

Multi-scale habitat models for reintroduced bird populations: a case study of South Island saddlebacks on Motuara Island

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Abstract: Understanding resource selection by animals is important when considering habitat suitability at proposed release sites within threatened species recovery programmes. Multi-scale investigatory approaches are increasingly encouraged, as the patchy distribution of suitable habitats in fragmented landscapes often determines species presence and survival. Habitat models applied to a threatened New Zealand forest passerine, the South Island saddleback (*Philesturnus carunculatus carunculatus*), reintroduced to Ulva Island (Stewart Island) found that at landscape scale breeding pairs' preferences for sites near the coast were driven by micro-scale vegetation structure. We tested these results by examining models of breeding site selection by a reintroduced saddleback population on Motuara Island (Marlborough Sounds) at two scales: (1) micro-scale, for habitat characteristics that may drive breeding site selection, and (2) landscape scale, for variations in micro-scale habitat characteristics that may influence site colonisation in breeding pairs. Results indicated that birds on Motuara Island responded similarly to those on Ulva Island, i.e. birds primarily settled at the margins of coastal scrub and forest and later cohorts moved into larger stands of coastal forest where they established breeding territories. Plant species composition was also important in providing breeding saddleback pairs with adequate food supply and nesting support. However, Motuara Island birds differed in their partitioning of habitat use: preferred habitats were used for nesting while birds were foraging outside territorial boundaries or in shared sites. These differences may be explained because Motuara has a more homogeneous distribution of micro-scale habitats throughout the landscape and a highly bird-populated environment. These results show that resource distribution and abundance across the landscape needs to be accounted for in the modelling of density–bird–habitat relationships. In the search for future release sites, food (invertebrates and fruiting tree species) should be abundant close to available nesting sites, or evenly spread and available throughout the landscape.

Keywords: bird–habitat models; food availability; landscape ecology; nest characteristics; *Philesturnus carunculatus carunculatus*; vegetation structure

Introduction

Worldwide, the decline of suitable habitat has been a major factor contributing to the decline and extinction of many species. Recently, wildlife management projects have focused increasingly on transferring threatened species to safe havens in order to prevent further extinctions (Wilson & Peter 1988; Wilson 1992; IUCN 1998; Ramade 2003). Understanding processes influencing resource selection has thus become an important component of translocation programmes as attempts to re-establish species in areas where they formerly occurred must consider the suitability of habitats at proposed release sites (IUCN 1998; Wolf et al. 1998). Habitats need to provide individuals with resources that best satisfy their requirements, including adequate

food, water and suitable places to successfully reproduce and survive (Manly et al. 2002). Without these high quality habitats, translocation programmes have a low chance of success, regardless of how many individuals are released or how well they are prepared for the release (Griffith et al. 1989; Veitch 1994; Lindenmayer 1995; Lovegrove 1996). However, determining habitat requirements and suitability 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).

New Zealand's unique endemic fauna and flora in particular are highly vulnerable to extinction as a result of ecological changes (mainly through the introduction

of exotic species). Emphasis has been placed on the restoration of offshore island sanctuaries, and more recently on the creation of mainland islands through predator-proof fencing (Saunders & Norton 2001). Threatened species are increasingly reintroduced where threats can be controlled (Saunders 1994; Armstrong & McLean 1995). Although analysis of fossil records and museum specimens has attempted to determine species' historical distribution, little is known of the original habitat used by locally extinct populations (Williams 1973; Worthy & Holdaway 2002). There is a need in New Zealand to further understand the mechanisms of habitat selection by its endangered and threatened fauna, in order to establish relationships between the dynamics of translocated populations and the characteristics of the environment in the recipient habitat. Determining the effect of specific habitat components on species biology can potentially help characterise habitat suitability beyond a species' actual range and help identify sites for future releases.

Increasingly, detailed habitat studies have contributed to the understanding of a species' biological requirements for the success of wildlife recovery programmes (Ontiveros & Pleguezuelos 2000; Luck 2002a). Various computer-based ecological modelling approaches have been used to predict habitat suitability and identify potential release sites for reintroduction programmes, and regression models are by far the most commonly used techniques to examine vegetative and environmental factors influencing the distribution and abundance of species (Berry 1986; Lindenmayer 1995; Luck 2002b). Resource selection in natural populations occurs on a hierarchical scale from the geographic range of a species to its individual

home range, or from general features (habitat) within a geographic or home range to the selection of particular elements (food items or nest cavities) (Morrison et al. 1998; Manly et al. 2002). In the investigation of resource selection by animals, empirical studies have traditionally described species distributions in relation to landscape characteristics and dynamics (Roshier et al. 2001; Roshier 2003; Gavashelishvili 2004; Gibson et al. 2004a,b; Väli et al. 2004; Díaz 2006), but increasingly focus is being given to a micro-scale approach (Bollman et al. 2005; Maguire 2006). Further, because patchy distribution of suitable habitats in fragmented landscapes often determines species presence and survival (Quevedo et al. 2006), multi-scale approaches in habitat studies have been encouraged to further acknowledge the influences of spatial variation on species behaviour (Levin 1992; Luck 2002a; Sergio et al. 2003; Graf et al. 2005; Manzer & Hannon 2005).

New Zealand has a long history of native bird translocations (Armstrong & McLean 1995) with some recent and current efforts presenting the opportunity to explore habitat selection at several scales. One such example is that of the threatened New Zealand forest passerine, the South Island saddleback (*Philesturnus carunculatus carunculatus*), reintroduced onto Ulva Island (Fig. 1). In this case, the saddlebacks exhibited selective preferences for sites located near to the coast. Habitat selection models in this species supported the notion that site preferences at a landscape scale were being driven by vegetation structure at a micro-scale. In particular, territorial establishment in this species was dictated by mixed-sized stands of broadleaved species,

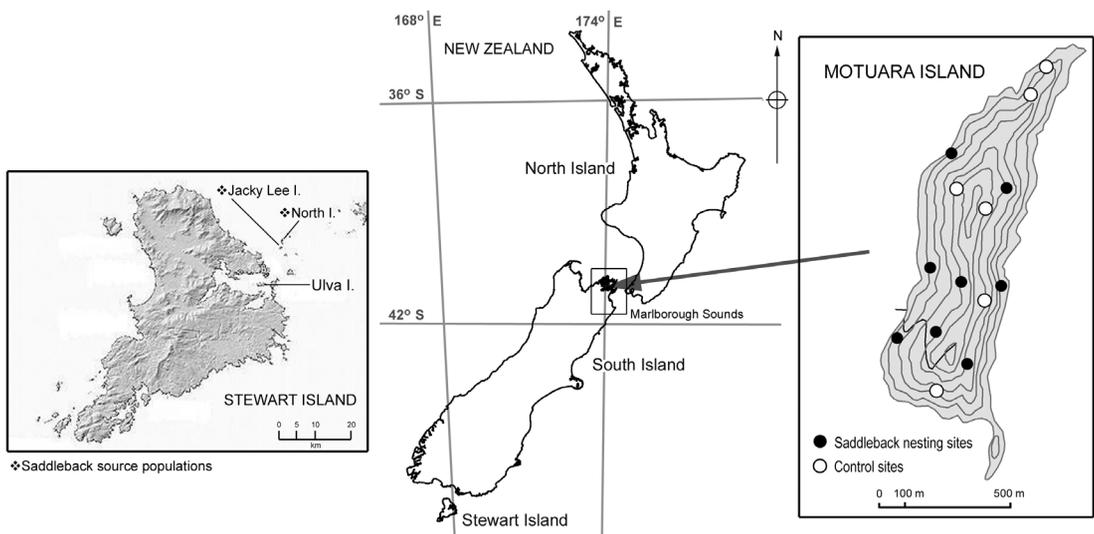


Figure 1. Map of Motuara Island, within Marlborough Sounds (South Island, New Zealand), showing sampled sites used in the study and its saddleback source populations, off Stewart Island.

where food supply and nesting support were adequate to breed successfully and maintain fitness (Steffens et al. 2005; Michel 2006). These results may, however, be specific to saddlebacks on Ulva Island, as bird-habitat models tend to be highly dependent on the data collected at a particular location (Fielding & Haworth 1995). Thus validating predictions beyond the geographic range of the model data, or current habitat structure, is necessary to determine the usefulness of models as management tools (Luck 2002b; Bollmann et al. 2005).

