

Habitat selection in reintroduced bird populations: a case study of Stewart Island robins and South Island saddlebacks on Ulva Island

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Abstract: An understanding of the mechanisms influencing habitat selection in reintroduced bird populations is fundamental for successful translocation programmes. Plant species composition, abundance, structure and food availability are likely to influence animal movement and habitat choice, but few studies have evaluated their combined effect on habitat selection of translocated birds. Stewart Island robins (*Petroica australis rakiura*) and South Island saddlebacks (*Philesturnus carunculatus carunculatus*) are two threatened New Zealand bird species that have been reintroduced to Ulva Island (Stewart Island). We hypothesised that their initial settlement patterns were driven by habitat quality. We tested this hypothesis by comparing habitat components between occupied and unoccupied habitats as the population grew after initial translocation. We also modelled probabilities of site selection as a function of the composition and structure of vegetation, availability of food (invertebrate composition) and nesting resources (cavity type). Founding pairs of both species first established territories in coastal habitat in the western part of the island, which is characterised by structurally complex broadleaved vegetation. Birds also selected sites with a greater abundance and diversity of food resources. Thus in the early stages of population establishment robins and saddlebacks appear to select high quality habitat that offers enhanced cover and foraging opportunities.

Keywords: food availability, habitat selection, nest characteristics, territory establishment, vegetation structure

Introduction

For successful recovery of threatened species it is important to understand the processes influencing habitat selection, as the re-establishment of species in areas where they formerly occurred is often influenced by the suitability of habitats at proposed release sites (IUCN 1998; Wolf et al. 1998). Without high quality habitats that provide adequate food, water and suitable places to roost and nest, translocation programmes have a low chance of success, regardless of how many individuals are released or how well they are prepared beforehand (Griffith et al. 1989; Veitch 1995; Lindenmayer 1995; Lovegrove 1996). However, determining habitat requirements of endangered bird species can be difficult, as relict populations are often at the edge of their former natural range, and species might do better in habitats and with diets outside those currently utilised (Gray & Craig 1991; Veitch 1994; Armstrong & McLean 1995). Assessing how habitat characteristics affect reproduction is often intricate, and studies have instead focused on habitat preferences and resource availability (Manly et al. 2002). Identifying the mechanisms influencing animals' decisions to settle in a habitat is also difficult, as it normally requires experimental manipulation of the environment, which may not be appropriate or desirable for an endangered species. Translocation of species to a new or unoccupied island habitat can provide an ideal experimental framework for investigating patterns of habitat preferences in natural populations while limiting or controlling the confounding effects of competition from residents, predator pressure, and dispersal opportunities.

Traditionally habitat selection studies have focused on landscape characteristics, but recently there has been increasing attention given to a micro-scale approach (Bollman et al. 2005; Maguire 2006). Micro-scale habitat selection refers to the behavioural response of an animal to local variation in particular vegetative or environmental elements (foliage density or food items) that often results in an uneven use of the habitat, thus influencing individual survival or fitness. Quantifying prime habitat has generally involved measures of plant abundance or food availability (Manly et al. 2002), but few studies have attempted to quantify habitat as an interaction of plant

composition, abundance, structure and food availability. From a habitat selection viewpoint, these factors together could be expected to influence animal movement and choice.

Stewart Island robins (*Petroica australis rakiura*) and South Island saddlebacks (*Philesturnus carunculatus carunculatus*) are two threatened insectivorous forest passerines that have been reintroduced to many offshore islands throughout New Zealand. On Ulva Island (Stewart Island), both species settled around the periphery of the island, mainly in coastal scrub habitat, avoiding the mature podocarp forest that occupies the vast majority of island area (Hooson & Jamieson 2004; Steffens et al. 2005). There could be two explanations for this pattern. First, coastal scrub is prime, high quality habitat and is preferred by the newly released birds. Second, the mature forest is prime habitat, but is unfamiliar to the birds (i.e. not part of their recent evolutionary history) and they have been drawn toward more familiar but less suitable habitat.

This study uses the recent reintroduction of these two endemic forest birds to explore habitat selection in natural populations. To understand how habitat affects territorial site selection during the establishment phase of a reintroduction, we first assessed territory quality by assuming that the regions that were first colonised were preferred habitat, and investigated differences between these areas and those settled subsequently as the population grew. We specifically asked: (1) whether habitat components of territories that were established soon after translocation differ from those established later on; and (2) how habitat components differ between territorial and randomly chosen unused sites. More generally, the study aims to understand the relationship between habitat components and breeding area selection in forest passerines reintroduced to sites that were unoccupied by conspecifics.

Methods

Study site and species

Ulva Island (46°55.9' S, 168°07.7' E, Paterson Inlet, Stewart Island) has been free of introduced mammalian predators since 1996. It

is covered predominantly by dense podocarp forest of *Dacrydium cupressinum* (rimu), *Podocarpus hallii* (Hall's tōtara) and *Prumnopitys ferruginea* (miro), surrounded by a coastal forest containing the angiosperms *Metrosideros umbellata* (southern rātā), *Griselinia littoralis* (broadleaf), *Weinmannia racemosa* (kāmahi) and *Dicksonia squarrosa* (tree fern) (Fig. 1). A narrow fringe of coastal scrub consisting mainly of *Olearia colensoi* (leatherwood), *Brachyglottis rotundifolia* (muttonbird scrub) and *Dracophyllum longifolium* (inaka) borders the coastline.

New Zealand robins still exist on the mainland of New Zealand but have increasingly fragmented populations due to loss of habitat and predation by introduced mammals. The Stewart Island subspecies (*Petroica australis rakiura*) was once widespread among podocarp (Podocarpaceae) forest but is now confined to stunted mānuka forest (*Leptospermum scoparium*, Myrtaceae), where densities of rats and feral cats are low relative to other parts of Stewart Island (Greer 2000; Harper et al. 2005). Between September 2000 and December 2001, 25 Stewart Island robins were released on Ulva Island, of which 12 survived and started breeding in 2001 (I. Jamieson unpubl. data).

