

Variation in breeding success among reintroduced island populations of South Island Saddlebacks *Philesturnus carunculatus carunculatus*

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South Island Saddlebacks *Philesturnus carunculatus carunculatus* were once found throughout the South Island of New Zealand, but by the early 1960s were confined to the island of Big South Cape, in the extreme south of the country. All subsequent reintroduced populations of South Island Saddlebacks are derived from 36 surviving birds from this relict population. The aim of this study was to compare the breeding success of three recently reintroduced populations of Saddlebacks relative to their distance from, and habitat similarity to, the relict population. The three study islands show a latitudinal cline with Ulva, Breaksea and Motuara Islands located 60, 190 and 810 km north of Big South Cape, respectively. Saddlebacks on Ulva and Breaksea appeared to prefer to establish breeding territories in coastal scrub, the dominant habitat feature of Big South Cape. The area of coastal scrub habitat was much smaller on Motuara, where breeding territories were instead scattered through broadleaf forest habitat. Nesting success, calculated using Mayfield's method, was significantly greater on Ulva (73%) than on Breaksea (32%) or Motuara (19%) owing primarily to higher egg fertility and hatching success. Although egg failure rates were highest on Motuara, the island least similar to Big South Cape, they were also relatively high on Breaksea where the habitat was similar to Ulva and Big South Cape. Therefore, the results only partially support the hypothesis that nesting success should decrease with increasing habitat difference associated with increasing latitudinal distance from the source population. The data from this 1-year study lay the groundwork for examining further hypotheses on the effects of reintroducing endangered species outside their contemporary range, but within their historical range.

The reintroduction of endangered species to areas within their historical range is increasingly important as a conservation strategy (Griffith *et al.* 1989, Wolf *et al.* 1996, IUCN 1998). One factor that can clearly affect reintroduction success is habitat suitability. The standard strategy used to determine the suitability of potential release sites is to compare proposed sites with the species' current habitat (Armstrong & McLean 1995). However, Gray and Craig (1991) argued that the current habitat of a species, particularly an endangered species confined to a relict population, may be suboptimal, and that consideration of the historical distribution and habitat it encompassed may be as important as the present distribution.

Furthermore, they argued that an animal's behavioural phenotype is generally flexible because of developmental plasticity, potentially allowing it to survive in habitats outside its current or even historical range.

Gray and Craig (1991) and Clout and Craig (1995) pointed to the successful translocation of two highly endangered birds with specific habitat requirements, New Zealand's Takahe *Porphyrio hoshstetteri* and Kakapo *Strigops habroptilus*, to support their arguments. Both species were introduced to offshore islands far outside the birds' present-day natural distributions and with habitats that differed substantially from those of their source populations. Both were confined to relict populations in alpine and semi-alpine habitat in cool-temperate parts of southern New Zealand and were subsequently

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transferred successfully to warm-temperate habitats on coastal islands further north, but within their historical distributions.

Although Takahe and Kakapo had high survival rates in their new habitats, Jamieson and Ryan (2000) noted that both species experienced marked declines in breeding success relative to that in their source populations, owing primarily to high egg infertility and low fledging success. Jamieson and Ryan (2000) postulated that although these species had a broad distribution historically, the individuals comprising the remnant populations might be better adapted to these localized environments. In addition, relict populations of both Takahe and Kakapo were likely to have been highly inbred, and reintroducing inbred individuals to novel environments can expose new genetic load (cf. Miller 1994, Bijlsma *et al.* 1999), resulting in higher egg infertility and lower fledging rates (Jamieson & Ryan 2000, Jamieson *et al.* 2003).

One other endangered New Zealand bird species, the South Island Saddleback *Philesturnus carunculatus carunculatus*, has been transferred from a relict population in the extreme periphery of its range and reintroduced to several islands within its historical range, whose habitats and environmental conditions differ substantially from those of the source island population. As in the Takahe and Kakapo cases, South Island Saddlebacks were confined to southern New Zealand and reintroduced to offshore islands further north, but their breeding success has not been evaluated.

The Saddleback is a medium-sized (*c.* 25 cm, bill to tail), cavity-nesting forest passerine and a member of the endemic New Zealand wattlebird family Callaeidae. Saddlebacks have two distinct geographical subspecies: *P. c. rufusater* in the North Island and *P. c. carunculatus* in the South Island, although Holdaway *et al.* (2001) now consider that the subspecies should be regarded as full species. Subfossil and historical records indicate that South Island Saddlebacks were formerly abundant and widespread throughout the South Island of New Zealand, including many offshore islands, and inhabited a variety of indigenous forest habitats such as beech, podocarp, broadleaf and dense coastal scrub (Williams 1976, Hooson 2000). Because of their habit of nesting and roosting on or close to the ground, Saddlebacks are extremely vulnerable to introduced mammalian predators. They declined rapidly following European settlement and were virtually extinct on the mainland by 1905 except for rat-free Big South Cape (939 ha) off the southern coast of Stewart Island (Fig. 1) (Merton 1975, Roberts 1994, Lovegrove 1996). Vegetation there is primarily coastal and low-lying scrub habitat.

