

Breeding variation in female kakapo (*Strigops habroptilus*) on Codfish Island in a year of low food supply

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Abstract: We investigated why some mature females of New Zealand's critically endangered parrot, the kakapo (*Strigops habroptilus*), did not attempt to breed during the 2005 breeding season on Codfish Island. At a population level, the initiation of kakapo breeding appears to correspond with years of mast fruiting of rimu (*Dacrydium cupressinum*) trees, with the proportion of females that breed each season dependent on the quantity of rimu fruit available. This research investigates possible links between habitat quality within individual home ranges and the breeding status of adult females during 2005, when the abundance of available rimu fruit was low. We assessed the importance of both home range size and habitat characteristics in determining breeding attempts. Foraging home ranges were characterised using radio-tracking and triangulation techniques. The relative importance of habitat variables in optimal breeding habitat was assessed using ecological niche factor analysis. Our results show that female kakapo breeding in 2005 had, on average, home ranges twice the size of those females that did not breed that season and the ranges contained a significantly greater quantity of mature rimu forest. Multivariate analysis illustrates female kakapo were effectively partitioning available habitat, as breeders' foraging locations were positively correlated with high-abundance rimu forest with a tall canopy, described as optimal breeding habitat. In contrast non-breeders' locations were weakly correlated with short forest containing little or no mature rimu forest. To maximise reproductive output each breeding season, conservation managers need to ensure that all breeding-aged females occupy optimal breeding habitat on Codfish Island. Removal to other islands of kakapo not required in the breeding population may enable females to increase their home range size and occupy better breeding habitat.

Keywords: ecological niche factor analysis; habitat selection; habitat quality; home range size; radio tracking; reproduction; rimu

Introduction

Despite having an annual gonadal cycle (Cockrem & Rounce 1995; Cockrem 2006), kākāpō (*Strigops habroptilus*) breed only once every 2–5 years on Codfish Island, the location of the entire population of breeding-aged females, in response to the mast fruiting of rimu (*Dacrydium cupressinum*) trees (Elliott et al. 2001; Eason et al. 2006). The recovery of this critically endangered parrot is slowed even further by considerable variation in the number of females that nest in some rimu-fruiting years. On a population level, breeding in this lek species (Merton et al. 1984) appears to be correlated with the quantity of rimu fruit available, with most females nesting in years of high rimu fruit production (Elliott et al. 2006; Table 1). However, in low rimu fruiting years only some female kākāpō in the population nest (Elliott et al. 2006), causing concern for conservation managers as there is no explanation for what might be preventing some females from breeding.

Hypotheses advanced to explain what triggers kākāpō to breed all focus on the females receiving cues that there will be sufficient ripe rimu fruit to raise their young. Whether these triggers are cognitive (Lignon 1974) or nutritional (Powlesland et al. 1992), or mediated via weight gain (Harper et al. 2006) or hormonal stimulation (Cockrem 2006; Fidler et al. 2008) remains unresolved. In a given breeding year, variation in the proportion of females that breed may reflect

either the patchiness of the fruit crops that trigger breeding or differences in female condition (Eason et al. 2006). This research investigates the hypothesis that variation in breeding attempts between females in low fruit years is associated with the quality and quantity of critical food resources available within their individual foraging ranges.

To test this hypothesis we estimate foraging home ranges of adult female kākāpō on Codfish Island in a non-breeding year (2006) and compare home range characteristics between females that did and did not breed in the previous (2005) summer. We predict that individual female kākāpō that bred will have larger foraging home ranges, since having a larger home range should increase the likelihood that an individual will be able to access more abundant, higher quality resources required for breeding (Millsbaugh & Marzluff 2001). We also predict that there will be distinct differences in vegetation composition and environmental conditions within the home ranges of breeding compared with non-breeding individuals, reflecting differences in habitat quality and resource availability.

Specifically we investigate whether (1) foraging home range sizes or vegetation selection differ between females that bred the previous summer and those that did not, (2) tenure on the island correlates with home range size or nesting, (3) the prevalence of vegetation types with a high rimu component inside foraging ranges differs between breeding and non-breeding females, and (4) the relative importance of

Table 1. Breeding years on Codfish Island (since the first translocation of kākāpō in 1987) showing the level of the rimu mast, percentage of rimu branches bearing fruit and the number of breeding-aged females that nested (Kakapo Recovery Programme, unpubl. data) compared with the total number on the island. The breeding year of 1992 is not included as rimu mast and breeding attempts were not accurately recorded.

Breeding year	Rimu mast level	Rimu bearing fruit (%)	No. of breeding-aged females* that nested (total no. on island)
1997	Low	14	6 (10)
2002	High	35	20 (21)
2005	Low	11	10 (21)
2008	Low	13	5 (38)
2009	High	39	27 (38)

*Note breeding age was defined as 9 years or older prior to 2008 (Eason et al. 2006), and as 6 years or older from the 2008 breeding season onwards as 6-year-old females nested that year (Moorhouse 2009). If a breeding age of 6 years or older had been used for the earlier years there would have been 26 breeding-aged females in 2005, but no change to the 2002 or 1997 figures.

a range of habitat variables in characterising the ecological niche required for females to breed in a low-rimu-mast year. The results of these analyses assist us in predicting optimal breeding habitat for female kākāpō on Codfish Island, thus providing an additional tool for managing this critically endangered species.

Methods

Codfish Island / Whenuahou (1475 ha) is situated 3 km off the north-west coast of Stewart Island in southern New Zealand (46°46.07' S, 167°37.23' E; Fig. 1). Habitat on the island is dominated by mixed-podocarp forest with pakahi scrub in elevated areas and dense scrub around coastal margins (Meurk & Wilson 1989). At the time of this research in 2006, Codfish Island was home to the only known breeding population of kākāpō as all 21 adult females of breeding age (9 years or older; Eason et al. 2006) resided there, along with 20 adult males and 13 juveniles. Our research involved 18 of the 21 breeding-aged females; one female was excluded from the study because she was hand-reared and had formed attachments to staff and two others were excluded because they were in inaccessible locations on the island. We assigned a breeding status (i.e. breeder or non-breeder) to each of the remaining 18 adult females, based on the birds' breeding status from the previous year (2005), which was the most recent breeding year (Table 1).

