory (based on 19 territory locations) |

Table 2 Known territorial hihi present at Maungatautari at the start of 2011/2012 breeding season (October 2011), by age and sex, and resident/release status

| Age | Male | Female | Total |
|-----|------|--------|-------|
| Resident adults ≥ 1 | 16 | 13 | 29 |
| First year resident, bred at site in 2010/2011 season (natal dispersers) | 7 | 8 | 15 |
| First year, translocated to site in April 2011 (post-release dispersers) | 5 | 5 | 10 |
(natal dispersers, m3), and the other using the location of post-release dispersers translocated to the site that year (post-release dispersers, m4) to enable a comparison between breeding site selection in natal and post-release dispersers.

**Results**

**Physical characteristics as predictors of preferred habitat**

In the first few years following release, hihi have primarily selected breeding territories within 150 m of a stream (Figs 2a, 3a), and closer to the release site/supplementary feeders than expected by chance (most within 3 km) (Figs 2b, 3b). There was also a slight tendency for hihi to select podocarp–broadleaf forest over montane and logged podocarp–broadleaf forest and secondary forest; however, these factors contributed relatively little under either model in comparison to distance to stream (Fig. 2a, b). There was also a slight tendency for hihi to select podocarp–broadleaf forest over montane and logged podocarp–broadleaf forest and secondary forest; however, these factors contributed relatively little under either model in comparison to distance to stream (Fig. 2a, b). Aspect did not influence territory selection in either model. PP appeared to have a weak influence under m1 (with lower PP being preferred habitat), but this effect disappeared when distance to release site was also included (Fig. 2a, b).

**Comparison between natal and post-release dispersal**

Natal dispersers appeared most strongly driven by social factors, with proximity to a conspecific territory being the most influential factor of those tested. The majority of natal dispersers settled within 500 m of an established conspecific territory. Distance to stream and distance to release site were less influential factors but still important, and aspect, vegetation class and PP had no influence. The predictive map generated from the maximum entropy model (Fig. 3c) clearly demonstrates the stronger social effect in territory selection for natal dispersers.

The model does not suggest an effect of conspecific presence in territory selection for post-release dispersers, although this is the weaker of the SDM models built, and from the lowest sample size. Distance to streams appears to be the only environmental variable we could show influencing territory selection in this group, but less strongly than previously with the majority within 500 m rather than 150 m (Figs 2d, 3d). Interestingly, there was no detectable effect of distance to release site/supplementary feeders for post-release dispersers, despite it being one of the most significant influences overall for all birds at the reserve (Fig. 2b).

**Discussion**

There were striking differences between the patterns of territory establishment in natal and post-release dispersal that may have implications for the establishment of reintroduced populations. We found a strong effect of conspecific attraction in the breeding territory selection of natal dispersers, but no detectable effect of conspecific attraction was detected in recently translocated individuals. In addition, we have identified environmental variables that play a role in breeding territory selection in hihi in mature forest habitat.

**Habitat selection in hihi**

Our results provide the first assessment of hihi habitat preferences in a reintroduced population, and suggest that habitat selection is non-random. Proximity to a stream is the pri-

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**Figure 2** Percentage variable contribution from maximum entropy species distribution models examining habitat preference in hihi at Maungatutari. Percentage variable contribution of environmental characteristics, (a) not including distance to release site (m1) (n = 34) and (b) including distance to release site (m2) (n = 34). Percentage variable contribution of environmental and social characteristics, (c) natal dispersers (m3) (n = 15) and (d) post-release dispersers (m4) (n = 10).
mary environmental variable predicting breeding territory occurrence. A strong effect of either distance to release site or to the established supplementary feeders is evident, but the results suggest this may only be important in the early stages of population establishment as it was not a significant factor for natal dispersers, or for the post-release dispersers from the third release, although the latter may have been confounded by the presence of established residents close to the release site and supplementary feeders. Both vegetation class and PP had a weak effect, and incorporating additional data into the model as the population grows may help determine if this is a real effect, or an artefact of small sample size.

Our data do not enable us to ascertain the exact mechanisms linking hihi preference to stream proximity. However, this result aligns with our observations during field work at this site. At Maungatautari, the majority of hihi nests were located in pukatea *Laurelia novae-zelandiae*, an endemic slow-growing tree which often has multiple natural cavities and typically occurs in swampy areas or in close proximity to streambeds. However, potentially suitable cavities also occurred in other tree species that are found away from streambeds, and further investigation would be needed to determine if stream proximity is linked to availability of suitable nest cavities, or other factors such as vegetation complexity or food availability.