The size of the Saddleback population on Big South Cape is unknown, but extrapolating from the densities of Saddlebacks on other islands (Hooson & Jamieson 2003a), Big South Cape could have supported at least 1000 birds. However, this remnant population was decimated when Ship Rats *Rattus rattus* invaded in 1962 (Merton 1975, Bell 1978). The New Zealand Wildlife Service (now Department

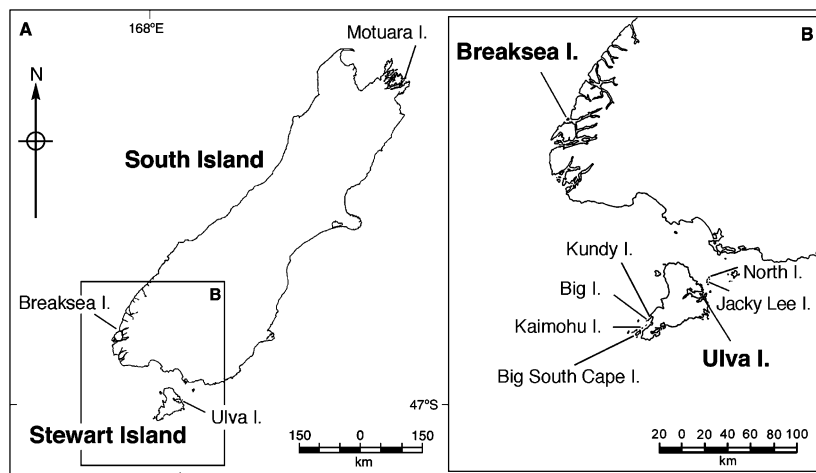


Figure 1. (A) Map of the South Island of New Zealand showing location of the three study sites: Ulva, Breaksea and Motuara Islands. (B) Location of islands from where reintroduced populations of South Island Saddlebacks on the three study sites were sourced (see Fig. 2).

of Conservation) transferred 36 Saddlebacks to two nearby rodent-free islands, Big Island (21 birds) and Kaimohu Island (15 birds), before the remaining population on Big South Cape was exterminated. Between 1964 and 1986, further translocations were made to several small, coastal islands lying just north of Big South Cape (Fig. 1). Most of these translocations resulted in established populations and the total number of birds is currently estimated to be 1200, spread among 15 island populations. (For a full account of the South Island Saddlebacks' translocation history and status, see Hooson & Jamieson, 2003a.)

Saddlebacks have more recently been translocated further north to Ulva (2000), Breaksea (1992) and Motuara (1994) Islands located 60, 190 and 810 km north of Big South Cape, respectively (see Fig. 1). Saddlebacks on Motuara experience substantially different environmental conditions and habitat from those of Big South Cape or the other nearby islands from where translocated Saddlebacks were sourced (see below). The founding lineages on Motuara had also gone through one more prior founding event than those on Breaksea, and two more than those on Ulva, although the numbers of birds released on the three islands were relatively large (Fig. 2).

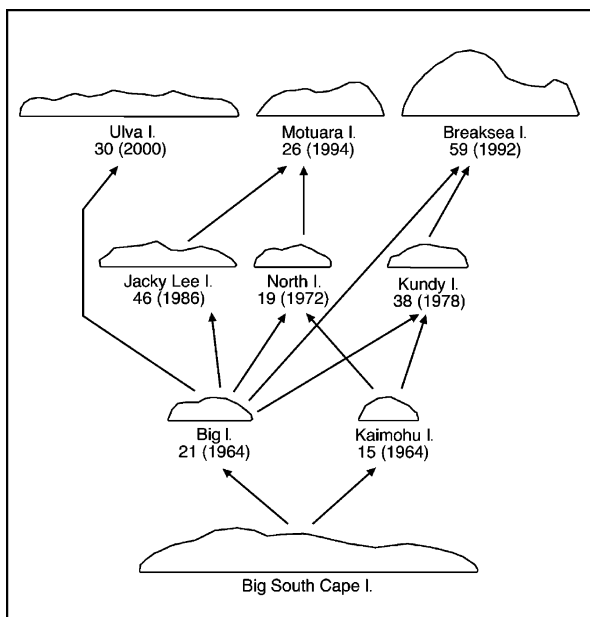


Figure 2. Diagram showing the translocation history of the South Island Saddlebacks from the three island study sites. The number of founders (year of translocation) are given below each island. Islands are not drawn to scale.