The South Island subspecies of saddleback (*Philesturnus carunculatus carunculatus*) became extinct from mainland podocarp forests and was confined to a single offshore island (Big South Cape, Stewart Island) (Fig. 1), where the birds inhabited dense, low-lying areas of coastal scrub consisting of *Olearia colensoi*, *Brachyglottis rotundifolia* and *Dracophyllum longifolium*, as well as small patches of coastal forest (*Metrosideros umbellata*, *Weinmannia racemosa* and *Leptospermum scoparium*) in more sheltered parts of the island (Hooson & Jamieson 2004). Saddlebacks from Big South Cape were subsequently transferred to nearby Big and Kaimahu islands, and from there to various other rat-free island sites off the coast of Stewart Island. As an inshore island, Ulva is less exposed than Big Island, and as a consequence its vegetation is more a mixture of

coastal vegetation and mature forest (Hooson & Jamieson 2003a). Thirty birds (28 adults and 2 yearlings) were transferred in 2000 from Big Island to Ulva, of which 17 survived to breed, including six pairs that established territories and produced offspring during the 2000–01 breeding season. A further five females formed pairs with five yearling males that were produced from the first breeding season, and established territories in the 2001–02 season (I. Jamieson unpubl. data). Robins build open-cup nests in tree forks or inside tree cavities (Higgins & Peter 2002). South Island saddlebacks nest mostly in tree cavities, but occasionally in cavities in banks or under upturned tree roots (Hooson & Jamieson 2003a, b). Although both species are insectivorous, robins mainly search for invertebrates in ground litter while saddlebacks primarily forage for insects on tree trunks and branches (Powlesland 1981; Pierre 2001).

Field sampling

Nest monitoring and mapping

Nesting success of the translocated populations of robins and saddlebacks on Ulva Island have been intensively monitored following the methods of Hooson & Jamieson (2003b) and Steffens et al. (2005), with all nestlings or fledglings being individually colour-ringed. Nest height, tree species, cavity orientation, and general habitat description were noted for most monitored nests (in total up to 111 robin nests and 131 saddleback nests). GPS coordinates of all nests were recorded with an estimated positional error (EPE) of no more than 10 m. Distance to nearest neighbour was estimated for each breeding pair, using the GPS location of the first nest established in a breeding season. The coastal topographic profile of Ulva Island was downloaded from the Oracle2 database, and converted into points of 5-m separation. Distances to nearest neighbour and to the coast were calculated using Hawthorne's analysis tools in ARCGIS 9.0.

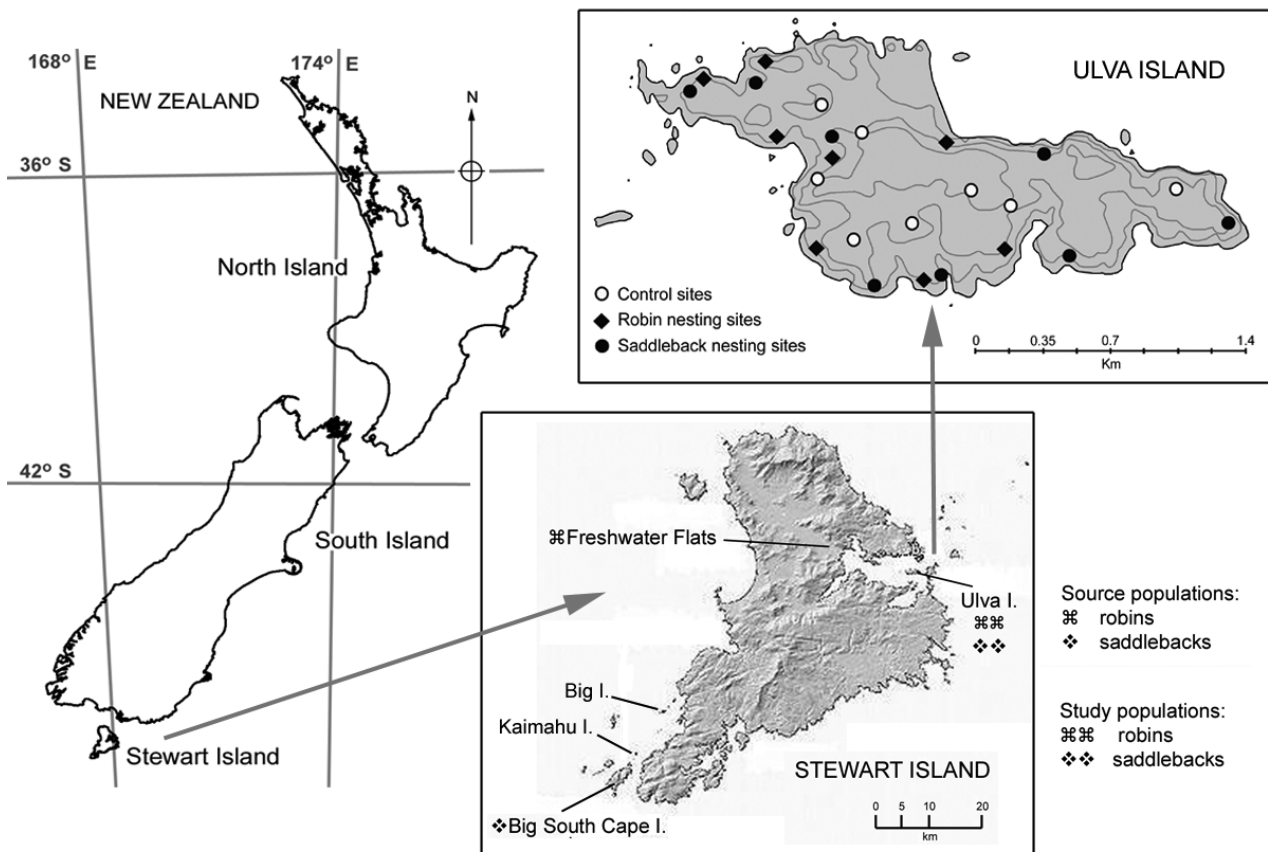


Figure 1. Maps of New Zealand, Stewart Island, and Ulva Island. Map of Stewart Island shows the source populations of Stewart Island robin and South Island saddleback reintroduced to Ulva Island, and the map of Ulva Island shows robin and saddleback nesting sites and unused control sites that were sampled during the study.

Vegetation sampling

In 2003, eight breeding territories for each species and eight control sites located in areas unused by birds were randomly selected across the island to be sampled for vegetation structure, nest characteristics and food availability (Fig. 1). Two foraging locations within robin and saddleback territories were determined by observing individuals (or pairs) feeding for more than 20 min in the same area during the pre-nesting period (October–November). For each observation, we recorded the location on the island, general habitat type, date and time of day, and bird–colour-ring combination. We identified plant species, size (diameter and height) and structure (leaf, branch or trunk) where foraging occurred, and estimated the height above ground.