Models can be tested at different levels. Such tests can involve the base assumptions, variables, components or overall output, but generally habitat models are tested at the overall output level (Schamberger & O'Neil 1986). Although testing individual variables or assumptions might provide better information for determining and improving model reliability, this approach remains site specific. A potentially more powerful approach is to compare predictions resulting from one case and apply those to another. This approach may better explain interactions between habitat quality and breeding site selection in reintroduced bird populations (Schamberger & O'Neil 1986; Luck 2002b; Sedgely & O'Donnell 2004) and also indicate the degree of site generalisation that can be derived from models. Habitat selection models for reintroduced bird populations had been developed for saddlebacks (and New Zealand robins) reintroduced onto Ulva Island (Michel 2006). Consequently, we used this case to assess the model predictions of breeding site selection by comparing them with another reintroduced saddleback population in a different landscape at a second island site, Motuara Island (Marlborough Sounds).

In this study, we asked (1) at a micro-scale level, what characteristics of the habitat drive breeding site selection in the Motuara Island population, and (2) how does landscape-scale variation in micro-scale habitat characteristics influence site colonisation in breeding pairs? To this end, we defined habitat quality in terms of vegetation structure and composition, nest availability (characteristics of available cavities), and food accessibility (invertebrate composition on tree trunks) between known breeding territories and unused control sites; and between territories established soon after reintroduction and those occupied later on. In considering these questions, we aimed to understand mechanisms of habitat selection in South Island saddlebacks, which may clarify the species' historical range and define requirements for future release sites.

Methods

Study species

Saddlebacks (*Philesturnus carunculatus*) are members of the ancient endemic family of New Zealand wattlebirds (Callaeidae), which have poor powers of flight and are

highly susceptible to predation by reintroduced mammals, especially rats (Higgins et al. 2006).

The South Island subspecies (*Philesturnus c. carunculatus* (Gmelin)) was extirpated from mainland podocarp (Podocarpaceae) and *Nothofagus* (beech) forests and confined to a single offshore island (Big South Cape) on the exposed south-western coast of Stewart Island. Here, the subspecies inhabited dense, low-lying areas of coastal scrub consisting of *Olearia colensoi* (leatherwood) (nomenclature follows Allan Herbarium (2000)), *Brachyglottis rotundifolia* (muttonbird scrub) and *Dracophyllum longifolium* (inaka) as well as smaller patches of coastal forest dominated by *Metrosideros umbellata* (southern rātā), *Weinmanniaracemosa* (kāmahi) and *Leptospermum scoparium* (mānuka) in more sheltered parts of the island (Hooson & Jamieson 2004). This single saddleback population was subsequently used to re-establish the species elsewhere, first on two nearby rat-free islands, and from there, to various other rat-free islands off the coast of Stewart Island; all with similar habitat types to the remnant source population.

Saddlebacks were later transferred from two of these small islands off the eastern coast of Stewart Island: Jacky Lee Island (30 ha, max. elevation 40 m) and North Island (8 ha, max. elevation 20 m) (Lovegrove 1996), onto Motuara Island, an inshore island in the Marlborough Sounds, which is much further north and drier than the islands from where they were sourced (Fig. 1).

Study site

Small and rugged (59 ha, max. elevation 128 m), Motuara Island (41°05.5' S; 174°16.5' E) lies at the entrance of Queen Charlotte Sound, in the Marlborough Sounds (Fig. 1). The island landscape was drastically modified following Māori and non-Māori occupation, during which gardens were established, and sheep and goats farmed (Walls 1984). Motuara was made a nature reserve in 1926 and since then a mosaic of vegetation has vigorously regenerated. A tall (3–12 m) canopy of *Kunzea ericoides* mostly dominates the inland, with a dense understorey of *Pseudopanax arboreus*, *Myrsine australis*, *Pittosporum tenuifolium*, *Cyathea* spp., *Coprosma lucida*, *C. robusta*, *C. rhamnoides* and *Pteridium esculentum* (Cash & Gaze 2000; Walls 1984). Low coastal forest is more abundant in the western and southern sections of the island and includes *Meliclytus ramiflorus*, *Hedycarya arborea*, *Brachyglottis repanda*, and *Macropiper excelsum*. The shore fringe is covered with scrub of *Pittosporum tenuifolium*, *Myoporum laetum*, *Coprosma repens*, *Olearia paniculata*, above dense *Phormium cookianum*. Patches of remnant vegetation are still occasionally found on the island, mostly along steep gullies, and include large stands of *Dysoxylum spectabile*, *Alectryon excelsum*, *Beilschmiedia tawa*, *Streblus banksii*, *Elaeocarpus dentatus*, and *Aristotelia serrata*.

Motuara Island was made mammalian-predator-free in 1991 when kiore (*Rattus exulans*) were eradicated and

South Island saddlebacks were translocated in 1994. The first breeding season after reintroduction, saddlebacks on Motuara Island were observed to have established primarily in forested areas along the coast, and plant species composition did not appear to be important (Pierre 2001). It was suggested that birds in this population preferred forest to scrub, and as population density increased, birds would move to colonise the less desirable coastal-scrub-dominated areas. Saddlebacks on Motuara Island foraged up to 4 m height, mostly on *Pseudopanax arboreus*, and males appeared to spend more time feeding on the ground than do the North Island subspecies (Pierre 2000, 2001). Territories on Motuara Island were not areas of exclusive use, and birds attended water points beyond territorial boundaries. In 2002, saddlebacks suffered a population crash, declining from over 100 to less than 50 within a period of 1–2 months as a result of a disease outbreak. The population has since recovered and was estimated to be at 119 individuals in 2004 (Hale 2007).

To determine habitat selection by saddlebacks on Motuara Island, vegetation composition, nest characteristics and food availability (invertebrate abundance and taxonomic diversity) were sampled during the 2004–05 breeding season. Nests were located by searching the area surrounding known nest sites from previous years, or walking a transect line in unused areas. During the period of the present study, the monitoring of nests started at the beginning of the breeding season in November 2004 and continued until the end of the fledging period in early March 2005. Eight breeding territories were randomly chosen from the identified nests (Fig. 1), in which foraging locations were determined during the nesting period (November–December) by observing individuals (or breeding pairs) feeding for more than 20 minutes in the same area. For each observed foraging location, the location on the island, date and time of the day, and bird colour-ring combination were recorded. We identified the tree species and the particular component (leaf, dead or live branch, trunk or fruits) where foraging occurred and estimated the height above ground. Because the density of birds on the island was high, there were few areas where saddlebacks did not nest or forage. Only six unused control sites could be identified with confidence.