Ideally, a control population(s) that best replicated the conditions and habitats encountered by the (now extinct) population on Big South Cape would have been included in this study. The most suitable control islands with established populations of Saddlebacks are the Titi Islands on which indigenous Māori harvest Titi or Muttonbird *Puffinus griseus*, but access to these is prohibited outside the harvesting season (early April to May). Therefore, at the initiation of this study, Ulva, Breaksea and Motuara Islands were the only three populations of South Island Saddleback to which access could be obtained.

The objectives of this study were to compare habitat selection and nesting success among three island populations of South Island Saddleback, which varied in their distance from the last remnant population, but which were all within the historical range of the species. One prediction is that breeding success should decrease with increasing habitat and environmental differences associated with increasing latitudinal distance from Big South Cape Island. Thus nesting success should be greater on Ulva and Breaksea than on Motuara. Alternatively, if species exhibit ecological flexibility when translocated within their historical range (Gray & Craig 1991, Clout & Craig 1995), then breeding success might actually be enhanced on Motuara because its climate is more benign than is that of either Ulva or Breaksea.

METHODS

Study sites

Ulva Island (267 ha, maximum elevation 72 m asl) lies inside Paterson Inlet on the eastern side of Stewart Island (168°07.7'E, 46°55.9'S) and only 60 km north of Big South Cape (Fig. 1). The island has been free of exotic mammalian predators since Norway Rats *Rattus norvegicus* were eradicated in 1996, although Weka *Gallirallus australis*, a large flightless rail and an occasional predator of South Island Saddlebacks (A. Roberts pers. comm.), are present. Thirty adult Saddlebacks of unknown sex were reintroduced from Big Island in 2000 (Figs 1 & 2) (B. Beaven pers. comm.). Dense, low-lying forest, termed coastal scrub, and dominated by Leatherwood *Olearia colensoi*, Inaka *Dracophyllum longifolium* and Muttonbird Scrub *Senecio reinoldii* is found in a narrow fringe around most of the island (Fig. 3). Slightly further from the shore, the coastal scrub

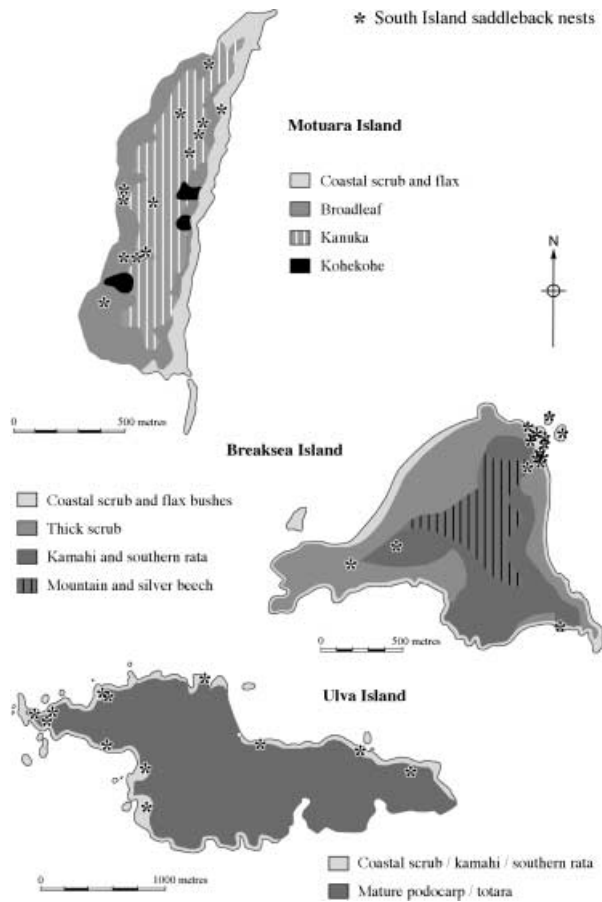


Figure 3. Nest locations of South Island Saddleback in relation to vegetation type on Motuara, Breaksea and Ulva Islands.

species intermix with Southern Rata *Metrosideros umbellata* and Kamahi *Weinmannia racemosa* (where most Saddlebacks built their nests; Fig. 3) before merging with mature podocarp forest. Podocarp forest consists primarily of Rimu *Dacrydium cupressinum*, Miro *Prumnopitys ferruginea* and Totara *Podocarpus hallii*; it dominates the island's habitat away from the coast (Fig. 3). Ulva's vegetation is similar in composition to that of Big South Cape, which consists of large areas of low coastal forest and scrub (Leatherwood and Inaka), intermixed with stunted Manuka *Leptospermum scoparium*, and flax bushes *Phormium cookium* at higher elevations above the coastal scrub, with patches of taller Inaka, Muttonbird Scrub, Manuka, Southern Rata, Kamahi and Rimu forest restricted to a few sheltered parts of the island (Hooson 2002).