During January and February 2003, vegetation composition and structure were sampled within four subplots (10 × 10 m) within a quadrat 20 × 20 m around a nest and at one foraging location for eight territories of each species, and at a centre point in eight unused sites, using the Recce method (Allen 1992). The percentage cover of individual plant species was recorded in classes (1: <1%, 2: 1–5%, 3: 6–25%, 4: 26–50%, 5: 51–75%, 6: 76–100%) for each tier height (Tier 1: >12 m, Tier 2: 5–12 m, Tier 3: 2–5 m, Tier 4: 30 cm to 2 m, Tier 5: <30 cm, Tier 6: epiphytes). Diameter at breast height (dbh; at 1.35 m) was measured for all trees greater than 10-cm dbh for each 20 × 20 m quadrat. Ground cover was assessed by percentage of vegetation, moss, lichen, litter, bare ground, rock, and dead logs, and total canopy cover was visually measured.

Nest characteristics

To determine whether robins and saddlebacks showed preferences for sites with particular tree cavities, we used a flexible metal measuring tape to measure cavities found in used and unused sites. All cavities within Recce plots (20 × 20 m) that were more than 1 m above the ground, could contain a nest cup of 13–23 cm, and had an entrance larger than 10 cm were considered as potential nesting cavities. Three

internal cavity characteristics were considered (Sedgeley 2003): (1) entrance height, (2) internal cavity height, (3) horizontal cross-section (internal widths *i* and *ii*); and four external characteristics: (1) tree species, (2) height above ground, (3) orientation of the cavity entrance, and (4) branch or trunk diameter.

Invertebrate sampling

Due to the differences in foraging behaviour, estimating food availability for robins and saddlebacks required separate estimates of invertebrate abundance in ground litter and on tree trunks. Within each quadrat (20 × 20 m) in foraging and unused plots, three soil-surface and litter samples were taken. For each sample, an area of leaf litter 30 × 30 cm was scraped to 0.5-cm soil depth and placed into a paper bag. Samples were kept in cool boxes, and invertebrates were later heat-extracted from the litter, using modified Tullgren funnels as described by Crook et al (2004). The bark of eight trees from the three dominant species was also searched. Invertebrates were collected using forceps and a paintbrush from within small (30 × 30 cm) quadrats at breast height (1.35 m). Invertebrates were collected into 70% ethanol and 5% glycerol and identified to order level. Invertebrate larvae of all taxa were combined and considered as a separate group.

Statistical analysis

To determine if nesting site characteristics changed with an expanding breeding population, we investigated differences in nest location (distance to the coast and nearest neighbour), and in nest characteristics (height, cavity and tree species) since reintroduction. We hypothesised that areas occupied soon after reintroduction would offer better nesting and foraging opportunities than those more recently established. To test this hypothesis, we demarcated nest site locations according to the year when that area was first occupied by a breeding pair (Fig. 2). Compositional variables (plant species cover and invertebrate

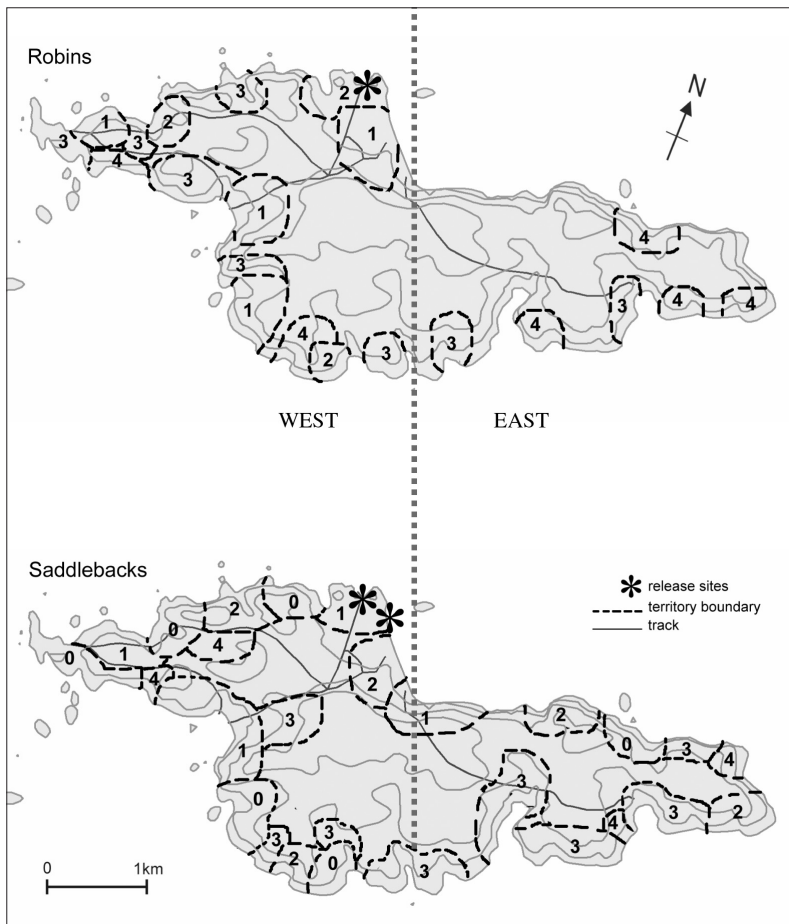


Figure 2. Map showing areas of Ulva Island where robins and saddlebacks had established territories since reintroduction, and coded by the year that an area was first occupied by a breeding pair (0 = 2000, 1 = 2001, 2 = 2002, 3 = 2003 and 4 = 2004).

abundance) were analysed using non-parametric multivariate analysis in the computer software package PRIMER (Clarke 1993; Clarke & Warwick 1998; Clarke et al. 2006). To explore differences in habitat compositional components between territories, we also tested dissimilarity distances between territories used in the first breeding season after reintroduction (2000 for saddlebacks; 2001 for robins) and sites occupied the following years, using one-way ANOSIM (999 permutations) for: (1) plant species cover per tier height, (2) number of stems per tree species per diameter class, and (3) number of individual invertebrates per order. The percentage contribution of each variable, to the level of 90% dissimilarity between and within sites, was estimated using SIMPER analysis (Clarke & Warwick 2001).