Field sampling

Vegetation composition

Vegetation sampling aimed to quantify the vertical and horizontal vegetation architecture of preferred nesting areas. For vertical structure, we wanted to know how the foliage cover varied in height, density and species dominance. For horizontal structure, we wanted to know the dominant plant species and how each was distributed through the vegetation. Vegetation structure was measured in February and March 2005 using the Recce method (Allen 1992), in four subplots (10 × 10 m) within a larger quadrat

(20 × 20 m) around the chosen nests in bird territories or around a random point in the unused control sites. In each, the percentage cover of individual plant species was recorded similarly for each class (1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%) and each tier height (Tier 1 = >12 m, Tier 2 = 5–12 m, Tier 3 = 2–5 m, Tier 4 = 30 cm – 2 m, Tier 5 = <30 cm, Tier 6 = epiphytes). Diameter at breast height (dbh at 1.35 m) was measured using a flexible tape measure for all trees greater than 10-cm dbh, while total canopy cover was visually established. The ground cover was assessed by percentage of vegetation, moss, lichen, litter, bare ground, rock, and dead logs.

Nest characteristics

To determine whether saddlebacks showed preferences for nesting in particular cavities, we measured used and unused randomly chosen cavities, with a flexible metal measuring tape. All cavities within the Recce quadrats (20 × 20 m) that could contain a nest cup of 13–23 cm and had an entrance larger than 10 cm were considered as potential nesting cavities. Four internal cavity characteristics were considered: (1) entrance height, (2) internal cavity height, (3) horizontal cross section (internal width *i* and *ii*); and four external characteristics: (1) tree species, (2) height of cavity above ground, (3) orientation of the cavity entrance, and (4) branch or trunk diameter (Sedgely 2003).

Food availability

Saddlebacks are known to feed mostly by searching for invertebrates under bark or by gleaning leaves on trees (Pierre 2001). Thus, the leaves, branches and bark of eight trees from the three dominant species within each quadrat (20 × 20 m), in foraging and control plots, were searched. Invertebrates were collected using forceps and a paintbrush from within a small (30 × 30 cm) quadrat at breast height (1.35 m) on tree trunks and preserved in plastic bottles containing 70% ethanol and 5% glycerol. All specimens were identified to order level. Invertebrate larvae of all taxa were considered as a separate group.

Statistical analysis

To determine differences in structural composition of vegetation and invertebrate abundance and taxonomic diversity between control and saddleback breeding sites, we plotted a non-metric multidimensional scaling (NMDS) ordination based on a Bray–Curtis dissimilarity distance matrix, and performed a one-way ANOSIM in the computer software package PRIMER[®] (Plymouth Routines in Multivariate Ecological Research, Plymouth Marine Laboratory, UK) on: (1) plant species cover per tier height, (2) number of stems per dbh class, and (3) number of specimens per invertebrate order (Clarke 1993; Clarke & Warwick 1998). To establish which plant or tree species and invertebrate order drove the dissimilarity between

treatment sites, we estimated the percentage contribution for each variable to 90% dissimilarity between and within sites using SIMPER analysis in PRIMER[®] (Clarke & Warwick 1994). The first five contributing variables were then plotted in a principal component analysis (PCA) to derive indices (first three principal components explaining >80% of variation between sites) of structural composition in vegetation and invertebrate composition. When required we normalised by log or fourth-root transformation (Clarke & Warwick 1994).

Comparisons of mean and standard deviation between treatment sites for environmental and nest variables were performed in SPSS using *t*-tests, ANOVA (or their non-parametric equivalents), and chi-squared analysis. Cavity orientations were tested for uniformity around an assumed circle, using the Rayleigh's test; and for differences in mean angle between treatment sites using the Watson-Williams test for two samples (Zar 1999). Principal components and variables of structural composition in vegetation, nest characteristics, and food availability showing significant differences between control and saddleback breeding sites were modelled in a binary logistic regression to derive the probability of a site being used by saddlebacks. The second-order Akaike Information Criterion corrected for small sample size (AIC_c) was calculated to determine the model that 'best' explained the variation in the data (Burnham & Anderson 2002). The use of AIC_c is recommended when the ratio of sample size (n) to number of variables (K) is less than 40 (Burnham & Anderson 2002), which applies in this study. We estimated models with AIC_c differences (ΔAIC_c) less than 2 to be best, and considered models with ΔAIC_c ranging from 2 to 7 to underline influential ecological processes (Burnham & Anderson 2002). Wald's chi-squared statistic was used to test the null hypothesis that regression coefficients were equal to 0 and to assess the contribution of individual variables to the model.

Positive parameter coefficients in the logistic regression equations indicated that an increase in the value of a variable raised the probability of a bird selecting a site for breeding, and negative parameter coefficients indicated that this probability decreased.

Saddlebacks were reintroduced in 1994 onto Motuara Island where they have successfully established. To determine variation in habitat quality between territories, we thus considered sites occupied during the first breeding season after reintroduction (1995) according to Pierre's mapping (1999), and those occupied since 2002 (2002–2004). We then explored differences in vegetation structure and composition, and tree invertebrate abundance and taxonomic diversity between territories, as described above, using NMDS, ANOSIM, and SIMPER analysis in the computer software package PRIMER[®]. We compared territorial differences in nest characteristics (tree species, cavity type and measurements) using Kruskal-Wallis or Pearson chi-squared tests.

Results

Breeding site selection

Vegetation structural composition

A total of 148 vascular plant species were recorded on Motuara Island during our Recce survey, with a mean of 90 in unused random control sites, and 115 in saddleback territories. Vegetation composition was significantly different ($R_{anosim} = 0.447$, $P = 0.01$) between control and saddleback territories (Fig. 2a), and the average dissimilarity of all pairwise coefficients of plant species cover per tier height between unused control plots and nest sites was 65.85% (Table 1). However, variables contributed to less than 2% of the dissimilarity. The canopy within saddleback sites was dominated by broadleaved species

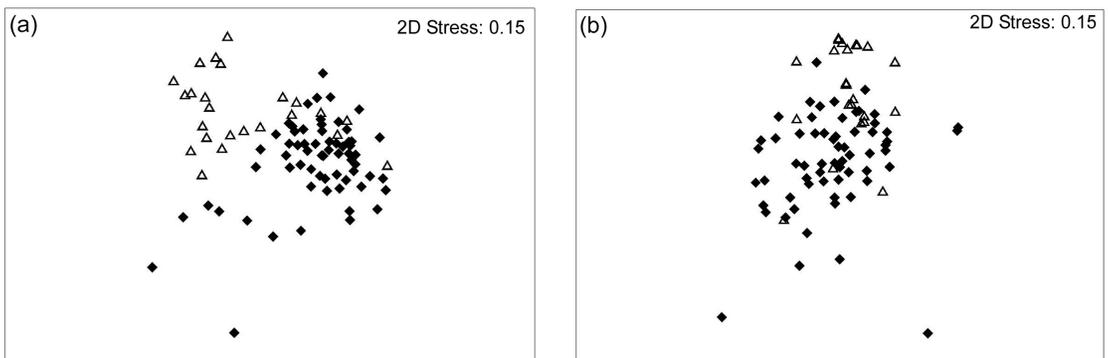


Figure 2. Two-dimensional NMDS ordination derived from all 10 × 10-m subplots at each site, showing differences in vegetation composition (a) per tier height and (b) in tree sizes, between unused control (\triangle) and saddleback breeding (\blacklozenge) sites on Motuara Island.