Breaksea Island (170 ha, maximum elevation 350 m) lies c. 2 km off the coast of Fiordland

(166°38.5'E, 45°35'S) and c. 193 km north-west of Big South Cape. It is much more exposed to the open ocean than Ulva or Motuara Islands (Fig. 1). The island is now predator-free as Norway Rats were eradicated in 1988 (Taylor & Thomas 1993). Fifty-nine Saddlebacks of unknown sex (including 34 adults, 10 subadults and six fledglings) sourced from Big and Kundy Islands (Figs 1 & 2) were reintroduced in 1992 (Rasch & McClelland 1993). The island is steep, rugged and densely vegetated and can be divided into four major habitat types: coastal scrub and flax bushes particularly prominent on the lower elevations at the north-east end of the island (where many of the Saddleback nests were subsequently located); thicker scrub composed of Inaka, Mahoe *Melicetyx ramiflorus*, Tree Fuchsia *Fuchsia excorticata* and Tree Ferns *Dicksonia squarrosa* along the exposed seaward slopes and ridges; Kamahi and Southern Rata on the more protected slopes; and Mountain Beech *Nothofagus solandri* and Silver Beech *N. menziesii*, which dominate the canopy at mid to higher elevations (Fig. 3) (Allen *et al.* 1994). Except for the beech forest, vegetation composition on Breaksea is also similar to that of Big South Cape (see above).

Motuara Island (59 ha, maximum elevation 128 m) lies in the outer Queen Charlotte Sound (174°16.5'E, 41°05.5'S) 1.8 km from the mainland and 813 km north-east of Big South Cape Island (Fig. 1). Pacific Rats or Kiore *Rattus exulans* were eradicated in 1991 and the island is now free of mammalian predators (Cash & Gaze 2000). Twenty-six Saddlebacks (including seven adult and five subadult males, 11 adult and one subadult females and one adult and one subadult of unknown sex) were transferred from North and Jacky Lee Islands in 1994 (Figs 1 & 2) (Lovegrove 1996, Pierre 1999). Although extensively modified for farming until it was designated a Scenic Reserve in 1926, the vegetation is regenerating vigorously and the island is now predominantly covered by a low 3–8 m broad-leaf forest dominated by Five-finger *Pseudopanax arboreus* (Cash & Gaze 2000). Kanuka *Kunzea ericoides* is abundant along the main ridge and upper slopes and small patches of Kohekohe *Dysoxylum spectabile* forest persist in moister parts of the island. A narrow, coastal scrub habitat including flax and *Olearia paniculata* is only found along the eastern side of the island (Fig. 3). The composition of the vegetation on Motuara Island is least similar to that of Big South Cape, presumably owing to its warmer temperatures and drier summers.

Field methods

The three island study sites were first visited between April and June 2001 to locate and map Saddleback territories, which remain occupied year-round. The same sites were revisited between October and January 2001/02 during the breeding season. Motuara Island was visited between 1 and 26 October 2001 while Saddlebacks were courting and nest-building, and between 15 and 20 December 2001 and 14 and 15 January 2002 while they were incubating, brooding and caring for dependent fledglings. Breaksea Island was visited between 30 October and 22 November and 11 and 13 December 2001. Saddlebacks were also monitored on Ulva Island at all stages of the nesting cycle, from early September 2001 to 16 February 2002, as part of a larger study.

Saddleback nests were located by searching likely nesting cavities within a territory, following the flight paths of adults transporting food or nesting material and listening for calls indicative of nesting females returning to nests (Hooson & Jamieson 2003b). Nest contents were checked, and the development stage of eggs was estimated by candling and the ages of nestlings were estimated by their plumage development. Nests were revisited approximately once a week to limit the level of disturbance.

The clutch size of South Island Saddlebacks is almost invariably two (Hooson & Jamieson 2003b). Eggs that failed to hatch were opened, their contents examined and recorded as infertile if no signs of development were visible. The number of dependent fledglings was determined by locating and following parent Saddlebacks. As Saddlebacks are strongly territorial, pairs with dependent young do not move outside their home territory. If no fledglings were seen after observing both members of a pair continuously and simultaneously for 30 min, it was concluded the pair had no dependent fledglings.

Calculating nesting success

Mayfield (1961, 1975) demonstrated that the shorter the period over which nests are monitored, the lower the probability of observing nest losses. Thus the 'exposure' of each nest needs to be incorporated into calculations of nesting success to avoid biased estimates. The 'exposure' of a nest is defined as the time (in days) from when it was confirmed to contain eggs or chicks until it either failed or the chicks fledged (Mayfield 1961, 1975). Nests that failed at some point between visits were assigned

exposure days equal to 50% the length of the visiting interval for intervals < 15 days apart and 40% for intervals \geq 15 days (Johnson 1979).