To explore differences in habitat characteristics between used and unused sites, we plotted Bray–Curtis similarity distances between sites, using non-metric multidimensional scaling (NMDS) in the computer software package PRIMER to establish sites' resemblance in vegetation composition (Clarke 1993; Clarke & Warwick 1998; Clarke et al. 2006). On an ordination, the closer the points were to each other, the more similar their vegetation composition, and at a stress level < 0.2 the ordination gives a good two-dimensional representation of the data. The three compositional variables measured were: (1) plant species cover per tier height, (2) number of stems per tree species per diameter class, and (3) number of individual invertebrates per taxonomic group. One-way ANOSIM (999 permutations) was performed to test for significance. The contribution percentages for each variable to 90% dissimilarity between and within sites were estimated using SIMPER analysis (Clarke & Warwick 2001). When required, data were normalised by log or fourth root transformations (Clarke & Warwick 2001). Cavity orientations were tested for uniformity around an assumed circle, using a Rayleigh's test; and for differences in mean angle between treatment sites using the Watson–Williams test for two samples (Zar 1999).

To determine whether habitat characteristics or their interactions influenced the probability of a bird using a site, compositional variables were first converted into indices of vegetation structure and invertebrate composition, using principal component analysis (PCA; based on the first three principal components explaining >80% of variation between sites). These indices were then modelled, along with all habitat variables, using binary logistic regression models. The second-order Akaike Information Criterion corrected for small sample size (AIC_c) was calculated to determine the model that 'best' explained variation in the data (Burnham & Anderson 2002). We estimated models with AIC_c differences (ΔAIC_c) < 2 to be best, and considered models with ΔAIC_c ranging from 2 to 7 to underline influential ecological processes (Burnham & Anderson 2002).

Results

Territorial establishment

Robin territories that established soon after reintroduction (2001) were predominantly in the northern (areas that were relatively close to the original release sites) and southern coast of the western section

of Ulva Island (Fig. 2). In the following years, robins progressively settled in the eastern part of the island, but territories remained close to the coast (Fig. 2). Nests in more recently occupied territories were built higher above ground, in areas with greater canopy cover and in larger trees (Tables 1 & 2). Areas that were first occupied were characterised by a dense cover of *Brachyglottis rotundifolia* at low height (2–5 m) and abundance in small stems (10–30 cm) of *Coprosma foetidissima* (stinkwood), *Pseudopanax crassifolius* (lancewood) and *Dracophyllum longifolium* (Table 2). In contrast, areas occupied later on had a denser cover of *Ripogonum scandens* (supplejack) from 2 to 12 m, and *Asplenium bulbiferum* (hen and chicken fern) above 30 cm, and greater abundance of small *Dicksonia squarrosa* (tree fern) (10–30 cm dbh) (Table 2). Although food availability (invertebrate abundance and diversity in litter) did not differ between sites ($R_{anosim} = 0.050$, $P > 0.05$), food accessibility could have been affected by the dense cover of *Asplenium bulbiferum* (Table 2).

Soon after reintroduction (2000 and 2001), saddleback breeding pairs settled mostly along the west coast of Ulva Island, with the exception of one pair that settled in the eastern part of the island (Fig. 2). Progressively more territories were established in the eastern section of the island. In 2003, birds established territories further inland or on the far eastern coast (Fig. 2). In 2004, few new areas were colonised and saddlebacks appeared to fill the available gaps on the coastline. Although not significant ($P = 0.063$), results suggested that saddleback founders nested closer to the coast than birds from subsequent generations (Table 1). Vegetation composition and structure (i.e. diameter of host tree) also differ significantly between areas occupied by saddleback soon after reintroduction (2000) and those occupied later on (Table 2). First-occupied areas were characterised by a greater abundance of small (10–30 cm dbh) *Dracophyllum longifolium*. Areas occupied later on had a denser cover of *Ripogonum scandens* at 2–5 m height, *Metrosideros umbellata* and *Weinmannia racemosa* at 5–12 m, and a greater abundance of small *Dicksonia squarrosa* and *Coprosma foetidissima*.

Breeding site characteristics

Vegetation structure

The structural composition of vegetation was distinctly different between robin and saddleback breeding sites and unused sites, as well as separating saddleback sites located in the far eastern part of island (Fig. 3), and were highly significant for both species (all $P < 0.001$). Each of the first five variables (species cover per tier height), however, contributed to less than 2% of the dissimilarity (Table 3). The indices of structural composition in vegetation derived from these five variables were expressed by two principal components (accounting for more than 80% of the variation) comparing unused sites and robin sites, and three principal components comparing unused sites and saddleback territories. Along axis one the principal component clearly separated sites dominated by dense covers of podocarp species (*Dacrydium cupressinum*, *Prumnopitys ferruginea* and moss cover) from those dominated by dense cover of coastal broadleaved tree species (*Metrosideros umbellata* and *Ripogonum scandens*).

Table 1. Variation in site characteristics for all recorded nests since reintroduction (maximum 111 robin nests and 131 saddleback nests), between areas of Ulva Island first occupied by a breeding pair soon after reintroduction (robins in 2001 and saddlebacks in 2000) and areas occupied later on (robins in 2002–2003 and saddlebacks in 2001–2003).

Year area was first occupied	Robin sites				Saddleback sites			
	2001	2002–2003			2000	2001–2003		
Variables	Mean ± SD	Mean ± SD	<i>n</i>	χ^2	Mean ± SD	Mean ± SD	<i>n</i>	χ^2
Distance to coast (m)	65.2 ± 48.3	71.6 ± 30.1	107	0.585	53.2 ± 67.7	74.5 ± 66.4	131	3.454
Distance to nearest neighbour (m)	220.2 ± 133.2	204.7 ± 130.7	111	0.373	274.5 ± 216.7	216.9 ± 114.9	131	0.046
Nest height (m)	5.5 ± 2.8	7.02 ± 3.6	109	4.701*	2.3 ± 2.0	2.2 ± 1.4	112	0.206
% nests in cavity	14.7	27.9	111	2.824	51.9	48.1	125	0.266

*Variables were significantly different at $P < 0.05$.

Table 2. Test of dissimilarity between areas of Ulva Island occupied by a breeding pair soon after reintroduction (robins in 2001 and saddlebacks in 2000) and areas occupied later on (robins in 2002–2003 and saddlebacks in 2001–2003), for the first explanatory variables of plant species cover per tier height and number of tree species per dbh class.