that determined the vertical structure of the vegetation: *Pseudopanax arboreus* at 5–12 m, *Melicytus ramiflorus* at 2–5 m, and *Macropiper excelsum* at 30 cm – 2 m (Table 1; Appendix 1). In unused sites, the ground cover contained more rocks in comparison with bird territories, and *Kunzea ericoides* cover dominated the upper canopy at 5–12 m. Indices of vegetation composition, derived from PCA analysis of plant species cover per tier height, expressed 78.8% of the variation between sites with three principal components (PC). The first PC separated sites according to *Kunzea ericoides* cover at 5–12 m height and rock cover (positive coefficients) from the cover of broadleaved species (*Pseudopanax arboreus* at 5–12 m, *Melicytus ramiflorus* at 2–5 m and *Macropiper excelsum* at 30 cm – 2 m) (negative coefficients); and the second PC axis according to *K. ericoides* and *P. arboreus* (5–12 m) cover (positive coefficients) from *Melicytus ramiflorus* (2–5 m), *Macropiper excelsum* (30 cm–2 m), and rock cover (negative coefficients) (Appendix 1).

Stand structure was also significantly different ($R_{\text{anosim}} = 0.194, P = 0.01$) between control and saddleback territories (Fig. 2), and the average dissimilarity of all pairwise coefficients of number of tree stems per dbh class between unused control plots and nest sites was 78.74% (Table 1). Five variables, the dbhs (10–30 cm) of *Kunzea ericoides*, *Pseudopanax arboreus*, *Melicytus ramiflorus*, *Dysoxylum spectabile* and *Cyathea dealbata*, accounted for more than 50% of the dissimilarity. A second index of structural composition was derived from

the three principal components of these five variables which explained 74.7% of the variation between sites (Appendix 1). The first PC separated sites according to the number of small *Kunzea ericoides*, *Cyathea dealbata* and *Pseudopanax arboreus* (positive coefficients) from the number of small *Melicytus ramiflorus* and *Dysoxylum spectabile* (negative coefficients). In general, saddleback breeding territories on Motuara Island contained more tree stems (especially those with dbh of 30–50 cm) in comparison to unused control sites, resulting in larger mean and maximum tree dbh and denser canopy cover (38% mean canopy cover) (Table 2).

Nest characteristics

The total number of available cavities for nesting was not significantly different between control and saddleback breeding sites (Table 2). Cavities in saddleback breeding territories were found in trees with larger diameters (mean dbh = 41 cm) than in control sites (mean dbh = 23 cm), but did not differ otherwise (Table 2). Measured cavities were mostly found in live trees, predominantly *Melicytus ramiflorus* (Table 3), and all except one were in tree hollows. Although tree species that provided available cavities were not significantly different between control and saddleback breeding sites, cavities in saddleback territories were found in a wider range of tree species (Table 3). Cavities in control sites were not uniformly oriented ($Z_{0.05, 10} = 0.381, P < 0.05$) but faced mostly south-east (median angle = 145°); however, the mean

Table 1. Test of dissimilarity between unused control and nest sites of saddlebacks, in terms of plant species cover per tier height and number of tree stems per dbh class, on Motuara Island.

Variables	Control (<i>n</i> = 24)	Saddlebacks (<i>n</i> = 64)	Dissimilarity
	Average abundance	Average abundance	Percentage contribution
<i>Plant species cover per tier height</i>			
Overall dissimilarity = 65.85%			
Explanatory variables			
<i>Pseudopanax arboreus</i> (5–12 m)	1.00	2.67	1.77
<i>Macropiper excelsum</i> (30 cm – 2 m)	0.54	2.72	1.76
<i>Melicytus ramiflorus</i> (2–5 m)	0.38	2.20	1.49
Rock	2.67	2.23	1.41
<i>Kunzea ericoides</i> (5–12 m)	1.92	1.06	1.29
<i>Number tree stems per dbh class</i>			
Overall dissimilarity = 78.74%			
Explanatory variables			
<i>Kunzea ericoides</i> (10–30 cm)	3.91	0.77	16.24
<i>Pseudopanax arboreus</i> (10–30 cm)	2.65	4.90	14.06
<i>Melicytus ramiflorus</i> (10–30 cm)	0.26	1.73	10.95
<i>Dysoxylum spectabile</i> (10–30 cm)	0.39	0.90	6.46
<i>Cyathea dealbata</i> (10–30 cm)	0.17	0.73	5.12

Table 2. Comparison of mean (\pm SD) for measures of vegetation structure and cavity size, between unused control sites and saddleback territories on Motuara Island. (^avariable failed the Levene's test of homogeneity and a Mann-Whitney *U* test was performed instead).

Variables	Control	Saddlebacks	F/U	P
	Mean \pm SD	Mean \pm SD		
<i>Vegetation structure</i>	(n = 24)	(n = 64)		
Canopy cover (%)	21.2 \pm 16.3	38 \pm 22.3	11.2	0.001
Canopy height	9.1 \pm 3.6	10.9 \pm 3.8	3.3	0.072
Number of cavities	0.3 \pm 1.2	0.4 \pm 0.8	646.5 ^a	0.133
Total number trees (10–30 cm)	8.3 \pm 4.6	10.6 \pm 6.4	628.5	0.190
Total number trees (30–50 cm)	0.1 \pm 0.5	1.1 \pm 1.3	447.5	0.001
Total number trees (50–70 cm)	0.0 \pm 0.0	0.0 \pm 0.1	744.0	0.384
Total number trees (> 70 cm)	0.0 \pm 0.0	0.0 \pm 0.0	756.0	0.540
Total number trees	8.5 \pm 4.5	11.8 \pm 6.3	535.0	0.029
Mean dbh	15.7 \pm 1.4	19.5 \pm 6.2	414.0	0.001
Maximum dbh	24.4 \pm 8.9	34.5 \pm 15.4	398.5	0.001
<i>Nest (cavity) characteristics</i>	(n = 9)	(n = 29)		
Entrance (cm)	36.5 \pm 25.9	43.4 \pm 25.1	0.157	0.695
Internal cavity height (cm)	108.8 \pm 102.0	90.3 \pm 42.2	120.5 ^a	0.736
Branch/trunk diameter (cm)	23.3 \pm 5.2	41.0 \pm 26.2	9.253	0.004
Internal-cross-section width <i>i</i> (cm)	20.7 \pm 4.8	20.4 \pm 7.7	0.014	0.906
Internal-cross-section width <i>ii</i> (cm)	19.4 \pm 7.3	23.2 \pm 11.7	0.805	0.376
Height above ground (cm)	74.7 \pm 59.5	108.0 \pm 78.6	1.356	0.252

Table 3. Comparison of percentage of measured cavities for each tree species or support, between unused control sites and saddleback territories on Motuara Island ($U_{9, 29} = 100.5$, $P > 0.05$).