Two native avian nest predators of Saddlebacks, the Australasian Harrier *Circus approximans* and the Morepork *Ninox novaeseelandiae*, are rare on the islands and unlikely to disturb nests inside tree cavities. The only other nest predator was the aforementioned flightless Weka on Ulva, which will occasionally predate nests that are close to the ground. Mayfield's method was developed primarily for calculating nest success (i.e. the probability of all nest contents surviving the complete nesting period) where nest losses result from predation or desertion. We were primarily concerned with nesting success where failures resulted from other causes such as egg infertility, or embryonic and nestling mortality. Therefore, instead of calculating exposure as 'nest-days', we calculated 'egg-days' and 'nestling-days' to measure the exposure of individual eggs and nestlings. Addled eggs were grouped with infertile eggs and the timing of egg loss assigned to the day of laying (Day 1). The timing of embryonic deaths during the incubation period (~20 days; Guthrie-Smith 1925, Hooson & Jamieson 2003b) was approximated from the stage of development (e.g. Days 1–5; 6–10; 11–15; 16–20). Hatching dates were similarly approximated from the nestling's plumage development (~26-day nestling period; Hooson & Jamieson 2003b). Fledging dates also had to be approximated in a few cases when fledglings were seen accompanying parent birds within their territory subsequent to the last nest visit.

Daily probabilities of loss during the incubation, nestling or nesting stage (incubation and nestling stages combined) were calculated as the total number of losses during each period, divided by the total number of egg or nestling exposure-days (Mayfield 1961). Daily probabilities of loss were converted to daily survival probabilities for each period. Daily survival probabilities were then raised to the power of the length of the period (in days), converting them to success probabilities over the entire incubation, nestling or nesting period (Johnson 1979).

Hensler (1985) developed a series of mathematical formulae for estimating nesting success parameters and their variances, which are functions of Mayfield's (1961, 1975) daily survival probabilities (see Appendix 1). Using these parameters and their variances, it is possible to make statistical comparisons between two or more populations, and between incubation and nestling stages of the nesting cycle. There are no

known statistical tests to compare directly nesting success proportions of three or more populations derived from Mayfield's method, so multiple pairwise comparisons following Hensler and Nichol's (1981) formula (also given in Hensler 1985, p. 294) were employed to test for significant differences between the three islands. The level of significance was adjusted accordingly, from 0.05 to 0.01 to reduce the probability of a Type I error occurring (Zar 1999).

The computer package Minitab (Minitab Inc. 1991) was used to analyse the data. Normality was examined by constructing scatterplots of residuals against fits, and histograms of the residuals. Where appropriate, normality was improved by $\log(x + 1)$ transforming the data (Zar 1999). Parametric multiple comparisons between the islands were tested using one-way ANOVA. The Kruskal–Wallis test was employed when the assumptions of the parametric tests could not be met. Unless otherwise indicated, $\alpha = 0.05$.

RESULTS

Nest locations in relation to habitat type

A wide range of vegetation types and habitats was available to Saddlebacks on the three islands, but territories and nest-sites were found in some habitat types more often than in others. All 12 of the Saddleback pairs holding territories on Ulva Island located their nest-sites near the coastline and within, or on the margin of, coastal scrub habitat (Fig. 3). Most nests were located on the northern and western coasts where the fringe of coastal scrub is wider. Thirteen of 16 nests on Breaksea Island were built in or alongside the coastal scrub and flax vegetation on the leeward (northern) end of the island, with the remaining three nests located in thick scrub on other parts of the island (Fig. 3). The clumped distribution of nests is probably an artefact of the early flowering of flax bushes on the northern part of Breaksea, as Saddlebacks are known to nest in other parts of the island later in the season (S. Hooson unpubl. obs.). Only a single pair nested in the coastal scrub on the exposed eastern side of Motuara Island, whereas eight of 13 pairs nested in the broadleaf forest, and four pairs nested in Kanuka forest on the island's main ridge (Fig. 3).

Nesting success

In total, 48 active Saddleback nests or pairs with dependent fledglings were found and monitored on