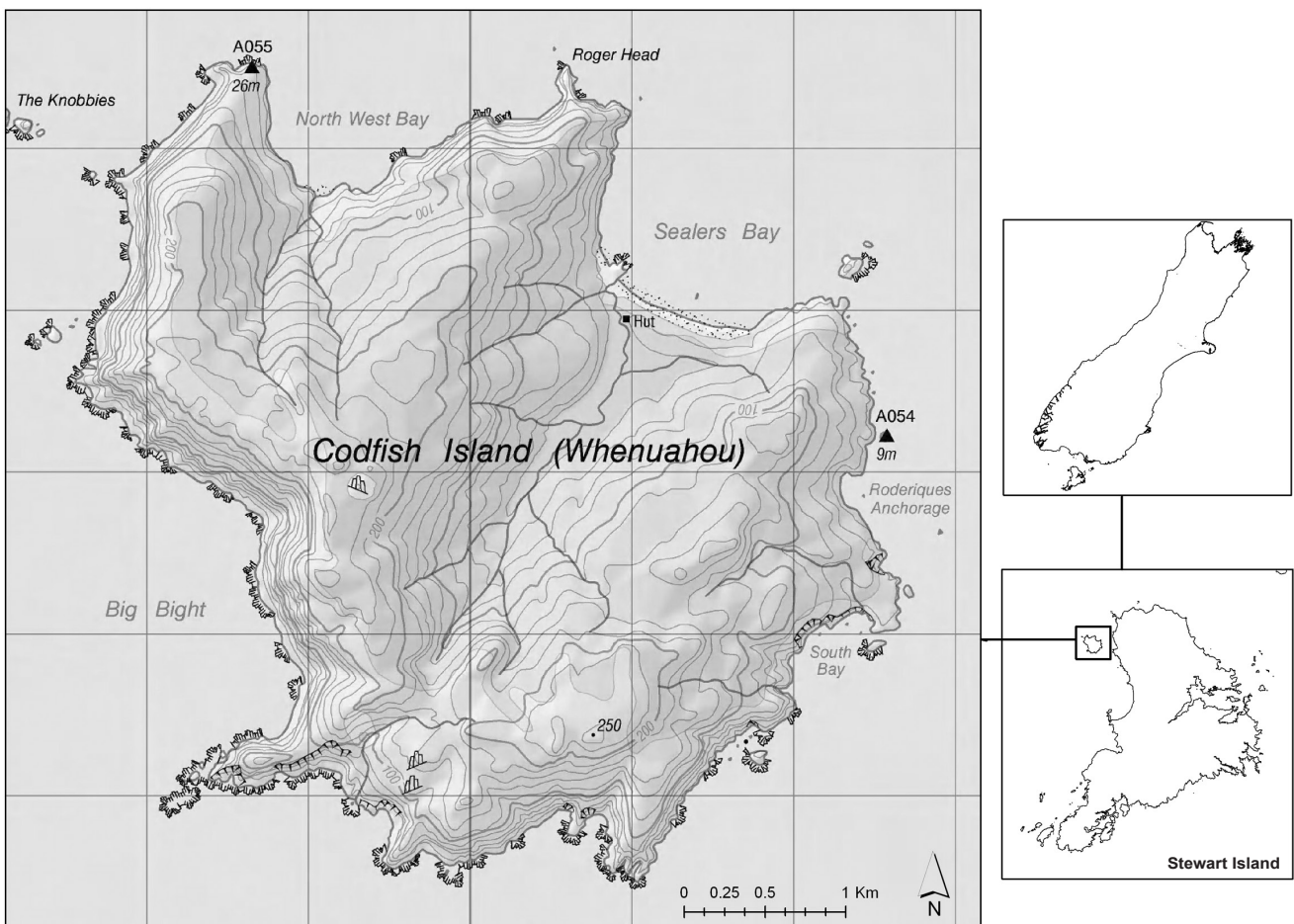


Figure 1. Codfish Island / Whenuahou, located 3 km off the north-west coast of Stewart Island, New Zealand (NZMS260 1:50 000 scale map series provided by Land Information New Zealand).

Radio tracking of foraging locations

All kākāpō on the island are fitted with back-mounted radio transmitters, for management purposes. Foraging locations were estimated for each of the 18 female kākāpō between 15 March and 30 May 2006, using standard radio-tracking techniques (Clout 2006). We used TR4 radio receivers (Teleonics, AZ, USA) and three-element Yagi hand-held aerials fitted with sighting compasses (Sirtrack, Havelock North, NZ) to locate females at night. Once located, a female's foraging position was estimated from the walking tracks on the island, using triangulation (White & Garrott 1990). Triangulations were estimated by recording the direction of the transmitters' strongest signal as a bearing from marked locations along the tracks and intersecting these bearings using an existing Microsoft Access database designed by the Department of Conservation's Kakapo Recovery Programme (DOC unpubl.). Up to 10 bearings were recorded in the field with the five having the closest intersection used for the final location estimate.

As triangulations are location estimates rather than exact fixes (Springer 1979) we used a number of approaches to minimise errors and obtain the greatest possible data accuracy (Whitehead 2007). To ensure we were estimating foraging rather than roosting locations we collected data during the night but not within 2 h of sunset or sunrise. The time of night that individuals were tracked was varied throughout the study period. Bearings were taken from as close as possible and from a variety of angles around the bird while the researcher remained on formed tracks.

Bearings were recorded simultaneously by two or more people situated at different locations along the tracks, or by one person moving quickly between locations. It is unlikely that a kākāpō would have moved any significant distance during the time taken to complete a triangulation as bearings were not recorded if the transmitter signal indicated the bird was moving (Mech 1983). If a kākāpō did move a significant distance, the triangulation would not have been accurate enough to include in later analysis, as any triangulations that had an estimated location triangle greater than 40 m in width were excluded. If movement did occur, we expect that the location error would have been relatively low since kākāpō are known to move at rates of up to 50 m h⁻¹ while foraging (Walsh 2002) and the mean time taken to complete a triangulation was 14.6 ± 7.6 min.

We calculated the error of our triangulation technique by comparing the estimated and actual locations of 25 transmitters hidden in the forest at similar locations and distances from where we encountered kākāpō (Walsh et al. 2006). Occasional sightings of kākāpō on or near tracks were recorded using a handheld global positioning unit (GPS) and recorded as additional locations. Only one foraging location was collected per bird per night to allow for independence of the data.

Estimating foraging home ranges

We estimated foraging home ranges using two estimation techniques that had previously been used in kākāpō home range studies (Trinder 1998; Farrimond et al. 2006, Walsh 2006) – minimum convex polygons (MCP) and kernels (50%, 75% and 95%). The MCP method connects the outermost locations to form a polygon and is one of the most widely used methods of estimating home range (Harris et al. 1990; Kernohan et al. 2001). Kernel estimators are being increasingly used in home range analysis as they provide information on how different parts of the home range are used disproportionately (Worton

1989; Harris et al. 1990). We used a fixed kernel and the least-squares cross-validation technique (Seaman & Powell 1996). Home ranges were estimated using the software Ranges6 v.1.2 (Kenward et al. 2003). We used a regression model to determine whether the number of locations used to estimate a foraging range influenced its size.