Year area was first occupied	Robin sites			Saddleback sites		
	2001	2002–2003	Dissimilarity	2000	2001–2003	Dissimilarity
	(<i>n</i> = 16)	(<i>n</i> = 40)		(<i>n</i> = 40)	(<i>n</i> = 28)	
	Average	Average	Percentage	Average	Average	Percentage
	abundance	abundance	contribution	abundance	abundance	contribution
<i>Plant species cover per tier height</i>	Overall dissimilarity = 53.34% $R_{\text{anosim}} = 0.11, P = 0.013$			Overall dissimilarity = 56.25% $R_{\text{anosim}} = 0.294, P = 0.010$		
<i>Metrosideros umbellata</i> (5–12 m)	2.31	2.44	1.75	1.71	2.61	1.70
<i>Ripogonum scandens</i> (5–12 m)	1.88	2.13	1.66	-	-	-
<i>Brachyglottis rotundifolia</i> (2–5 m)	2.06	0.75	1.58	-	-	-
<i>Ripogonum scandens</i> (2–5 m)	1.94	2.94	1.57	1.50	2.34	1.74
<i>Asplenium bulbiferum</i> (30 cm – 2 m)	0.94	2.31	1.52	1.79	1.61	1.67
<i>Weinmannia racemosa</i> (5–12 m)	-	-	-	1.46	2.32	1.59
<i>Metrosideros umbellata</i> (2–5 m)	-	-	-	1.79	1.75	1.43
<i>Number of tree stems per dbh class</i>	Overall dissimilarity = 72.64 % $R_{\text{anosim}} = 0.261, P = 0.030$			Overall dissimilarity = 71.44% $R_{\text{anosim}} = 0.176, P = 0.010$		
<i>Brachyglottis rotundifolia</i> (10–30 cm)	1.42	0.10	8.06	0.63	0.61	4.89
<i>Dicksonia squarrosa</i> (10–30 cm)	3.08	7.05	8.05	4.00	4.77	5.51
<i>Weinmannia racemosa</i> (10–30 cm)	1.25	1.40	7.23	1.04	1.80	6.98
<i>Coprosma foetidissima</i> (10–30 cm)	1.17	0.90	7.15	0.58	0.84	5.18
<i>Weinmannia racemosa</i> (30–50 cm)	0.83	0.45	6.59	-	-	-
<i>Pseudopanax crassifolius</i> (10–30 cm)	1.25	0.05	5.63	-	-	-
<i>Dracophyllum longifolium</i> (10–30 cm)	1.50	0.10	5.60	2.04	1.45	5.64

Table 3. Average abundance and percentage contribution for the first five variables driving the dissimilarity between unused and robins' and saddlebacks' nest sites, in terms of plant species cover per tier height and number of tree species per dbh class.

Variables	Control	Robins		Saddlebacks	
	(<i>n</i> = 32)	(n = 56)		(n = 68)	
	Average	Average	Percentage	Average	Percentage
	abundance	abundance	contribution	abundance	contribution
<i>Plant species cover per tier height</i>					
Moss cover	3.41	0.56	2.15	0.97	2.02
<i>Prumnopitys ferruginea</i> (5–12 m)	2.38	0.19	1.74	0.34	1.79
<i>Ripogonum scandens</i> (2–5 m)	0.66	2.44	1.61	2.04	1.5
<i>Metrosideros umbellata</i> (5–12 m)	1.78	2.38	1.58	2.29	1.56
<i>Dacrydium cupressinum</i> (5–12 m)	2.00	0.31	1.46	-	-
<i>Podocarpus hallii</i> (5–12 m)	2.19	-	-	0.57	1.52
<i>Number of tree stem. per dbh class</i>					
<i>Dicksonia squarrosa</i> (10–30 cm)	1.66	5.56	12.20	4.5	11.34
<i>Podocarpus hallii</i> (10–30 cm)	1.94	0.16	8.20	0.32	8.08
<i>Weinmannia racemosa</i> (10–30 cm)	2.06	1.34	7.71	1.53	8.03
<i>Prumnopitys ferruginea</i> (10–30 cm)	1.34	0.03	6.54	0.04	6.47
<i>Coprosma foetidissima</i> (10–30 cm)	0.13	1.00	5.28	-	-
<i>Dracophyllum longifolium</i> (10–30 cm)	0.97	-	-	1.66	6.19

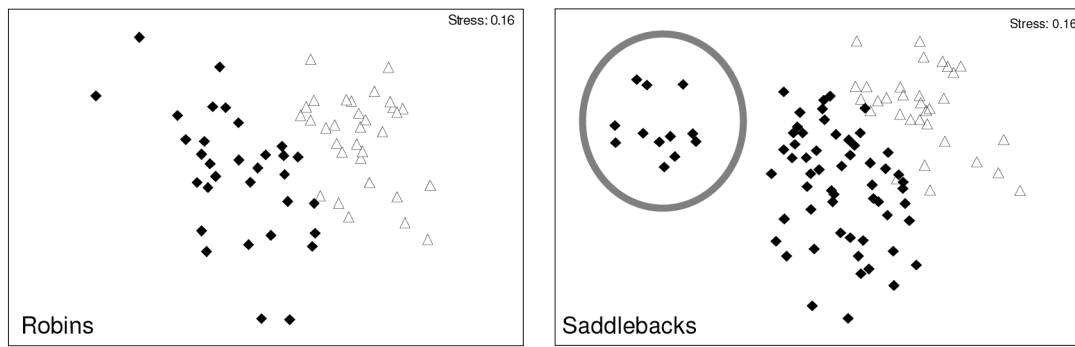


Figure 3. Two-dimensional NMDS (non-metric multidimensional scaling) ordination, showing differences in vegetation composition per tier height between control (Δ) and bird nesting sites (\blacklozenge). (Saddleback sites circled by a grey solid line were located in the far eastern section of Ulva Island.)

For both bird species, the number of tree stems per dbh class of 10–30 cm for five species – *Dicksonia squarrosa*, *Podocarpus hallii*, *Weinmannia racemosa*, *Prumnopitys ferruginea* and *Coprosma foetidissima* or *Dracophyllum longifolium* – accounted for more than 40% of the dissimilarity (Table 3). A second index of structural composition was derived from the first three principal components of these five variables, which explained more than 80% of the variation and clearly separated podocarp forest (*Prumnopitys ferruginea* and *Podocarpus hallii*) and coastal forest (*Dicksonia squarrosa* and *Coprosma foetidissima*).