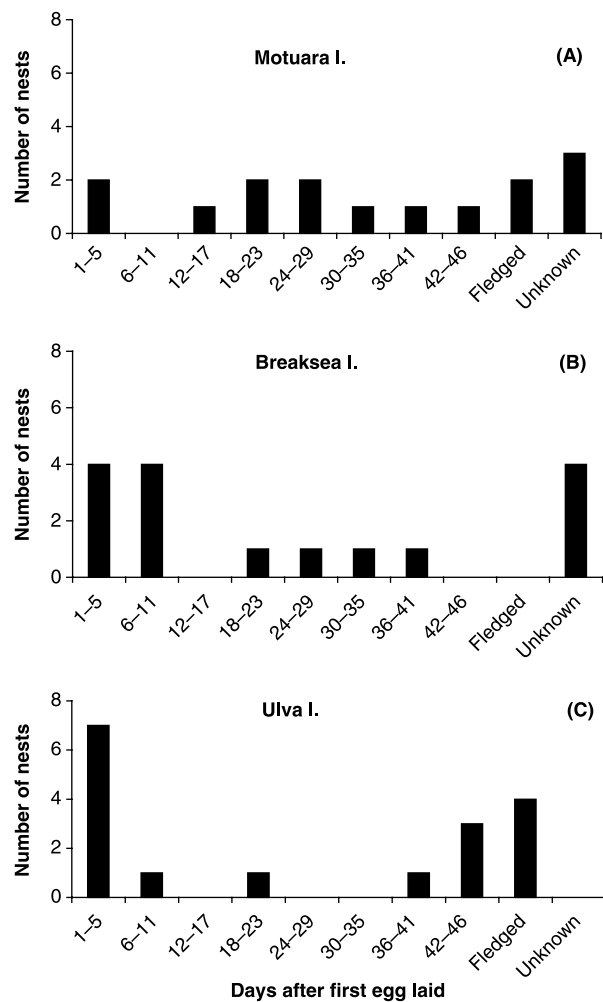


Figure 4. Frequency of South Island Saddleback nests found with regard to days after laying of the first egg for (A) Motuara, (B) Breaksea and (C) Ulva Islands. Where necessary, ages of eggs and nestlings were estimated from embryo development and plumage development.

Motuara (15), Breaksea (16) and Ulva Islands (17) between 1 October 2001 and 16 February 2002. Pairs were found at all stages of the breeding cycle: prior to hatching (65%), with nestlings (21%) and with fledged young (14%) (Fig. 4). Several nesting parameters varied significantly between the islands, with pairs on Ulva producing significantly more clutches, fledglings per clutch and total numbers of fledglings than pairs on Motuara and Breaksea (Table 1). Apparent nesting success was also significantly higher on Ulva (Table 1), but this value, along with apparent hatching and fledging success, is not adjusted for monitoring bias (see below).

Table 1. Reproductive parameters of South Island Saddleback on Motuara, Breaksea and Ulva Islands.

Nesting parameter	Mean \pm se (No. of breeding pairs)			F	P
	Motuara	Breaksea	Ulva		
No. clutches/pair	1.1 ^a \pm 0.07 (14)	1.0 ^a \pm 0.00 (16)	1.5 ^b \pm 0.16 (11)	11.17	< 0.001
No. eggs/clutch/pair	2.0 \pm 0.00 (14)	1.9 \pm 0.06 (16)	2.0 \pm 0.05 (11)	0.50	0.613
No. nestlings/clutch/pair	1.3 \pm 0.22 (12)	1.1 \pm 0.21 (14)	1.7 \pm 0.15 (7)	1.59	0.221
No. fledglings/clutch/pair	0.9 ^{ab} \pm 0.23 (12)	0.6 ^a \pm 0.30 (7)	1.6 ^b \pm 0.18 (8)	4.28	0.026
Total no. fledglings/pair	0.9 ^a \pm 0.23 (12)	0.6 ^a \pm 0.30 (7)	1.9 ^b \pm 0.28 (10)	6.53	0.005
Apparent hatching success	0.63 \pm 0.11 (12)	0.57 \pm 0.10 (14)	0.89 \pm 0.074 (7)	2.15	0.135
Apparent fledging success	0.75 \pm 0.16 (8)	0.75 \pm 0.25 (4)	0.92 \pm 0.071 (7)	0.46	0.641
Apparent nesting success	0.46 ^{ab} \pm 0.12 (12)	0.29 ^a \pm 0.15 (7)	0.75 ^b \pm 0.134 (8)	5.31	0.013

Different superscript letters indicate significant differences between islands (pair-wise comparisons, $\alpha = 0.05$).

Table 2. Daily survival probabilities of eggs and nestlings and percentage nesting success for the incubation, nestling and overall nesting (incubation + nestling) periods estimated using Mayfield's method for South Island Saddlebacks on Motuara, Breaksea and Ulva Islands.

Reproductive period	Estimated parameter	Mean \pm se (No. of breeding pairs)		
		Motuara	Breaksea	Ulva
Incubation	Daily survival probability	0.937 ^a \pm 0.0217 (8)	0.955 ^a \pm 0.0147 (12)	0.995 ^b \pm 0.0050 (8)
	Percent success	26.9 ^a \pm 12.49 (8)	39.8 ^a \pm 12.22 (12)	90.5 ^b \pm 9.07 (8)
Nestling	Daily survival probability	0.987 \pm 0.0076 (12)	0.992 \pm 0.0059 (12)	0.992 \pm 0.0057 (11)
	Percent success	70.7 \pm 14.15 (12)	80.3 \pm 12.46 (12)	80.9 \pm 12.14 (11)
Overall nesting	Daily survival probability	0.969 ^a \pm 0.0093 (12)	0.975 ^{ab} \pm 0.0075 (15)	0.993 ^b \pm 0.0039 (12)
	Percent success	19.0 ^a \pm 9.78 (12)	32.0 ^a \pm 11.10 (15)	73.2 ^b \pm 13.25 (12)

Different superscript letters indicate significant differences between daily incubation, nestling and overall survival probabilities and success (%) (pairwise multiple comparison, $\alpha = 0.01$).