We analysed the influence of 2006 foraging home range size on breeding status, which was determined using breeding information collected from the summer of the previous year (2005). Previous analyses (Whitehead 2007) had shown there to be no significant difference between home ranges of females in breeding and non-breeding years for these birds on Codfish Island. This finding is consistent with previous research showing that kākāpō generally stay within similar home ranges for a number of years (Merton et al. 1984; Moorhouse & Powlesland 1991; Powlesland et al. 1992) and that breeding is not thought to alter home range size (Farrimond et al. 2006). We were unable to make comparisons with 2007 as no breeding occurred that year (Table 1). As a further test of this assertion, we plotted nesting locations from 2005 onto the 2006 home range locations for each female. Each female's nest fell inside (or within 100 m of) 95% kernel foraging ranges, supporting the idea that kākāpō use similar home ranges between breeding and non-breeding years. Statistical comparisons were made between home range sizes between breeding and non-breeding female kākāpō. Two-sample *t*-tests were used to compare mean home range sizes for MCP and 95% kernels. The 75% and 50% kernels were not normally distributed so were compared using the non-parametric Wilcoxon rank sum test (unpaired).

Initially, we considered whether other factors such as age, body condition or time spent on the island (tenure) may have influenced a female's home range size or breeding ability, but due to insufficient data we were only able to test the effect of tenure. Using a Wilcoxon rank sum test (with a continuity correction) we tested whether tenure was correlated with her breeding status during the 2005 breeding season. A Kendall's rank correlation was used to determine whether tenure was correlated with foraging home range sizes.

Vegetation use analysis

The vegetation of Codfish Island was mapped in 2005 using a combination of aerial photos, infrared images and ground surveys (Kakapo Recovery Programme, DOC unpubl. data). Sixteen vegetation types were described according to the main canopy and subcanopy species, with some reference to the understorey vegetation (Table 2). To enable statistical analysis of vegetation selection by kākāpō, the original 16 vegetation types were combined into five aggregate classes based on the similarity of the species and area of the island occupied by each vegetation type. All vegetation types occupying 10% or less of the island's area were included as an 'other' class, along with the four vegetation types not used by adult female kākāpō in this study. A chi-squared test was used to determine if vegetation selection by female kākāpō (within 75% kernel home ranges) differed from the available vegetation on the island.

To investigate the importance of mature rimu trees for breeding in individuals, a second map illustrating the relative abundance of mature rimu trees was created by combining vegetation types described to have a high, moderate or low abundance of mature rimu trees (Table 2, Fig. 3). The areas of low-, medium- or high-abundance rimu forest in the foraging ranges (75% kernel) of breeders and non-breeders

Table 2. The original 16 vegetation types on Codfish Island reclassified into three columns for analysis: aggregated classes; rimu abundance and canopy height (Kakapo Recovery Programme, New Zealand Department of Conservation unpubl. data).

Original vegetation types	Description	Aggregated classes	Rimu abundance	Canopy height (m)
Miro–rimu	Dense miro (<i>Prumnopitys ferruginea</i>) and rimu forest, > 20 m tall, with a predominance of miro. Additional secondary species include kāmahi (<i>Weinmannia racemosa</i>), rātā (<i>Metrosideros umbellata</i>) and occasional tōtara (<i>Podocarpus hallii</i>).	Rimu–miro	High	20
Rimu–miro	Dense rimu forest, > 20 m tall. Secondary species include miro and rātā, but kāmahi can be locally common. Interspersed with occasional tōtara.		High	20
Rātā	Predominantly rātā forest, typically < 5 m tall, often with patches of mānuka (<i>Leptospermum scoparium</i>). Understorey often consists of <i>Dracophyllum</i> spp.	Rātā–podocarp	Low	5
Rātā–podocarp short	Short rātā-dominated forest interspersed with podocarps that are generally < 5 m tall. Occasional kāmahi. Understorey is commonly <i>Dracophyllum</i> spp. Possibly regenerating forest.		Moderate	5
Mixed podocarp stunted	Predominantly mixed rimu, miro and tōtara forest, 10–20 m tall, with numerous rātā, occasional kāmahi and an understorey often consisting of <i>Dracophyllum</i> spp.	Mixed podocarp stunted	High	15
Coastal daisy	Daisy forest scrub with <i>Olearia</i> spp. and <i>Dracophyllum</i> spp.	Coastal daisy – pakahi scrub	Low	5
Pakahi scrub	Mānuka and <i>Dracophyllum</i> spp. scrub, predominantly 1–2 m tall, interspersed with rātā, <i>Olearia</i> spp. and mingimingi (<i>Cyathodes juniperina</i>). Mostly in pakahi soils.		Low	5
Coastal scrub	Scrub with strong coastal influence including <i>Brachyglottis</i> spp., broadleaf (<i>Griselinia littoralis</i>), <i>Hebe</i> spp. and kāmahi. In wetter areas fern.	Other	Low	5
Rimu–rātā	Rimu forest interspersed with rātā and miro. Canopy height is typically > 20 m. Rātā dominates over miro as the predominant secondary species.		High	20
Kāmahi–podocarp	Mixed kāmahi–podocarp forest typically > 20 m tall, with occasional rātā. Kāmahi is a canopy species and comprises of approximately half the forest-type composition.		Moderate	20
Rātā–podocarp	Tall rātā-dominated forest interspersed with podocarps that are generally < 10 m tall. Occasional kāmahi. Understorey is commonly <i>Dracophyllum</i> spp.		Moderate	15
Mixed podocarp tall	Predominantly mixed rimu, miro and tōtara forest generally > 20 m, with some rātā. Found in the valley floor. Typically no <i>Dracophyllum</i> spp. Widespread podocarp seedlings.		High	20
Kāmahi*	Predominantly kāmahi forest, often in pure stands, but occasionally interspersed with podocarps and rātā.		Moderate	15
Kāmahi–rātā*	Predominantly kāmahi forest with frequent rātā. Also occasionally interspersed with podocarps.		Moderate	15
Mānuka–broadleaf*	Mix of mānuka, broadleaf, and <i>Hebe</i> found around the hut.		Low	5
Sand dune*	Sand dunes		Low	5

*indicates vegetation types not occupied by adult female kākāpō in this study.

were compared using a non-parametric Wilcoxon rank sum test (unpaired).