Tree species	Control (n = 9)	Saddlebacks (n = 29)
<i>Meliccytus ramiflorus</i>	88.9	79.4
<i>Pseudopanax arboreus</i>	0	7.0
<i>Kunzea ericoides</i>	0	3.4
<i>Olearia paniculata</i>	0	3.4
<i>Cortaria arborea</i>	0	3.4
Dead tree	11.1	3.4
Total (%)	100.0	100.0

degree of orientation of available cavities did not differ ($F_{0.05, 41} = 0.128$, $P > 0.05$) between unused control plots and saddleback sites.

Foraging behaviour and food availability

During 12 out of 43 observations, individual saddlebacks were foraging on the ground, amongst litter (6% of the observations), under fallen dead branches and logs (1.2%), on fallen *Macropiper excelsum* and *Corynocarpus laevigatus* berries (2.4%), under roots (1.2%) or under seaweeds and rocks on the beach (1.2%). More often, birds were observed foraging on trees from 30 cm to 5 m in height, independently of tree species ($F_{4, 20} = 1.046$,

$P > 0.05$). They fed mostly on *Pseudopanax arboreus*, *Kunzea ericoides* and *Meliccytus ramiflorus*, and on invertebrates, and occasionally on fruits (Table 4). The part of a tree that birds were observed foraging on was significantly related to the tree species itself ($\chi^2 = 19.853$, $P < 0.05$). For example, birds fed on live branches and leaves of *Meliccytus ramiflorus*, *Pseudopanax arboreus* and *Macropiper excelsum*, on trunks of dead trees, *Kunzea ericoides* and *Leptospermum scoparium*, and on dead branches of *P. arboreus*.

Invertebrate composition on tree trunks was significantly different ($P_{\text{anosim}} = 0.133$, $P = 0.02$) between saddleback foraging and unused control sites, with saddleback territories containing more Gastropoda and Isopoda, and control sites more Hemiptera, Blattodea and invertebrate larvae (Table 5). Invertebrate numbers were highly patchy between sampled trees, and larvae, Hemiptera, Coleoptera and Blattodea appeared the more variable orders between tree species (Appendix 2). Larvae and Araneae were abundant on the trunks of *Griselinia lucida*, *Meliccytus ramiflorus*, *Macropiper excelsum*, *Pseudopanax arboreus*, *Dysoxylum spectabile* and *Kunzea ericoides* (Appendix 2); leaves of *P. arboreus* and *D. spectabile* trees hosted a large number of Hemiptera (scale insects), and Coleoptera were significantly more numerous on *M. ramiflorus*, *M. excelsum* and *G. lucida*. A great number of Annelida and Amphipoda were present on tree ferns (*Cyathea* spp.) (Appendix 2). Indices of invertebrate composition, derived from PCA analysis of

Table 4. Percentage of foraging observations per tree species or support, and part of tree in saddlebacks on Motuara Island.

Variables	Observations (%)
Live tree	87.8
Dead tree	12.2
<i>Tree species/support</i>	
<i>Pseudopanax arboreus</i>	34
<i>Kunzea ericoides</i>	19.1
<i>Melicytus ramiflorus</i>	19.1
<i>Macropiper excelsum</i>	6.4
Dead tree	4.3
<i>Cyathea</i> spp.	4.3
<i>Coprosma lucida</i>	2.1
<i>Dysoxylum spectabile</i>	2.1
<i>Leptospermum scoparium</i>	2.1
<i>Pseudowintera colorata</i>	2.1
<i>Cupressus macrocarpa</i>	2.1
<i>Pseudopanax crassifolium</i>	2.1
<i>Part of tree</i>	
Leaves	33.3
Live branches	24.4
Trunk	22.2
Dead branches	15.6
Fruits	2.2
Pine cones	2.2

the number of specimens per order, expressed 86.9% of the variation between sites with three principal components. The first and second principal components separated sites according to the number of larvae and Hemiptera at one end of the axis from the number of Gastropoda and Isopoda at the other end (Appendix 1).

Habitat selection models

Derived from the above results, variables that were significantly different between unused sites and territorial sites were selected to describe a bird's habitat and were thus entered in a binary logistic regression model. However, due to small sample sizes, only seven parameters allowed calculations for the construction of regression models: number of trees with dbh 30–50 cm, mean and maximum dbh, first and second principal components of vegetation composition per height tier, tree species per dbh class, and invertebrate abundance on tree trunks. Of these, models that considered the first two principal components of vegetation composition presented the best fit (Models 1 and 2, Table 6).

The probability of a saddleback using a site for breeding increased with dense cover of *Macropiper excelsum* at 30 cm–2 m and *Melicytus ramiflorus* at 2–5 m; and decreased with dense canopy cover of *Kunzea ericoides* at 5–12 m (Models 1 and 2, Table 6; Appendix 1). Although

Table 5. Test of dissimilarity for total number of invertebrate specimens per order in tree samples, between unused control sites and saddleback foraging sites.

Tree invertebrates	Control (<i>n</i> = 24)	Saddlebacks (<i>n</i> = 24)	Dissimilarity
	Average abundance	Average abundance	Percentage contribution
Overall dissimilarity = 42.61%			
Gastropoda	2.14	6.19	7.06
Hemiptera	97.67	3.67	6.81
Isopoda	3.62	7.56	6.81
Blattodea	4.05	1.89	6.56
Chilopoda	2.48	1.00	5.60
Larvae	47.86	28.70	5.33

Table 6. Explanatory variables included in each binary logistic regression model on habitat selection by saddlebacks on Motuara Island.

Model	Explanatory variables	Coef.	SE	Wald	<i>P</i>	–2LL ^a	<i>K</i> ^b	AIC _c ^c	ΔAIC _c ^d
1	Constant	2.089	0.514	16.532	<0.05	43.925	3	50.211	0.001
	1 st PC vegetation composition	–2.018	0.435	21.547	<0.05				
	2 nd PC vegetation composition	–0.938	0.369	6.474	0.011				
2	Constant	1.853	0.492	14.201	<0.05	41.505	5	52.237	2.027
	1 st PC vegetation composition	–2.197	0.507	18.805	<0.05				
	2 nd PC vegetation composition	–0.480	0.460	1.090	0.296				
	1 st × 2 nd PC vegetation composition	–0.624	0.426	2.149	0.143				

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

the cover of *Pseudopanax arboreus* at 5–12 m and rocks determined site differences between used and unused sites (Table 1), these did not influence the probability of a saddleback using a site for breeding (Models 1 and 2, Table 6, Appendix 1). Models that considered tree size (tree species per dbh class and number of stems with dbh 30–50 cm) in addition to vegetation composition, and food availability (abundance and diversity of invertebrate orders) showed less support than the best-fitted models ($\Delta AIC_c > 7$).

Territorial variation in habitat components

Territorial variation in vegetation structure

Soon after reintroduction, saddlebacks settled mostly on the west and south-east coast of Motuara Island (Fig. 3).