Applying Mayfield's method, eggs on Ulva had a significantly better chance of surviving the incubation period (90%) than on Motuara (27%) (pairwise comparison, $Z = 4.12$, $P < 0.001$) and Breaksea (40%) ($Z = 3.33$, $P < 0.001$) (Table 2). As the three islands differed little in nestling success, the greater hatching rate on Ulva was the primary reason for the significantly higher nesting success (73%) relative to Motuara (19%) and Breaksea (32%) (Motuara, $Z = 3.29$, $P < 0.001$; Breaksea, $Z = 2.38$, $P = 0.009$) (Table 2). Egg infertility was high on Motuara Island (18%, $n = 28$ eggs) and Breaksea (20%, $n = 30$), but was comparatively low on Ulva (3.3%, $n = 30$). Three embryonic deaths were recorded on both Motuara and Breaksea (11% and 10%, respectively), whereas none was recorded on Ulva. Failures as a result of nestling death were higher on Motuara (12.5%) than on Breaksea and Ulva (3% on both).

DISCUSSION

Estimated hatching success was highest on Ulva (90.5%), intermediate on Breaksea (39.8%) and lowest on Motuara (26.9%), the island furthest from, and with the least similar habitat type to, the remnant population. Low egg hatchability on Motuara and Breaksea was chiefly attributable to egg infertility and embryonic deaths. Although based on one season's data only, it is nevertheless difficult to see how such large differences in fertility and hatching success between sites could be due to seasonal effects. We discuss three possible explanations for our results.

Although confined to the coastal scrub, nests appeared to be much more dispersed on Ulva than on Breaksea and, to a lesser extent, on Motuara. Therefore, less competition for food among nesting pairs might have contributed to greater hatching

success on Ulva. This explanation, however, would not account for the substantially poorer hatching success on Motuara compared with Breaksea and does not explain why there were no significant differences in fledging success among the three islands.

Because of the more recent release, the overall density of Saddlebacks was also lower on Ulva (0.18 birds/ha) than on Breaksea (0.42) and Motuara (0.42) (Hooson 2002). Therefore, the lower density of birds on Ulva could have contributed to the higher hatching success. However, only the number of clutches laid and juvenile survival show significant density-dependent effects in Saddleback breeding pairs whereas hatching success shows little change with density (Davidson 1999, D. Armstrong unpubl. data).

A third explanation is that hatching success of translocated birds declines with increasing distance from source populations. In a similar pattern to that found in this study, New Zealand Takahe and Kakapo that were translocated to warmer, temperate islands at lower latitudes experienced reduced egg hatchability relative to their source populations in cooler, southern locations (Jamieson & Ryan 2000). Subfossil and historical records (Williams 1976, Hooson 2000) indicate that South Island Saddlebacks were previously distributed throughout unmodified indigenous beech forest, podocarp/broadleaf forest and coastal scrub prior to their extinction on the mainland. The distribution of territories on Ulva and Breaksea suggests that Saddlebacks there preferred coastal habitat comprised predominantly of a mixture of Leatherwood, Inaka, Muttonbird Scrub, Southern Rata and Kamahi – vegetation that was similar to that on Big South Cape. It is conceivable that a preference for coastal scrub habitat is primarily due to the birds that were originally released having been familiar with that habitat type on the southern islands from where they had been sourced. In this case, their preference might be unrelated to habitat suitability *per se* (cf. Gray & Craig 1991), although preliminary data from Ulva Island indicate that tree cavities are also more numerous in the coastal scrub – Rata/Kamahi mixture (K. Steffens unpubl. data). It is unknown why breeding pairs seemed to avoid nesting in the small area of coastal scrub (containing mostly flax bushes) on the eastern side of Motuara Island, although that coast is more exposed to the prevailing winds. Pierre (1999) also found that Saddlebacks avoided the eastern side of Motuara in their first breeding season after release.

The recommendation that endangered species be released into the core of their historical distribution (Griffith *et al.* 1989, Wolf *et al.* 1996) might need to be viewed with caution in cases where a species' historical distribution crosses a wide variety of habitat types and environmental conditions, and the relict population has been confined to one or a few refuge habitats at the far edge of its historical distribution. At the very least, the release of birds far removed from the area/habitat of the source population might result in lower nesting success, which could contribute to slower establishment rates.