All statistical tests described above were carried out using R statistical software v. 2.9 (R Development Core Team 2008).

Multivariate habitat analysis

The relative importance of a range of habitat variables in predicting optimal breeding habitat for adult female kākāpō on Codfish Island was assessed using Ecological Niche

Factor Analysis (ENFA; Hirzel et al. 2002) implemented in the software package Biomapper 3.2 (Hirzel et al. 2006a). ENFA predicts the ecological niche that a species occupies by contrasting the average value of a habitat variable across the study area with the average value in the cells occupied by the species, with any difference in these two values indicating habitat selection. As habitat variables are not independent, a factor analysis is used in ENFA to initially transform correlated variables into the same number of uncorrelated factors (Brotons et al. 2004), allowing the overall information explaining

the ecological niche of the species to be represented by two uncorrelated indices: marginality and specialisation.

The marginality value for each habitat variable is the ecological distance between the species optimum and the mean within the study area (Hirzel et al. 2002). The larger the absolute value of marginality, the more the species mean differs from the mean in the study area. The habitat variable with the highest marginality value has the most influence in determining the species' distribution (Hirzel et al. 2002). The second index, specialisation, shows the extent to which the use of habitat variables by the species is narrow compared with its overall distribution in the study area. Specialisation is calculated as the ratio of the standard deviation of the study area distribution to that of the species' distribution. In ENFA, the first axis accounts for all marginality of the species and some of the specialisation. The second and subsequent axes are then extracted orthogonally to explain the remaining specialisation of the species (Hirzel et al. 2002). Most of the information explained by marginality and specialisation is contained in the first few axes.

To compare the ecological niche of breeders and non-breeders we ran two ENFA models, one using kākāpō foraging locations from 10 breeding females and the other from eight non-breeding females. Foraging locations were buffered to a 20-m radius to account for triangulation error and converted to a 50-m grid, using ArcGIS 9.1 (Esri Inc. Redlands, CA, 2005). We were limited to using a grid resolution of 50 m as this was the margin of error estimated in the vegetation map.

Nine GIS-based raster layers were used to represent potential kākāpō habitat on Codfish Island at a spatial resolution of 50 m. Elevation, slope and aspect were derived from a digital elevation model, using spatial analyst functions in ArcGIS 9.1. Kākāpō may prefer short vegetation (Atkinson & Merton 2006; Butler 2006), so vegetation types with the same estimated canopy heights were merged to create three layers with canopy heights of approximately 20 m, 15 m and 5 m or less (Table 2). The high-, moderate- or low-abundance classes of mature rimu trees were used as the final three habitat layers in the ENFA as vegetation selection analysis had indicated the importance of rimu forest to breeding females.

ENFA requires quantitative rather than categorical data, so the canopy height and rimu-abundance layers were converted to binary raster grids, where 1 or 0 represented the presence or absence of the habitat variable, respectively. The focal statistics function of ArcGIS 9.1 was used to convert the layers from binary to continuous data, using a circular area the mean size of the 75% kernel home range (7.11 ha with a radius of 85 m).

The first few factors resulting from the ENFA of the breeders' model were used to predict suitable breeding habitat for female kākāpō on Codfish Island in a year of low food supply. A habitat suitability map was constructed using the distance geometric-mean algorithm as recommended by Hirzel and Arlettaz (2003). The explained information was maximised by determining the number of factors to include, using a comparison of the factors' eigenvalues based on MacArthur's broken-stick distribution (Hirzel et al. 2002). Habitat suitability values ranging from 0 to 1 were computed for each cell by delineating envelopes around various proportions of kākāpō locations and by counting the proportion of kākāpō locations they encompassed (Hirzel et al. 2006b). The map was reclassified into the following four habitat suitability classes: unsuitable (< 0.25), marginal (0.26 – 0.50), suitable (0.51 – 0.75) and optimal habitat (> 0.76).

The quality of the ENFA models was assessed by determining how they differed from a random model of kākāpō distribution relative to available habitat. Model accuracy was assessed using the continuous Boyce Index (Hirzel et al. 2006b), a 10-fold cross-validation procedure that spatially partitions the species dataset into independent partitions (Manly et al. 1993; Boyce et al. 2002). The continuous Boyce Index value was calculated as a measure of the increase in the mean predicted/expected (P/E) ratio as habitat suitability increases, using a Spearman rank correlation coefficient (Boyce et al. 2002). Results can vary from –1 to 1, with absolute values close to 1 indicating that the model is not different from a random model. Positive values indicate that the model correctly predicts presences based on habitat suitability values, while negative Boyce Index values indicate the model has poor predictive power (Hirzel et al. 2006b).

Results

Between 15 March and 30 May 2006 we recorded 506 foraging locations for the 18 adult female kākāpō in this study, using 482 triangulations and 24 sightings. The number of locations collected per individual ranged from 17 to 34, with a mean (\pm SD) of 28.1 ± 4.5 . The mean error associated with our triangulation technique was calculated to be 19.3 ± 12.2 m. There was no relationship between the number of location points used to estimate a home range and its size for all individuals ($R^2 = 0.05$; $P = 0.38$).

Foraging home ranges varied greatly in size between individuals for each of the home range methods (MCP: 3.1 – 33 ha; 95% kernels: 3.5 – 26.5; 75% kernels: 2.4 – 16.6 ha; 50% kernels: 1.4 – 9.7 ha) (Fig. 2), a finding consistent with previous research on kākāpō home ranges (Moorhouse 1985; Trinder 1998; Farrimond et al. 2006; Walsh et al. 2006). MCP and 95% kernel methods appeared to overestimate home range size, a criticism commonly cited for both methods (White & Garrott 1990; Seaman et al. 1999; Börger et al. 2006), while the 50% kernel provided only an estimate of core foraging area. The 75% kernel home ranges closely resembled the areas covered by foraging locations and excluded major outliers, so were considered the most accurate representation of kākāpō foraging areas and these borders were used in later analysis (Fig. 3).