**Habitat selection in natal versus post-release dispersers**

We demonstrated a clear difference in habitat selection patterns between natal and post-release dispersers, suggesting that making inferences about post-release dispersal behaviour from natal dispersal data may not always provide reliable information. We found that natal dispersers were strongly influenced by presence of conspecifics in selection of breeding territories. Natal dispersal data for another aspect of this project strongly indicates this conspecific attraction is not explained by natal philopatry (K.M. Richardson, J.G. Ewen, P. Brekke, L. Doerr, K.A. Parker, D.P. Armstrong, unpublished data), hence we believe it reflects active selection by natal dispersers. We found neither a positive nor negative effect of distance to conspecifics on territory selection by post-release dispersers, so there was no suggestion that recently translocated birds were actively avoiding resident conspecifics, or were driven away by aggressive encounters.

Using species distribution modelling in monitoring reintroduced populations

Investigating how, or if, these habitat preferences change at our study site as population densities increase will enhance our understanding of hihi habitat preference and patterns of density dependence. In particular this has relevance for predicting the carrying capacity of release areas and estimating population size. Predicted habitat with higher than 50% probability of occurrence (based on the map in Fig. 3a) covered an area of 663 ha, about a fifth of the total available forest habitat at the reserve. Frequently, population estimates assume an equal density of individuals across an area, but this may only rarely be a true assumption. Ongoing monitoring of the Maungatautari population will determine if hihi restrict themselves to the predicted habitat, or if habitat

![Figure 3 Predictive maps from maximum entropy species distribution models predicting preferred breeding habitat for hihi at Maungatautari.](image-url)
selection patterns change as the density increases, and this could provide information to assist in developing a stratified sampling monitoring design.

Species distribution modelling has the potential to assist in monitoring reintroduced populations (Hirzel et al., 2004; Mihoub et al., 2014), particularly at release areas where there are constraints in both the resources available and what is logistically practical. Refining, and testing, predictions about species habitat preferences could provide a guide to where best to focus effort on monitoring new and existing populations, and assist in generating population estimates where densities are known to vary spatially.

**Implications for reintroduction strategy**

Our results highlight the importance of understanding the role that habitat selection can play in establishing reintroduced populations, in particular the effect of conspecific attraction or repulsion. We emphasise the need to consider this from the outset in reintroduction planning, in particular where it is anticipated multiple releases may be required. It should not be assumed that individuals from subsequent releases will behave in a similar manner to those released first in the absence of conspecifics. In our low-density study population, it was hoped that resident birds would act as an anchor for new releases, hence increasing the probability of integration into the population and preventing individual birds from becoming isolated within a large area and remaining unpaired, as was observed with some individuals from the first two releases. Instead, our results suggest that while clustering of the resident population is apparent, integration of subsequently translocated birds with residents is less likely, at least initially.

The wider implications for reintroduction strategy will largely be dependent on the context in which subsequent releases occur. Where reinforcements occur primarily to boost numbers, integration of new individuals into a population may not be immediately critical, and higher rates of dispersal may aid spatial expansion of the population. However, in sites with high connectivity, or adjacent to unmanaged areas, later releases may be less successful if individuals are less likely to settle near conspecifics and form pairs, or more likely to disperse into unprotected areas thereby reducing probability of survival. Where the objective for reinforcements is to boost genetic variability, integration of new individuals into the breeding population is key, and a lack of conspecific attraction in post-release dispersal may undermine the success of such translocation attempts unless integration can be achieved in later generations.

As outlined by Mihoub et al. (2009), conspecific attraction has the potential to have both positive and negative effects on the establishment probabilities of a reintroduced population. Conspecific attraction is likely to lead to clusters of individuals in some areas, and if sub-optimal habitat was selected by the original individuals, this may lead to an ecological trap whereby the majority of the population resides in less optimal habitat. At our site, the effect on population growth is partially dependent on whether sub-optimal habitat was originally selected by hihi from the first release. Our results suggest that hihi are using some environmental indices to select habitat, which indicates non-random selection is occurring to some degree, but it is not possible to determine if the habitat selected is optimal based on available data.

**Conclusions**

Overall, our results support the predictions made by Mihoub et al. (2009) that conspecific effects on habitat selection can have unexpected consequences on the establishment of reintroduced populations, and we suggest that differential habitat selection between releases may be an additional behavioural factor that can influence the success of reinforcement translocations. We recommend consideration of these factors during the earliest stages of reintroduction planning.

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**Supporting information**

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

**Figure S1.** Environmental variables used in species distribution models with maps demonstrating variation across the release area, Maungatautari Ecological Island, for each variable.