Although translocated Motuara Saddlebacks might be less well adapted to their new environment, the possibility also exists that they are suffering from greater inbreeding depression. Numerous studies have shown that inbreeding can reduce egg fertility and hatching success in wild bird populations (Keller & Waller 2002). More specifically, patterns of inbreeding depression will vary as a function of a population's genetic structure or of the environment, and any interaction between the two (Hedrick & Kalinowski 2000). The extent to which South Island Saddlebacks on these islands are inbred is unknown, although low levels of genetic variation and differentiation have been found across several island populations of North and South Island Saddlebacks (T. King & D. Lambert unpubl. data; I. Jamieson unpubl. data). As Saddlebacks are weak fliers (Merton 1975, Newman 1980), there is no gene flow between current island populations. Consequently, the remnant population of South Island Saddlebacks confined to Big South Cape probably also had a long history of genetic isolation. Compounding this, all of the remaining South Island Saddleback populations are founded from fewer than 36 individuals whose genetic variability may have been impoverished further by additional population bottlenecks occurring during serial translocations from one island to another. For example, the source population of Saddlebacks for Motuara had gone through one more founding bottleneck than had that of Breaksea, and two more than had the Ulva population.

Although we assume that South Island Saddlebacks are inbred to some extent, the birds on Ulva showed remarkably little sign of inbreeding depression, at least in terms of hatching success. Indeed, the hatchability of eggs on Ulva (90.5%) was almost identical to the average reported for populations of birds in the Northern Hemisphere (90.6%, Koenig 1982). On the other hand, Saddlebacks on Motuara

exhibited relatively low hatching rates, although this has not prevented the population from increasing from 26 to 130 individuals over an 8-year period (Hooson & Jamieson 2003a). However, the Saddlebacks on Motuara did experience a population crash (declining by 50%) several months after our study was completed (S. Hooson & B. Cash unpubl. report). The crash is thought to have been caused by the outbreak of a disease that only affected Saddlebacks (K. Hale unpubl. data). Further disease and genetic work is underway at all three island sites, but it is possible that the apparent reduced fitness of Saddlebacks on Motuara is a consequence of a genetic \times environment interaction with Saddlebacks experiencing greater inbreeding depression in a habitat/environment that differs substantially from that of the source population (Miller 1994, Bijlsma *et al.* 1999, Jamieson & Ryan 2000). The results from this 1-year study lay the groundwork for research on the possible effects of inbreeding depression in populations of threatened species that are reintroduced outside their contemporary range, but within their historical range.

We should like especially to thank J. Lüring and B. Cameron (University of Otago), B. Beaven, S. Opper, B. Cash, M. Willans, A. Munn (Department of Conservation), M. McIntosh and J. Briskie (University of Canterbury) for assistance with data collection and logistics in the field. D. Armstrong kindly provided unpublished data on North Island Saddlebacks. P. Seddon, J. Briskie and S. Westgate made comments on earlier drafts of the manuscript. Funding for our research was provided by the Leslie Hutchins Conservation Foundation and the University of Otago, and logistical support was provided by the Department of Conservation (Marborough Sounds, Te Anau and Stewart Island Area Offices, and the Southland Conservancy Office).

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Received 6 January 2003; revision accepted 13 December 2003.

First published online early on 11 March 2004;

doi: 10.1111/j.1474-919x.2004.00275.x

APPENDIX 1

Hensler's (1985) formulae for estimating nesting success parameters and their variances, which are functions of Mayfield's (1961, 1975) daily survival probabilities.

Overall nesting success was calculated using

$$\hat{s} = \hat{p}_1^{J_1} \hat{p}_2^{J_2}$$

where \hat{s} = the maximum likelihood estimator (mle) of s = overall nesting success, \hat{p} = mle of the daily probability of an egg or nestling surviving a given period and J = the length of the periods in days; 1 = incubation period and 2 = nestling period. Standard errors for overall nesting success were calculated by taking the square root of

$$\hat{V}_s^2 = \hat{p}_1^{2J_1} \hat{V}_{\hat{p}_2}^2 + \hat{p}_2^{2J_2} \hat{V}_{\hat{p}_1}^2 + \hat{V}_{\hat{p}_1}^2 \hat{V}_{\hat{p}_2}^2$$

where \hat{V} = the mle of the variance of \hat{s} and $\hat{\beta}_1$ = a one-to-one transformation of \hat{p} (i.e. $\hat{\beta}_1 = \hat{p}_1^{J_1}$). Standard errors for daily survival estimates were calculated by taking the square root of

$$\hat{V}_p^2 = \hat{p}(1 - \hat{p}) / \sum_{k=1}^k T_k$$

where k = the number of active nests and $\sum T_k$ = total egg or nestling days of observation. Standard errors for daily incubation and nestling survival were calculated by taking the square root of

$$\frac{\hat{p}(1 - \hat{p})}{\sum_{k=1}^k T_k} (J\hat{p}^{J-1})^2$$