Comparisons of foraging home ranges between breeders (females that nested in 2005) and non-breeders (females that did not nest in 2005) showed some significant results. Breeders had foraging ranges on average twice the size of those of non-breeders, with these differences being statistically significant for three of the four home range estimation techniques (Fig. 2). Using the MCP method breeders had a significantly larger mean (\pm SD) home range size of 13.5 ± 8.2 ha, compared with the mean non-breeders' foraging range of 7.0 ± 3.6 ha ($t_{12.778} = 2.247$, $P = 0.043$). The 95% kernel method also estimated the mean foraging range of breeders to be significantly larger at 15.1 ± 7.5 ha compared with the 8.0 ± 4.2 ha mean foraging range estimated for non-breeders ($t_{16} = 2.238$, $P = 0.030$). The 75% kernel method showed that the breeders' mean foraging range of 8.9 ± 4.5 ha was larger than the non-breeders' foraging range of 4.9 ± 2.5 ha, but these differences were not quite statistically significant ($W = 61.5$, $P = 0.062$). The 50% kernel method estimating core foraging area showed that the breeders' mean core area was significantly larger at 5.0 ± 2.4

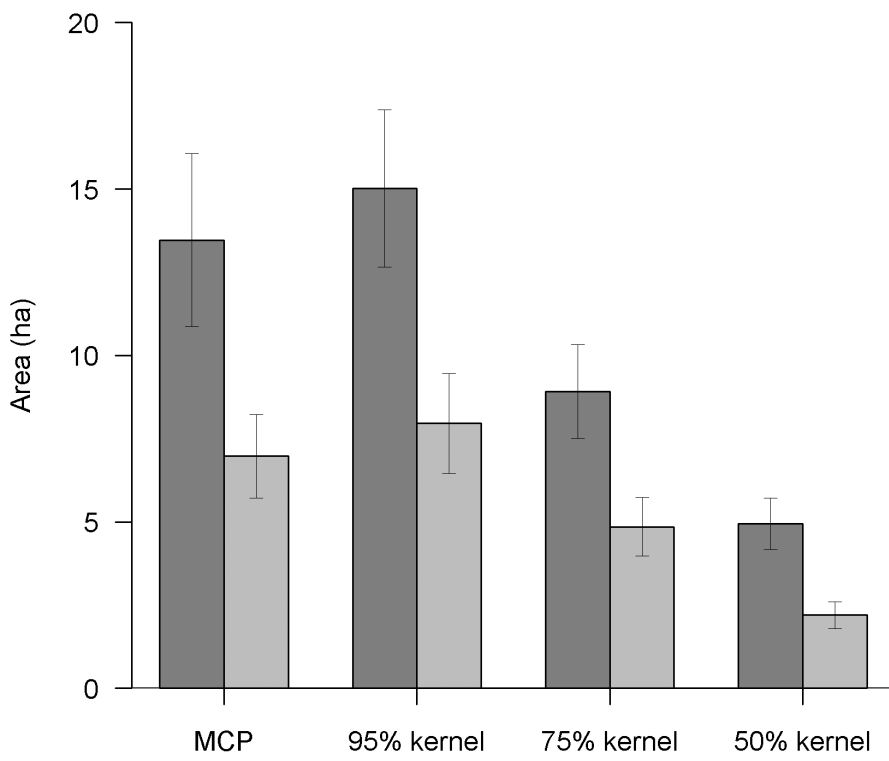


Figure 2. Comparison of mean (± 1 SE) foraging home range sizes for breeders (dark bars) and non-breeders (light bars) for the four home range estimation techniques used. Differences between breeders and non-breeders were statistically significant for all techniques except 75% kernels that were almost significant.

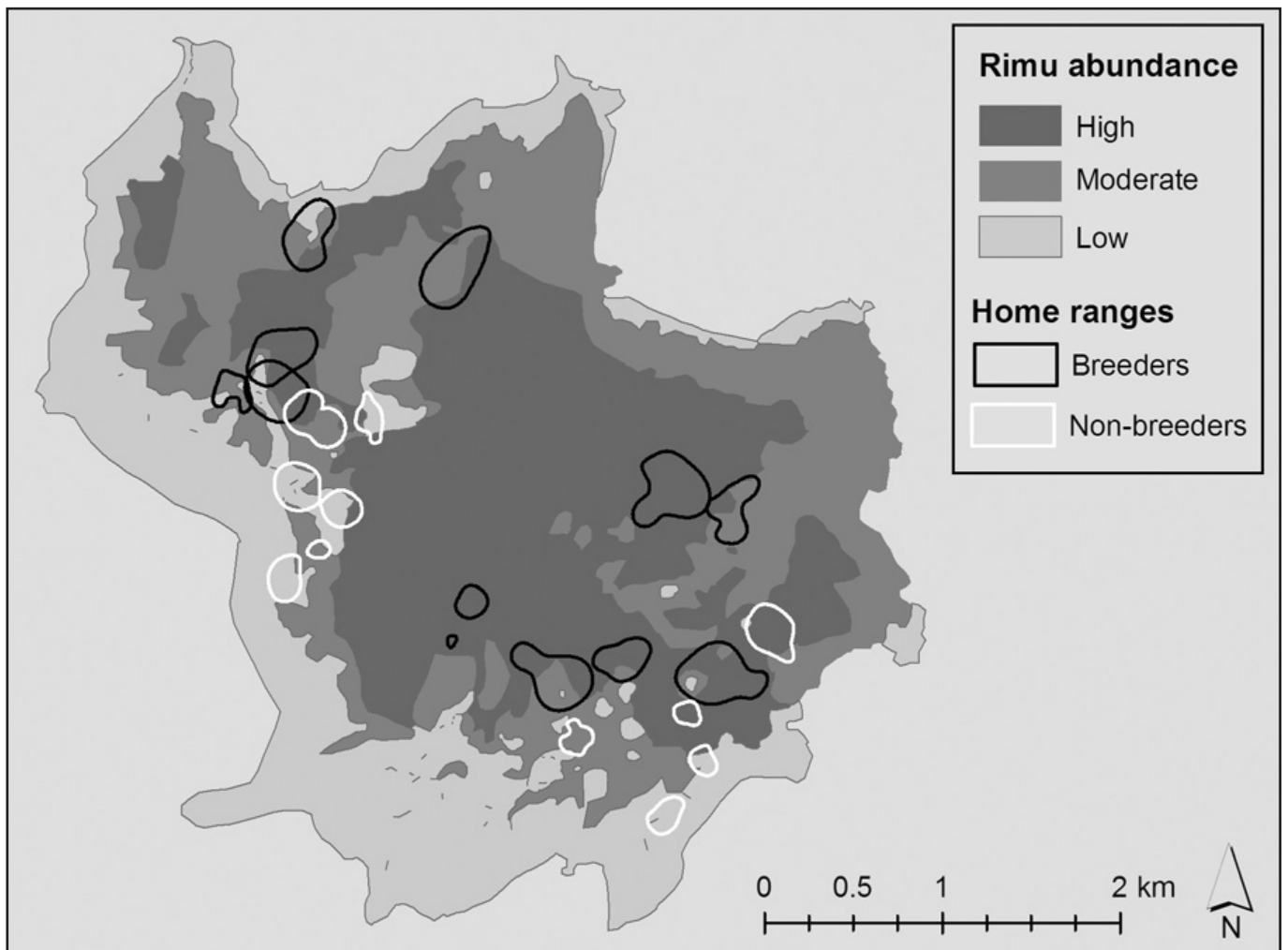


Figure 3. Distribution of forest with varying abundance of mature rimu trees on Codfish Island and the location of 75% kernel foraging ranges for females that bred during 2005 (breeders) and those that did not breed (non-breeders).

ha than the non-breeders' mean core area of 2.2 ± 1.2 ha ($W = 67.5$, $P = 0.016$; Fig. 2).