The percentage of the upper-canopy cover (for saddlebacks only) and the number of cavities did not differ significantly ($P > 0.05$) between nesting sites and unused sites (Table 4). In general, both robin and saddleback territories contained more *Dicksonia squarrosa* and broadleaved species and less podocarp species than unused sites. Within birds' territories, vegetation composition contributed to mixed-size stands with a mean canopy height (MCH) of 3 m, fewer trees of 30–50 cm dbh, and stems of smaller mean dbh than unused sites (Table 4).

Cavity characteristics

Cavities in saddleback and robin territories were predominantly found in live *Metrosideros umbellata* and *Griselinia littoralis*, while cavities in unused sites were mostly in dead trees and *M. umbellata* (Table 4). Cavities were significantly higher above ground in saddleback sites and the entrances wider and larger inside for robins, in comparison to those cavities found in unused sites.

Foraging and food availability

During 16 out of 18 observations, individual robins foraged on the ground with less than 50% vegetation cover (in 53% of the observations, no ground vegetation cover was recorded). Ninety-two percent of the observations occurred in gullies and half of these were in coastal habitat. During 23 of 32 observations, individual saddlebacks foraged on trees of which 89.6% were live trees and 10.4% were dead ones. Saddlebacks foraged at 2.66 ± 1.27 m mean height on trees of 27.17 ± 21.32 cm mean dbh, mostly on tree ferns *Dicksonia squarrosa* (21.2%) and *Cyathea smithii* (12.1%), *Brachyglottis rotundifolia*

Table 4. Mean and standard deviation for measures of stand structure and cavity size, between unused sites and robin or saddleback nesting territories.

Variables	Control		Robins			Saddlebacks		
	n	Mean \pm SD	n	Mean \pm SD	χ^2	n	Mean \pm SD	χ^2
<i>Stand structure</i>								
Canopy cover (%)	8	47.9 \pm 13.8	14	57.6 \pm 9.0	4.408*	17	55.2 \pm 13.8	1.554
Canopy height	8	14.8 \pm 3.4	14	12.4 \pm 3.9	1.992	17	18.9 \pm 9.7	1.422
Number of cavities	8	2.0 \pm 1.6	14	1.5 \pm 1.3	2.583	17	1.5 \pm 2.0	0.246
Total number trees (10–30 cm)	8	41.2 \pm 13.9	14	50.6 \pm 18.2	1.496	17	53.5 \pm 18.6	3.079
Total number trees (30–50 cm)	8	9.5 \pm 2.0	14	5.3 \pm 2.6	6.646**	17	5.94 \pm 2.88	8.640**
Total number trees (50–70 cm)	8	2.0 \pm 1.6	14	2.6 \pm 2.0	0.037	17	1.1 \pm 1.7	1.288
Total number trees (>70 cm)	8	0.7 \pm 1.0	14	1.0 \pm 2.1	0.003	17	1.0 \pm 0.8	0.439
Total number trees	8	53.5 \pm 13.9	14	57.6 \pm 15.6	0.431	17	61.7 \pm 17.9	1.445
Mean dbh	8	22.3 \pm 3.0	14	19.6 \pm 2.9	4.217*	17	19.4 \pm 2.5	5.862**
Max dbh	8	71.4 \pm 16.8	14	66.7 \pm 18.7	0.342	17	77.9 \pm 19.5	0.688
<i>Cavity measurements</i>								
Entrance (cm)	12	22.3 \pm 15.1	7	52.7 \pm 40.4	5.371**	19	28.3 \pm 27.1	0.558
Internal cavity height (cm)	12	89.8 \pm 80.9	7	136.0 \pm 116.7	1.077	19	79.3 \pm 45.9	0.221
Diameter (cm)	12	35.6 \pm 25.6	7	42.9 \pm 18.5	0.456	19	49.0 \pm 17.5	3.124
Horizontal width i (cm)	12	18.0 \pm 10.9	7	27.7 \pm 13.1	2.828	19	25.8 \pm 12.6	3.428
Horizontal width ii (cm)	12	17.0 \pm 8.4	7	27.7 \pm 10.9	4.930*	19	21.1 \pm 9.8	1.585
Height above ground (cm)	12	118.8 \pm 41.9	7	156.2 \pm 44.4	3.284	19	185.6 \pm 74.1	7.878**
Tree species (total number)	12		7		0.458	19		13.818**
Dead trees		5		0			2	
<i>Metrosideros umbellata</i>		4		3			8	
<i>Griselinia littoralis</i>		0		3			6	
<i>Weinmannia racemosa</i>		2		1			2	
<i>Carpodetus serratus</i>		0		0			1	

*Level of significance is indicated with asterisks: * $P < 0.05$, ** $P < 0.01$.

(19.7%) and *Metrosideros umbellata* (16.7%). The recorded height above ground and tree dbh of foraging observations were significantly ($P < 0.01$) related to tree species. Saddlebacks foraged on large (> 30 cm dbh) stems of *Metrosideros umbellata*, *Griselinia littoralis* and *Myrsine australis* at > 2.5 m height; or on small (< 20 cm) tree ferns and *Coprosma* species at < 0.5 m height.

Although invertebrate groups found in the litter samples showed greater dissimilarity between unused and bird foraging sites than within sites (robin: $R_{anosim} = 0.137$, $P < 0.05$; saddleback: $R_{anosim} = 0.176$, $P < 0.05$), invertebrate group contribution to group dissimilarity was low (< 25%) and NMDSs failed to represent sites dissimilarity at a 2D-level. This result suggests that dissimilarity in invertebrate communities between sites may be driven by factors not identified in this type of descriptive analysis (e.g. spatial variability). However, the numbers of Amphipoda, Coleoptera, and Diplopoda were greater in the litter at bird foraging sites compared with unused plots. In addition, Annelida were significantly more abundant in saddleback sites (Table 5).

The overall invertebrate community on tree trunks did differ significantly between foraging and unused sites (average % dissimilarity = 65%; $R_{anosim} = 0.048$, $P < 0.05$). Numbers of larvae, Amphipoda and Annelida were greater, and the number of Blattodea and Gastropoda lower, in saddleback foraging sites than in unused plots (Table 6). Invertebrate communities also differed amongst tree species ($R_{anosim} = 0.212$, $P < 0.05$) (Fig. 4). Larvae were more abundant in coastal scrub species (*Dracophyllum longifolium*, *Olearia colensoi*, *Brachyglottis rotundifolia* and *Dicksonia squarrosa*), Coleoptera on *Olearia colensoi*, and Amphipoda on *Weinmannia racemosa* and *Metrosideros umbellata*. In podocarp forest, invertebrate order diversity was relatively high but abundance was high only on *Dacrydium cupressinum* stems (Fig. 4).