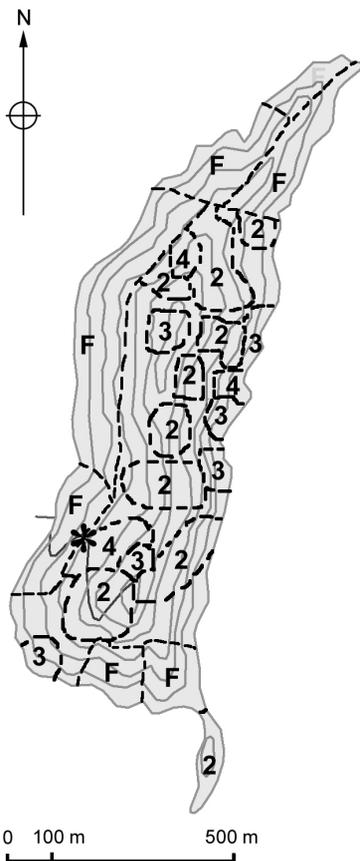


Figure 3. Map of sites colonised by reintroduced saddlebacks since reintroduction on Motuara Island. Boundaries of founders' territories (F), as mapped by Pierre (1999) the first breeding season after release in 1994–1995, are compared with areas colonised since 2002 (2), 2003 (3) and 2004 (4) (based on sightings and nesting records).

Areas first occupied for breeding in 2002 were mostly located on the eastern side of the island ridge. In 2003–04, newly occupied sites filled up gaps in the centre and along the eastern coast. Vegetation composition ($R_{anosim} = 0.375$, $P = 0.01$) and stand structure ($R_{anosim} = 0.173$, $P = 0.01$) differed significantly between areas occupied soon after reintroduction and those subsequently used after 2002, but invertebrate composition on tree trunks did not ($R_{anosim} = -0.012$, $P = 0.543$). Plant species' contribution to the 60% dissimilarity in vegetation composition between control and unused sites was still low (<2%), but small *Pseudopanax arboreus*, *Melicytus ramiflorus* and *Dysoxylum spectabile* stems contributed c. 30% of dissimilarity in stand structure between territories (Table 7). Areas occupied after 2002 had significantly denser canopy cover (mean canopy cover in areas occupied after 2002 = 41.7%, in comparison with 31.7% in first-occupied areas), greater number of trees with dbh of 30–50 cm, and in general, larger tree stems than in first-occupied sites (Table 7). Sites occupied soon after translocation were located closer to the coast than later occupied sites. Available cavities did not differ in number or in size between occupied areas, but were found in smaller branches or trunks in areas occupied after 2002 (Table 8).

Territorial variation in nest characteristics

In general, saddleback nests on Motuara Island were found mostly in cavities of *Melicytus ramiflorus* (44.1%), or under *Phormium cookianum* (flax) (19.1%) and rocks (10.3%) (Table 9). Nest height varied significantly according to tree species or substrates ($\chi^2 = 35.629$, $P < 0.05$) from ground level, under rocks or in *P. cookianum*; and up to 1.2 m above ground inside *Melicytus ramiflorus* and *Kunzea ericoides* cavities. However, in areas occupied soon after reintroduction, saddlebacks nested significantly ($U = 88.0$, $P < 0.05$) closer to the coast and at a lower height above ground (<1 m), mostly in flax (Tables 8 and 9). Later on, newly established breeding pairs built nests predominantly in cavities on *Melicytus ramiflorus* (64.9% of all nests).

Discussion

Modelling habitat components that influence site selection in reintroduced bird populations can be an important tool in the management of endangered species, because species interactions with the physical environment often determine the success of translocation programmes (Luck 2002b; Sergio et al. 2003; Gibson et al. 2004a,b; Bollmann et al. 2005). Multi-scale approaches in habitat studies have demonstrated the subtle relationships between animals and the environments they live in, where habitat preferences at a landscape level may be dictated by environmental variations at the micro-scale level (Penteriani et al. 2003;

Table 7. Test of dissimilarity between saddleback territories established soon after reintroduction and those occupied since 2002, in terms of plant species cover per tier height and number of tree stems per dbh class, on Motuara Island.

	First breeding season (<i>n</i> = 12)	Since 2002 (<i>n</i> = 20)	Dissimilarity
	Average abundance	Average abundance	Percentage contribution
<i>Plant species cover per tier height</i>			
Overall dissimilarity = 60.06%			
Explanatory variables			
<i>Pseudopanax arboreus</i> (5–12 m)	2.46	2.80	1.90
<i>Dysoxylum spectabile</i> (2–5 m)	0.21	2.23	1.79
<i>Dysoxylum spectabile</i> (5–12 m)	0.13	2.03	1.79
<i>Melicytus ramiflorus</i> (5–12 m)	0.96	1.90	1.47
Litter	4.08	4.88	1.44
<i>Melicytus ramiflorus</i> (2–5 m)	2.00	2.20	1.44
<i>Number tree stems per dbh class</i>			
Overall dissimilarity = 75.46%			
Explanatory variables			
<i>Pseudopanax arboreus</i> (10–30 cm)	4.95	4.88	11.07
<i>Melicytus ramiflorus</i> (10–30 cm)	1.86	1.65	10.85
<i>Dysoxylum spectabile</i> (10–30 cm)	0.00	1.40	7.71
<i>Kunzea ericoides</i> (10–30 cm)	0.64	0.85	6.76
<i>Olearia rani</i> (10–30 cm)	0.73	0.18	6.11
<i>Cyathea dealbata</i> (10–30 cm)	0.09	1.08	5.75

Table 8. Effect of year an area was first occupied by a breeding pair on environmental and cavities characteristics (mean \pm SD) in saddleback territories on Motuara Island.

Saddleback sites	First breeding season		Since 2002		<i>U</i> / χ^2	<i>P</i>
	<i>n</i>	Mean \pm SD	<i>n</i>	Mean \pm SD		
<i>Nest characteristics</i>						
Distance to coast	24	38.1 \pm 35.8	33	103.1 \pm 39.0	88.0	<0.05
Nest height	31	0.4 \pm 0.5	37	1.1 \pm 0.8	426.0	0.056
<i>Vegetation structure</i>						
Canopy cover	12	31.7 \pm 22.0	20	41.7 \pm 21.9	176.0	<0.005
Canopy height	12	8.1 \pm 3.7	20	12.5 \pm 2.8	351.0	0.073
Number trees (10–30 cm)	12	9.4 \pm 5.9	20	11.4 \pm 6.6	416.0	0.373
Number trees (30–50 cm)	12	0.5 \pm 0.7	20	1.5 \pm 1.5	282.0	0.004
Number trees (50–70 cm)	12	0.0 \pm 0.0	20	0.0 \pm 0.2	456.0	0.269
Number trees (>70 cm)	12	0.0 \pm 0.0	20	0.0 \pm 0.1	468.0	0.439
Total number trees	12	9.9 \pm 6.2	20	13 \pm 6.1	359.5	0.094
Mean dbh	12	16.2 \pm 6	20	21.6 \pm 5.5	249.0	0.001
Maximum dbh	12	27 \pm 11.9	20	39 \pm 15.6	262.0	0.002
Number cavities	12	0.3 \pm 0.7	20	0.5 \pm 0.9	442.0	0.512
<i>Cavity measurements</i>						
Entrance	6	33.4 \pm 11.7	19	46.6 \pm 27.6	43.0	0.400
Internal cavity height	8	77.8 \pm 43.3	21	95.1 \pm 46.0	64.0	0.349
Height above ground	8	110.2 \pm 91.2	21	107.1 \pm 75.7	84.0	1
Branch/trunk diameter	8	69.9 \pm 41.2	21	31.8 \pm 7.3	33.0	0.011
Internal-cross-section width <i>i</i>	8	21.6 \pm 9.1	21	20.0 \pm 7.4	72.0	0.582
Internal-cross-section width <i>ii</i>	8	21.5 \pm 8.0	21	23.8 \pm 13.0	83.5	0.981

Table 9. Mean height and percentage of saddleback nests per tree species or support type, on Motuara Island for all sites, for years an area has been occupied by a breeding pair since reintroduction, and for successful and unsuccessful nests.