Tenure was correlated with productivity as breeding females had on average been resident on Codfish Island for longer than non-breeders ($W = 68.5$, $P = 0.009$). However, tenure was not correlated with home range size ($z = 0.927$, $P = 0.354$).

Female kākāpō did not use vegetation at random on Codfish Island (breeders: $\chi^2_4 = 77$, $P < 0.01$; non-breeders: $\chi^2_4 = 34.8$, $P < 0.01$) but appeared to select for certain types. Vegetation use differed between breeders and non-breeders (Table 3). Although only 20% of the island contained rimu-miro forest, this vegetation type was heavily used by breeders, making up 39% of their foraging ranges compared with 25% of non-breeders' ranges. Breeders were not recorded in coastal daisy – pakahi scrub yet this vegetation made up 25% of non-breeders' foraging ranges. Both breeders and non-breeders used rātā-podocarp forest more than would have been expected assuming random habitat selection (Table 3).

Vegetation with a high, moderate or low abundance of mature rimu trees each occupied around one-third of the island's area (Table 4). Forest with a low abundance of rimu mostly occurred in coastal regions, while high-abundance rimu forest occupied central, higher elevation areas (Fig. 3). There was a significant difference in the quantity of high-abundance rimu forest in foraging ranges of breeders and non-breeders ($W = 65.5$, $P = 0.026$), with high-abundance rimu forest occurring in 60% of breeders' foraging ranges compared with only 31% of non-breeders' (Table 4). Low-abundance rimu forest was a lot more common in non-breeders' ranges, accounting for 45% of vegetation, compared with just 9% for breeders, although these differences were not statistically significant ($W = 21$, $P = 0.097$).

Multivariate habitat analysis

The main difference between the habitat of breeders and non-breeders as detected by the ENFA models was the abundance of tall, rimu-dominated forest (Table 5). Results of marginality for the breeders' model showed that the locations of breeding females were strongly biased towards forest containing a high (0.472) or moderate (0.204) abundance of mature rimu trees and biased against forest containing no mature rimu trees (−0.433). In contrast, non-breeders' locations were weakly correlated with forest containing no mature rimu trees (0.152), while they had no significant correlation with high- (0.012) or moderate-abundance (−0.029) rimu forest (Table 5). Breeders tended to occupy tall forest with a maximum canopy height of up to 20 m (0.233). Non-breeders occurred more frequently in short vegetation types with a maximum canopy height less than 5 m (0.318) and less often in vegetation types with a maximum canopy height of up to 15 m (−0.282).

Overall the most important factor in determining kākāpō locations was elevation as it produced the largest absolute marginality values in both the breeders (0.627) and non-breeders (0.710) models (Table 5). Kākāpō distributions were negatively correlated with slope, with both breeders (−0.313) and non-breeders (−0.515) occurring in areas of the island that were flatter than the mean available. Aspect did not appear to influence the location of breeders (−0.042) or non-breeders (−0.154) (Table 5) significantly, with both marginality coefficients showing only a small difference from the mean aspect available on the island.

Evaluation of the ENFA models resulted in a continuous Boyce Index of 0.25 ± 0.46 for the breeders' model and 0.25 ± 0.65 for the non-breeders' model. The positive values indicate that, on the whole, the models correctly predicted habitat suitability (Hirzel et al. 2006b) but the relatively low

Table 3. Proportions of aggregated vegetation classes (Table 2) on Codfish Island and within the foraging home ranges (75% kernel) of females that bred (breeders) and did not breed (non-breeders) in the low-rimu-mast year of 2005.

Aggregated vegetation classes	Proportion of each vegetation class on Codfish Island, and inside foraging ranges of breeders and non-breeders		
	Island	Breeders	Non-breeders
Other	0.32	0.12	0.03
Coastal daisy – pakahi scrub	0.23	0.00	0.25
Rimu-miro	0.20	0.39	0.25
Rātā-podocarp	0.14	0.33	0.40
Mixed podocarp stunted	0.12	0.16	0.07

Table 4. Comparisons of the relative abundance of mature rimu trees in the vegetation on Codfish Island and inside the foraging ranges (75% kernel) of females that bred (breeders) and did not breed (non-breeders) in the 2005 breeding season. (The proportions in bold highlight the distinct differences in high and low rimu abundances between breeders' and non-breeders' foraging ranges).

Relative abundance of mature rimu trees in vegetation	Proportion of rimu abundance on Codfish Island, and inside foraging ranges of breeders and non-breeders		
	Island	Breeders	Non-breeders
High rimu abundance	0.37	0.60	0.31
Moderate rimu abundance	0.32	0.31	0.24
Low rimu abundance	0.31	0.09	0.45

Table 5. Marginality (in rank order) and specialisation coefficients (SC) are shown for the nine habitat variables included in the ENFA breeders and non-breeders models for the first six ecological factors.

	Marginality	SC1	SC2	SC3	SC4	SC5
Breeders	(27%)	(33%)	(15%)	(7%)	(5%)	(5%)
Elevation	0.627	-0.08	-0.459	0.147	0.331	0.034
Frequency of high-abundance rimu forest	0.472	0.159	0.551	-0.576	-0.364	0.346
Frequency of no rimu forest	-0.433	-0.193	0.153	-0.439	-0.033	0.045
Slope	-0.313	0.083	-0.321	0.127	-0.338	0.182
Frequency of up to 20-m canopy	0.233	0.01	-0.279	0.486	-0.276	-0.588
Frequency of moderate rimu forest	0.204	-0.52	0.256	-0.382	-0.393	0.158
Aspect	-0.042	-0.003	-0.035	0.208	-0.004	-0.079
Frequency of up to 5-m canopy	0.027	0.808	-0.125	0.073	-0.577	-0.521
Frequency of up to 15-m canopy	-0.016	0.003	-0.445	-0.084	-0.281	-0.443
Non-breeders	(25%)	(31%)	(14%)	(9%)	(7%)	(5%)
Elevation	0.710	-0.286	0.289	0.248	-0.115	0.113
Slope	-0.515	0.08	0.205	0.247	-0.209	0.102
Frequency of up to 5-m canopy	0.318	0.431	-0.41	0.379	-0.527	-0.612
Frequency of up to 15-m canopy	-0.282	-0.343	-0.065	0.288	-0.39	-0.542
Aspect	-0.154	0.035	0.087	0.303	0.158	-0.108
Frequency of no rimu forest	0.152	-0.082	-0.1	-0.023	0.284	-0.188
Frequency of up to 20-m canopy	-0.051	-0.371	-0.713	0.739	-0.323	-0.455
Frequency of moderate rimu forest	-0.029	-0.026	0.027	-0.045	0.326	-0.146
Frequency of high-abundance rimu forest	0.012	0.68	0.418	-0.101	0.444	-0.182