Modelling habitat selection

Models of habitat selection by robins on Ulva Island, which considered vegetation composition (Model 1) and tree size (Model 2) respectively, presented the best fit with $\Delta AIC_c < 2$ (Table 7). More specifically,

Table 5. Average abundance (no. per sample) of invertebrates in litter samples and percentage contribution to dissimilarity between unused control sites and birds foraging sites of the most abundant invertebrate taxonomic groups found on Ulva Island (* variables were significantly different at $P < 0.05$ between control and bird sites).

Orders	Control (n = 48)	Robins (n = 48)		Saddlebacks (n = 48)	
	Average abundance	Average abundance	Percentage contribution	Average abundance	Percentage contribution
Amphipoda	12.56	23.73*	12.88	33.98*	11.35
Coleoptera	6.23	13.27*	10.39	12.94*	8.61
Collembola	61.77	60.82	9.01	66.90	8.00
Isopoda	6.25	7.48	8.85	10.52	7.89
Annelida	4.48	6.00	8.81	9.33*	9.74
Acarina	164.02	192.18	7.97	241.15	7.69
Araneae	6.29	5.97	7.01	6.65	6.84
Larvae	49.96	48.06	5.72	64.48	4.40
Diplopoda	0.81	4.03*	5.58	5.15*	7.59

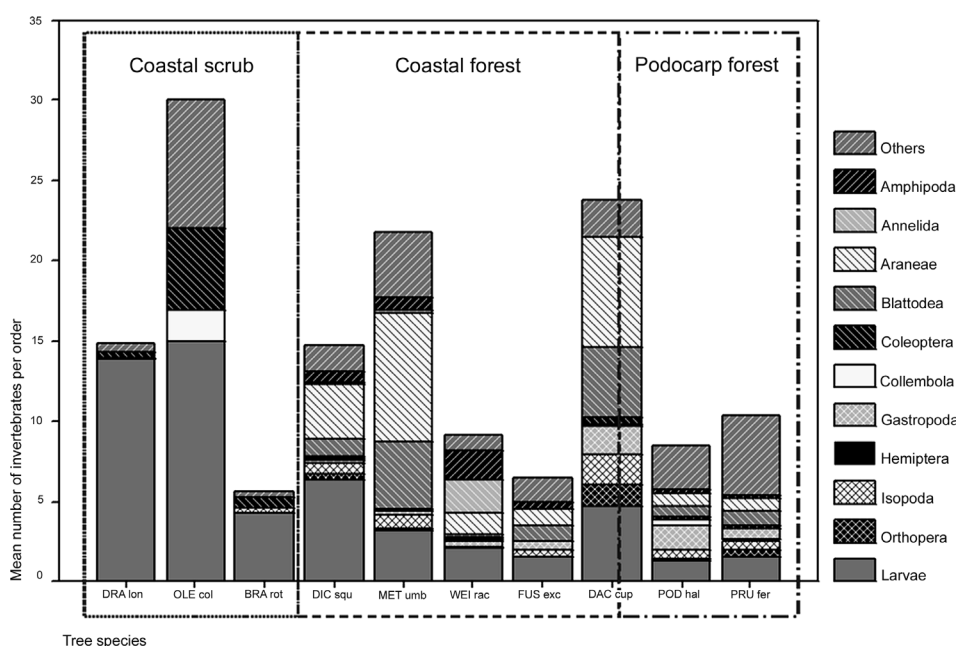


Figure 4. Mean number of invertebrates for each order, per tree species and habitat type, on Ulva Island. (Abbreviations: DRA lon = *Dracophyllum longifolium*, OLE col = *Olearia colensoi*, BRA rot = *Brachyglottis rotundifolia*, DIC squ = *Dicksonia squarrosa*, MET umb = *Metrosideros umbellata*, WEI rac = *Weinmannia racemosa*, FUS exc = *Fuchsia excorticata*, DAC cup = *Dacrydium cupressinum*, POD hal = *Podocarpus hallii*, PRU fer = *Prumnopitys ferruginea*)

Table 6. Average abundance (no. per sample) of invertebrates on tree trunks and percentage contribution to dissimilarity between unused control sites and saddleback foraging sites of the most common invertebrate taxonomic groups found on Ulva Island (* variables were significantly different at $P < 0.05$ between control and bird sites). [Robins tended not to forage on tree trunks.]

Orders	Control	Saddlebacks	
	($n = 48$)	($n = 48$)	
	Average	Average	Percentage
	abundance	abundance	contribution
Larvae	2.59	6.11*	11.99
Araneae	3.14	3.45	11.06
Blattodea	2.53	1.09*	10
Gastropoda	1.02	0.55*	9.81
Chilopoda	0.67	0.7	8.3
Isopoda	0.73	0.68	7.26
Amphipoda	0.24	0.81*	6.76
Opiliones	0.76	0.49	6.42
Coccidea	0.78	0.38	6.09
Orthoptera	0.55	0.21	5.25
Coleoptera	0.24	0.3	4.06
Annelida	0.06	0.53*	2.9
Collembola	0.08	0.17	2.72

the probability of robins selecting a site for breeding increased with an increasing cover of *Metrosideros umbellata* at 5–12 m and *Ripogonum scandens* at 2–5 m, and with an increasing number of small sized *Dicksonia squarrosa* and *Coprosma foetidissima* (Table 7). Models that considered the number of trees of 30–50 cm dbh and invertebrate composition provided only moderate support for the data ($2 < \Delta AIC_c < 7$).

The best fit for a model of habitat selection in saddlebacks on Ulva Island included tree species per dbh class (Model 1, Table 7). More specifically, the probability of saddlebacks selecting a site for breeding increased with an increasing number of small size *Dicksonia squarrosa* and *Coprosma foetidissima* (Table 7). Models that considered vegetation composition alone (Model 2) and vegetation composition in addition to tree species per dbh class (Model 3) also showed some level of support ($\Delta AIC_c < 2$). More specifically, the probability of saddlebacks selecting a site for breeding increased with an increasing cover of *Metrosideros umbellata* at 5–12 m and *Ripogonum scandens* at 2–5 m (Model 2), and with an increasing number of small size *Dicksonia squarrosa* and *Coprosma foetidissima* (Model 3) (Table 7). Thirteen other models showed considerably less fit with the data ($2 < \Delta AIC_c < 7$), suggesting a minor effect of vegetation composition, food availability and mean canopy height (MCH).