Tree species/support	All sites		Occupied areas	
	Mean nest height (m)	All nests (%)	First breeding season (%)	Since 2002 (%)
	(n = 67)	(n = 67)	(n = 30)	(n = 37)
<i>Phormium cookianum</i>	0.28	19.1	35.5	5.4
<i>Meliccytus ramiflorus</i>	1.28	44.1	19.4	64.9
Rocks	0.29	10.3	19.4	2.7
<i>Pseudopanax arboreus</i>	0.80	8.8	9.7	8.1
<i>Arthropodium cerratum</i>	0.00	2.9	6.5	0
Coastal bank	0.00	1.5	3.2	0
<i>Cyathea</i> spp.	0.00	2.9	3.2	2.7
Dead trees	0.43	4.4	3.2	5.4
<i>Kunzea ericoides</i>	1.10	5.9	0	10.8

Sergio et al. 2003; Gibson et al. 2004a; Graf et al. 2005). For example, Bonelli's eagles (*Hieraetus fasciatus*) showed preferences for water or open areas (landscape), which coincided with highest quality foraging habitats for this species (micro-scale) (Penteriani et al. 2003). In the modelling of bird-habitat, foliage or plant species cover and structural variation in vegetation density are variables that are the most widely cited to explain micro-scale habitat selection (Best & Bellingham 1991; Green et al. 2000; Ricketts & Ritchison 2000; Reich et al. 2004; Bollmann et al. 2005). Foliage density, for example, may affect habitat choice by birds by reducing the risk of predation or by creating microclimates that influence convection heat loss at the nest, for open as well as cavity nesters (Calder 1973; Walsberg 1981, 1985; Cody 1985; With & Webb 1993).

In the case study of reintroduced saddlebacks onto Motuara Island, the multi-scale approach of habitat selection showed a macro-scale preference for sites nearest to the coast that was primarily explained by micro-scale complex structural composition of the vegetation. Especially, breeding pairs showed preferences for sites dominated by mixed-broadleaved stands of *Macropiper excelsum* at 30 cm – 2 m, *Meliccytus ramiflorus* at 2–5 m and *Pseudopanax arboreus* at 5–12 m, which also contributed to a denser upper canopy. Similarly, a direct relationship was previously established between plant species composition and habitat selection in South Island saddlebacks on Ulva Island where preference was given for sites with denser cover of *Metrosideros umbellata* and *Ripogonum scandens* that contributed to a denser low canopy (Michel 2006).

In this study, the experimental design was established on the assumption that breeding site selection in this reintroduced bird population was determined first by high quality habitat as defined by dense vegetation structure, abundant food availability, and diverse nesting substrates.

However, if habitat selection was random or influenced by proximity to the release sites, bird territories chosen would not necessarily be of high quality. Although vegetation composition was very different on Ulva and Motuara islands, habitat selection in South Island saddlebacks showed similarity in response to vegetation structure, and preference for coastal habitat (Michel 2006). Differences in site locations and vegetation composition between areas occupied soon after reintroduction and those recorded after 2002 suggested reintroduced saddlebacks onto Motuara Island primarily settled at the margins of coastal scrub and forest. Later cohorts moved into larger stands of coastal forest where they established breeding territories. The pattern shown here was similar to that established for Ulva Island. For the Motuara Island reintroduced population, coastal scrub also reflected a familiar vegetative environment when compared with the birds' source location. Moreover, coastal habitats, in general, offered more abundant and diverse nesting support and food items for successful breeding than did inland habitats.

Plant species are an important component of bird habitats by determining fruiting density and invertebrate composition (food availability). Often, birds' presence and fitness are greatly dependent on prey or floristic abundance, diversity and quality (Ford & Paton 1985; Ontiveros & Pleguezuelos 2000). Plant species on Motuara Island were important in providing breeding saddleback pairs with adequate food supply. Invertebrate life, if not more abundant, was more diverse on tree trunks of broadleaved species. *Pseudopanax arboreus* was the primary plant species on which saddlebacks were observed to forage, and hosted a high abundance of Hemiptera and an average abundance of all other dominant invertebrate groups. Saddlebacks seasonally foraged on berries of *Macropiper excelsum* and *Corynocarpus laevigatus*, and occasionally on honeydew and *Phormium cookianum* (Pierre 2000, 2001).

Territorial overlaps appeared frequent on Motuara Island, and pairs were often observed sharing foraging sites or drinking outside territorial boundaries (Pierre 1999), most likely associated with the relatively high density of birds. Water sources on Motuara Island are highly localised and not readily available in the long hot summer. Although saddlebacks showed initial site preferences for coastal habitat, no habitat type was avoided as saddlebacks regularly visited the least preferred *Kunzea*-dominated bush during short foraging trips. Even though saddlebacks still fed predominantly on trees, they were often observed foraging on the ground. Fallen berries and seaweeds were mainly eaten by juvenile birds, and even if they were not a main food item for breeding birds, they might still be important for post-fledgling survival in this location. In contrast, on Ulva Island, where resources were highly patchy, birds exhibited highly territorial behaviour and preference for coastal habitats (Steffens et al. 2005; Michel 2006). On Ulva Island, coastal trees (e.g. *Dracophyllum longifolium*, *Olearia colensoi*, *Brachyglottis rotundifolia*, and *Dicksonia squarrosa*) hosted significantly more larvae and their litter contained a greater abundance of all the major groups of arthropods than on inland podocarp species (Michel 2006). Coastal habitats also provided supplementary food during the fledgling period, as saddlebacks often foraged seasonally on *Pseudopanax arboreus* fruits (Merton 1966; Pierre 2000).

Saddleback pairs on Motuara Island showed nesting preferences for cavities in trunks or branches c. 40–50 cm in diameter of live broadleaved trees, but number, size and orientation of available cavities did not determine the establishment of their breeding territories (Michel 2006) –again, similar results to those obtained for saddlebacks on Ulva Island. Likewise, successful nests on Motuara Island were more often built in cavities on coastal banks or on live broadleaved species than on dead trees (Michel 2006). Cavities in live trees with a canopy are further protected against aerial predators (e.g. morepork, falcon or harrier) and harsh weather conditions than those in dead logs. Cavities in dead logs may also have more porous walls which could further affect microclimate inside the cavity, such as heat conduction or relative humidity (McComb & Noble 1981). Thus, cavity location and properties may be important in saddleback breeding ecology and should be further investigated and taken into consideration in the selection of future translocation sites.