ENFA = Ecological Niche Factor Analysis (Hirzel et al. 2002)

Notes: Habitat variables are sorted by decreasing absolute value of coefficients on the marginality factor. Positive values on this factor mean that adult female kākāpō prefer locations with higher values on the corresponding habitat variable than the mean location on the island. Signs of coefficients have no meaning on the specialisation factors. The amount of specialisation accounted for is given in brackets in each column for breeders and non-breeders.

magnitude of the index values combined with large standard errors, particularly for the non-breeders' model, indicates a low degree of model robustness (Sattler et al. 2007).

Six significant factors of the breeder's ENFA model were retained for computing a habitat suitability map predicting optimal breeding habitat for female kākāpō in low-rimu-mast years (Fig. 4). Together the six factors explained 96% of the information contained in all variables (100% of the marginality and 92% of the specialisation). Optimal breeding habitats were mostly located in the central regions of the island at higher elevations (Fig. 4). Some large areas of optimal breeding habitat were not occupied by adult female kākāpō, possibly because they were inhabited by any of the 33 other kākāpō on the island including dominant adult males. Females that did not breed in 2005 were mostly located in habitat classified as marginal or unsuitable for breeding (Fig. 4).

Discussion

This study is the first to characterise home ranges based on the night-time foraging activities of female kākāpō on Codfish Island, as well as to make comparisons of foraging home range sizes between breeding and non-breeding female kākāpō. Previous reports of kākāpō home range sizes on various offshore islands, including Codfish Island, have been mainly based on day-time roosting locations (e.g. Best & Powlesland 1985; Moorhouse 1985; Farrimond et al. 2006), which have

likely resulted in an underestimation of the actual area used by kākāpō for foraging (Trinder 1998).

Importantly, our results show that home range sizes of breeding females are almost twice that of non-breeding females, and are largely non-overlapping (Fig. 4), regardless of the method employed for home range estimation. This suggests that there is a clear reproductive benefit to kākāpō with larger home ranges and that this habitat is generally not shared, at least not with other females. Our results also indicate that females with a longer tenure on the island are more likely to breed, although this relationship is not mediated by home range size, but perhaps by prior opportunity to occupy prime habitats. Thus, the implication is that individual kākāpō females on Codfish Island have effectively partitioned available habitat, both in space and time, based on the availability and quality of resources for successful reproduction.

Both the vegetation selection and ENFA multivariate analyses suggest that females were limited in their ability to breed if their access to mature rimu forest was limited. The importance of rimu fruit abundance in triggering kākāpō to breed on Codfish Island (Harper et al. 2006) and in increasing breeding attempts (Elliott et al. 2006) at a population level is well recognised. Our results go a step further by showing that at an individual level the ability of each female kakapo to breed in a low food supply year is limited by their access to food resources. Breeding females appear to select for certain vegetation types, particularly those containing rimu, at the home range scale. For individual females on Codfish