Discussion

Historically, Stewart Island robins and South Island saddlebacks were likely to have been present on Ulva Island (Roberts 1994; Worthy & Holdaway 2002). The reintroduction of these species provided a natural experiment to explore the mechanisms that influence breeding site selection and territorial establishment in natural populations while controlling for the effects of competition from resident conspecifics, introduced predators, and long-distance dispersal. In their first breeding year after reintroduction, robins and saddlebacks settled on territories in coastal habitat, predominantly in the western part of the island, and avoided sites dominated by podocarp species and dense ground cover of moss. Birds progressively settled in the eastern part of the island but still favoured coastal habitat.

The structural composition of the vegetation appeared to be the primary factor driving breeding site selection in robins and saddlebacks on Ulva Island. Specifically, the probability of birds selecting a site for breeding increased with an increasing cover of broadleaved coastal species such as *Metrosideros umbellata* and *Dicksonia squarrosa*, and with a decreasing number of medium-sized stems, contributing to a preference for a dense vegetation cover at c. 3 m height (see also Michel et al. 2008b). Dense low vegetation offers greater perching areas, protection against avian predators and harsh weather, and foraging surfaces for breeding passerines (Walsberg 1985).

Food availability appeared to be less important than vegetation structure per se in determining habitat selection in both saddlebacks and robins. Forest structure is often a reflection of community composition, where mixed-size stands reflect a mixed-species community (coastal forest) in comparison with regular-size stands of a few dominant species (podocarp forest). Forest composition and structure also dictate the invertebrate community and food availability for birds (see also Michel et al. 2008a). For example, trees in coastal habitat hosted more invertebrate larvae and spiders, and litter contained an abundance of major arthropods groups than in podocarp forest (Michel et al. 2008c). Invertebrate groups collected on litter and trees, and which were significantly more abundant in bird territories than unused random sites, coincided with observations of food items preferred by robins (Powlesland 1980, 1981) and saddlebacks (Merton 1966; Pierre 2000). Furthermore, fruiting tree species in coastal habitats such as *Pseudopanax arboreus* and *Coprosma* spp. are likely to provide supplementary food during the fledgling period.

Low food and nesting availability in the dense podocarp forest of Ulva Island may explain why saddlebacks and robins did not colonise these habitats even though both species were once widespread in the mixed podocarp–broadleaved forest type that characterised the mainland. The broadleaved tree species would have provided birds with more nesting and foraging opportunities than the dense monoculture stand of podocarp species found on Ulva Island.

The ground litter in western sites hosted a more diverse and accessible invertebrate community, with all groups being more abundant than in eastern parts of the island (Michel 2006). Further, robin territories established in the first year after reintroduction contained more Collembola, Coleoptera, and larvae in comparison with areas occupied later on. Thus, founding robins have settled most probably in prime habitat that supported successful nesting, and the following generations established territories adjacent to conspecifics, but possibly in lower quality habitat. Similarly, locations of saddleback nests in coastal scrub and coastal forest, which hosted the greatest number of larvae, could have been perceived as prime habitat for breeding, as nests located in these habitats also showed the highest productivity (Michel 2006). In later years, pairs colonised sites further from the coast, which offer poor nesting medium (dead trees) and fewer food items.

Overall, the apparent initial preference for the western section of Ulva Island by robins was probably influenced by forest type and food availability, and not nest site availability, as robins are known to exhibit high flexibility in nesting habitats – for example in pine–fir plantations (Duncan et al. 1999). Saddlebacks were spread more widely across the island, but still showed preferences for coastal habitat. Similar patterns of habitat colonisation with preferences for coastal habitats (scrub and forest) have been observed in the reintroduced saddleback population onto Motuara Island (Marlborough Sounds) (Pierre 2003; Michel et al. 2008a). Coastal habitat appeared to provide breeding pairs with the best foraging and nesting opportunities. Thus the observed patterns of habitat selection in robins and saddlebacks are likely to be driven by habitat quality, and habitat suitability is critical for the successful establishment of reintroduced individuals (Armstrong & Ewen 2002; Armstrong et al. 2005).

Habitat quality, however, is best defined as a combination of factors where the interaction between the structural composition of the vegetation, the abundance and diversity of food items, and nesting support quantifies bird requirements. Vegetation biomass is often considered a good surrogate measure of invertebrate abundance in

Table 7. Explanatory variables included in each binary logistic regression model on habitat selection by robins and saddlebacks on Ulva Island.

Model	Explanatory variables	Coef.	SE	$-2LL^a$	K^b	AIC_c^c	ΔAIC_c^d
<i>Robins</i>							
1	Constant VegComp1	0.299 -4.480	1.464 3.887	4.154	2	9.154	0.000
2	Constant TreeDBH1	-3.961 6.680	4.912 6.693	4.451	2	9.451	0.297
<i>Saddlebacks</i>							
1	Constant TreeDBH1	0.129 3.357	1.152 2.160	5.035	2	9.958	0.000
2	Constant VegComp1	1.173 -2.199	1.208 1.076	7.074	2	11.997	2.039
3	Constant VegComp1 TreeDBH1	0.383 -1.670 2.651	1.427 2.275 2.489	4.056	3	12.056	2.098

^a-2 Log Likelihood, ^b K = number of parameters in the model, ^cAkaike Information Criterion corrected for small sample size, ^d ΔAIC_c differences.

habitat modelling, but may fail to account for variation in invertebrate composition, resulting in high specialisation in plant–animal interactions (Blenden et al. 1986; Schamberger & O’Neil 1986). Plant physiology may determine litter content and quality, invertebrate assemblage, and cavity formation. From our results, structural composition of the vegetation (plant species cover at different heights) was the first variable explaining site selection in both studied populations. More generally, structurally diverse habitats such as ecotones often support a greater abundance and diversity of species by providing a diversity of substrates for foraging or reproduction (Odum 1958; Baker et al. 2002). In conclusion, vegetation composition should not be ignored in the modelling of bird–habitat relationships, as it could be a good indicator of food availability in reintroduced bird populations. Habitat quality may also be better assessed within an interacting ecosystem and as a functional-resource-based concept of habitat (Vanreusel et al. 2007). Consequently, the distribution of resources and suitable habitats across the available landscape could influence the survival and reproduction of reintroduced bird populations (Hobbs & Hanley 1990; Verboom et al. 1991; Armstrong et al. 2005; Armstrong & Davidson 2006).

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