Birds on Motuara Island showed partitioning in habitat use: preferred habitats were used for nesting while birds were foraging outside territorial boundaries or in shared sites. This behaviour had already been observed during the first breeding season after reintroduction (Pierre 1999), and thus is unlikely to be the result of increased density over time. Where high quality resources are clumped in distribution, animals hold and defend a territory, but where low quality resources are sparsely distributed animals roam over larger areas and are unable to viably

defend a territory (Davies & Houston 1984). Food and water availability appeared more sparsely distributed on Motuara Island than on Ulva Island and may explain the lack of territorial behaviour observed on the former. Consequently in the management of endangered species, the distribution of required resources and suitable habitats across the available landscape might also influence the survival and reproduction of saddleback populations. Therefore, resource distribution and abundance across the landscape may need to be accounted for in the modelling of density–bird–habitat relationships (Hobbs & Hanley 1990; Verboom et al. 1991). Increasingly, spatially explicit models (models that combine population simulators with the spatial distribution of landscape features) are used in wildlife management (Dunning et al. 1995; Liu et al. 1995; Reed et al. 2002) to account for these factors.

For conservation managers seeking predator-free translocation sites to establish new South Island saddleback populations, it seems necessary to evaluate habitat at both a landscape- and micro-scale. Vegetation structure and composition should provide nesting substrate on coastal banks or in flaxes (*Phormium* spp.), or in cavities of live broadleaved species. Food availability (invertebrates and fruiting tree species) should be abundant in close proximity to available nesting sites, or evenly spread and available throughout the landscape. In an environment where habitat quality is patchily distributed in the landscape (e.g. Ulva Island), birds may be confined to territorial boundaries avoiding unsuitable habitats, and reproduction may then become highly density-dependent. In contrast, in an environment where resources are scattered more homogeneously throughout the landscape (e.g. Motuara Island) birds may behave less territorially, thus counteracting a density-dependent effect on successful reproduction.

Resource distribution on Motuara Island may also reflect a mosaic vegetative pattern resulting from previous human-induced disturbance (cf. McGlone 1989). In New Zealand, young stands of regenerating *Kunzea ericoides* scrub were found to have low biological diversity in comparison with more botanically diverse broadleaved forests (Moeed & Meads 1992; Dugdale & Hutcheson 1997). Worldwide, ecotones are also known to support a greater abundance and diversity of species by providing a diversity of substrates for foraging or reproduction (Odum 1958; Baker et al. 2002). Likewise, structurally diverse forest habitats in New Zealand have been shown to be important for breeding mohua (*Mohoua ochracephala*) by providing more seasonal variety and availability of food items (Oppel & Beaven 2002). Stems of broadleaved species also provided saddleback populations on Ulva and Motuara islands with a diversity and abundance of food items and a complex vegetation structure, as well as cavities that enhanced birds' nesting success in comparison with cavities located in dead trees. Thus, mixed-sized stands with broadleaved species with a dense canopy appear

highly preferable in comparison to those dominated by *Kunzea ericoides* as future translocation sites.

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Appendix 1. Results of principal component analysis (PCA) comparing control sites with saddleback territories on Motuara Island for plant species composition, dominant tree structural composition, and invertebrate composition.

Principal components	1	2	3
<i>Vegetation composition</i>			
Eigenvalue	1.87	1.22	0.85
% variation	37.4	24.4	17.1
Cumulative % variation	37.4	61.7	78.8
<i>Kunzea ericoides</i> (5–12 m)	0.091	0.658	0.695
<i>Pseudopanax arboreus</i> (5–12 m)	-0.483	0.282	-0.368
<i>Melicytus ramiflorus</i> (2–5 m)	-0.565	-0.147	0.450
<i>Macropiper excelsum</i> (30 cm – 2 m)	-0.604	-0.272	0.156
Rock	0.274	-0.626	0.392
<i>Structural composition</i>			
Eigenvalue	1.63	1.14	0.97
% variation	32.6	22.7	19.3
Cumulative % variation	32.6	55.3	74.7
<i>Kunzea ericoides</i> (10–30 cm)	0.604	-0.003	0.095
<i>Pseudopanax arboreus</i> (10–30 cm)	0.076	-0.472	-0.865
<i>Melicytus ramiflorus</i> (10–30 cm)	-0.586	0.087	-0.181
<i>Dysoxylum spectabile</i> (10–30 cm)	-0.513	-0.405	0.296
<i>Cyathea dealbata</i> (10–30 cm)	0.154	-0.778	0.350
<i>Invertebrate composition on tree trunk</i>			
Eigenvalue	1.56	1.20	0.71
% variation	39.0	30.1	17.8
Cumulative % variation	39.0	69.1	86.9
Larvae	0.433	0.512	0.740
Gastropoda	0.649	-0.182	-0.302
Isopoda	0.600	-0.390	-0.031
Hemiptera	0.175	0.743	-0.600

Appendix 2. Comparison of invertebrate abundance in the dominant orders (mean \pm SD) per tree species in all sampled sites on Motuara Island.

	<i>Kunzea ericoides</i>	<i>Melicytus ramiflorus</i>	<i>Pseudopanax arboreus</i>	<i>Macropiper excelsum</i>	<i>Cyathea</i> spp.	<i>Dysoxylum spectabile</i>	<i>Griselinia lucida</i>	<i>Olearia paniculata</i>
Larvae	23.8 \pm 22.3	50.8 \pm 59.3	33.7 \pm 32.2	49.0 \pm 21.3	11.0 \pm 18.0	29.0 \pm 7.0	209.5 \pm 286.3	7.3 \pm 8.3
Hemiptera	3.4 \pm 3.6	10. \pm 6.0	114.7 \pm 324.1	1.6 \pm 1.9	5.7 \pm 8.2	249.5 \pm 351.4	3.0 \pm 2.8	0.3 \pm 0.5
Coleoptera	4.8 \pm 5.0	25.8 \pm 22.0	5.9 \pm 8.7	23.4 \pm 28	6.0 \pm 6.6	3.0 \pm 2.8	15.0 \pm 18.3	8.0 \pm 6.0
Blattodea	4.8 \pm 4.8	0.3 \pm 0.5	2.0 \pm 2.0	0.0 \pm 0.0	7.5 \pm 8.6	0.0 \pm 0.0	6.0 \pm 2.8	5.0 \pm 7.0
Araneae	19.5 \pm 20.1	23.3 \pm 27.6	6.7 \pm 4.6	11.0 \pm 8.4	9.5 \pm 9.9	29.0 \pm 15.5	12.0 \pm 8.4	17.0 \pm 26.0
Annelida	0.2 \pm 0.4	0.0 \pm 0.0	2.2 \pm 4.0	0.0 \pm 0.0	18.5 \pm 33.1	0.0 \pm 0.0	0.0 \pm 0.0	2.3 \pm 2.5
Amphipoda	0.0 \pm 0.0	0.6 \pm 0.8	2.0 \pm 4.8	0.0 \pm 0.0	16.0 \pm 31.3	0.5 \pm 0.7	0.0 \pm 0.0	0.0 \pm 0.0
Isopoda	3.6 \pm 6.2	6.5 \pm 6.7	12.0 \pm 24.8	0.2 \pm 0.4	10.2 \pm 14.5	3.0 \pm 4.2	0.0 \pm 0.0	0.0 \pm 0.0
Gastropoda	2.6 \pm 2.1	6.5 \pm 5.9	6.7 \pm 7.0	1.8 \pm 2.4	6.5 \pm 5.8	5.5 \pm 4.9	2.0 \pm 2.8	1.0 \pm 1.7