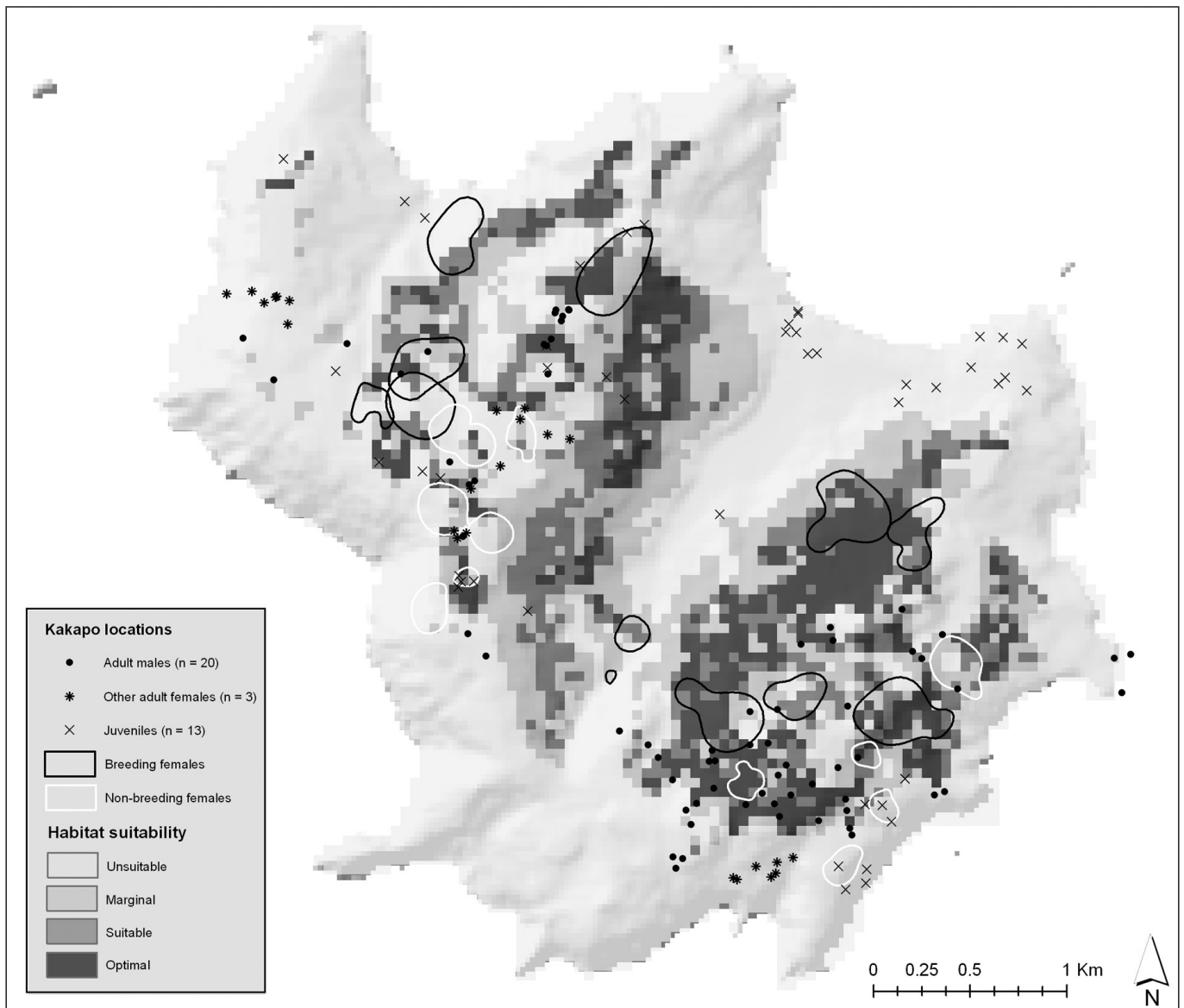


Figure 4. Relative suitability of habitat for adult female kākāpō to breed on Codfish Island in low-rimu-mast years (as predicted by the ENFA breeders' model), compared with actual foraging ranges (75% kernel) for females that bred (breeders, $n = 10$) and did not breed (non-breeders, $n = 8$) in 2005. Locations recorded during this study are also shown for the three adult females not radio-tracked, 20 adult males and 13 juvenile kākāpō also present.

Island, rimu availability is influenced by both the size and habitat composition of the home range. In 2005, only females that had home ranges with a moderate-to-high prevalence of rimu were able to breed in this relatively low rimu mast year. In high-rimu-mast years, such as 2002, the abundance of fruit apparently overwhelms the importance of home range characteristics, as all females were able to obtain sufficient fruit from fewer trees, resulting in successful nesting attempts by nearly all females (Table 1).

The importance of rimu forest in relation to kākāpō breeding was further supported by the ecological niche factor analysis that assessed the relative importance of a range of habitat variables to kākāpō breeding habitat. With the exception of elevation, the relative abundance (as measured by the relative degree of prevalence) of rimu forest had the highest marginality score, and was therefore considered more important than other variables such as slope, aspect or the canopy height

of the vegetation in describing high-quality breeding habitat. Locations of breeding females were strongly positively correlated with the presence of high-abundance rimu vegetation types and strongly negatively correlated with vegetation types with a low abundance of rimu forest. Elevation was given the highest importance value in models describing both breeding and non-breeding female kākāpō habitat, indicating that, in general, individuals prefer to inhabit higher elevation portions of the island. Indeed, past descriptions of kākāpō distributions and resource use have shown that kākāpō may prefer higher elevation ecotonal areas, such as those found near treelines and slips and where the birds can more easily access a variety of food sources (Atkinson & Merton 2006; Butler 2006).

Despite the generally low robustness reported for the ENFA models for both breeders and non-breeders, variables chosen for inclusion in the models were statistically important, and habitat suitability maps produced from the models (Fig. 4)

provided insight into the overall spatial distribution of kākāpō relative to the predicted distribution of habitat of differing quality. Such maps can be useful tools for conservation as they may, for instance, enable managers to identify likely candidates for translocation to new islands. By overlaying foraging home ranges onto the breeders habitat suitability map (Fig. 4) we were able to show that females only needed a small area of optimal breeding habitat in their home range to enable them to breed even in low-rimu-mast years, provided that the remainder of their foraging home ranges were mostly located in moderately suitable breeding habitat. The overlays also showed that non-breeding females mostly occupied unsuitable or marginal habitats despite there being large areas of optimal breeding habitat not occupied by breeding-age females. Locations collected for the 33 other kākāpō inhabiting the island during the study period, and overlaid onto the habitat suitability map (Fig. 4), showed that juveniles were largely inhabiting coastal areas of the island within marginal habitat; some adult males, on the other hand, were found in areas of optimal or suitable breeding habitat, suggesting that they may compete with females for higher quality habitat.

We suggest that further investigations into kākāpō habitat use and resource selection would benefit from an improved characterisation of the variability in kākāpō resource composition, quantity, and quality at the scale relevant to foraging kākāpō. A drawback of this study was the limited spatial resolution and compositional detail of the vegetation data used in our analyses, which limited our ability to investigate within-home-range resource selection. Aside from the overall importance of rimu abundance, the exact form and mechanisms of the available cues used by kākāpō to trigger nesting (Harper et al. 2006), and the importance of other fine-scale resources for nutrition (Elliot et al. 2001), remain unclear. As such, data on plant composition and abundance at different spatial scales, in combination with more direct tracking of movements (e.g. with GPS receivers) and dietary habits of kākāpō of varying age throughout the year, would help shed light on some of these issues.

Conclusions

The results of this research support two general hypotheses posed at the outset of the study. Specifically we found that: (1) female kākāpō that bred during the low-rimu-mast year of 2005 had larger foraging home ranges relative to females that did not breed that year; (2) home ranges of those that bred were situated in areas of higher quality breeding habitat, characterised in particular by a higher prevalence of mature rimu forest. We therefore conclude that female kākāpō are partitioning available space and resources on Codfish Island in ways that increase the likelihood of breeding.

The trend of reduced productivity of adult female kākāpō on Codfish Island in low-rimu-mast years is most likely caused by some individuals having insufficient critical resources to breed, a finding that will be valuable to managers as they try to increase the productivity of this critically endangered species. As the size of a home range is likely to be dependent on the number of potential competitors, it could be expected that as the Codfish Island kākāpō population grows, home ranges will likely reduce in size. Females in mostly unsuitable or marginal breeding habitat are unlikely to breed in low-rimu-mast years and so could be considered as candidates for translocation to another island where more suitable breeding habitat may be

available. Further, translocation of any juvenile kākāpō or adult males that are not currently required in the breeding population, to a non-breeding island, might allow breeding-age females to increase the sizes of their foraging home ranges on Codfish Island and, thus, the quality of the breeding habitat to which they have access.

Through this research we now know that there are factors limiting the ability of adult female kākāpō to breed in low-rimu-mast years on Codfish Island. Perhaps more importantly we also know that these factors – home range size and access to mature rimu forest – can be manipulated by conservation managers to give individual birds the best chance of being able to breed each breeding season. The principles applied in this management-focused research could easily be applied to other rare species to gain a better understanding of their ecology and the importance of a range of variables in their breeding performance.

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