NICHE OVERLAP AND FORAGING ECOLOGY OF ISLAND *Petroica* SPECIES

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ABSTRACT

We investigated foraging niche overlap in two allopatric and two sympatric island populations of *Petroica* species. We predicted that sympatric populations (Black Robins, Chatham Island Tits) would have narrower foraging niches than the allopatric populations (South Island Robins, Snares Tits), and that the foraging patterns of the allopatric populations would tend to be intermediate between the sympatric populations. These predictions were not supported. Rather, the two robins and two tits foraged in ways very similar to each other, and in ways suggesting that "robin" and "tit" foraging styles are a conservative feature in the evolution of this group.

INTRODUCTION

Attempts to investigate competitive interactions and ecological (or niche) overlap between original communities of New Zealand forest birds have been severely hampered by habitat fragmentation and extinctions. Members of many taxonomic and ecological groups that were originally sympatric are now either allopatric, or one or several members of the group no longer exist (e.g. the wattlebirds, Callaeatidae). Introduced mammalian predators and competitors in forests (King 1984) further confound ecological studies because of the lower densities of extant species of birds and unknown indirect effects. Consequently, ecological studies of relatively undisturbed bird faunas must now be conducted on islands. Islands, however, impose other historical and ecological constraints. Island faunas tend to be depauperate, species endemic to islands have usually evolved in the absence of taxonomically similar competitors, and the amount of time that the island population has been separated from its "parent" population is usually unknown (MacArthur & Wilson 1967, Shafer 1990). Island populations may also have been subjected to short-term disturbance (such as attempts at farming, or introduction and subsequent eradication of mammals) in historical times.

Where closely related species are sympatric (overlap in space) on islands, there should be strong ecological interactions, presumably with the potential to cause the extinction of one species (MacArthur & Wilson 1967). To survive, such species are likely to become more specialised and diverge morphologically, ecologically, and behaviourally (Schluter & McPhail 1993) and so exploit a realised niche that is more restricted than their fundamental niche (see Krebs 1985, and Figure 1 for an explanation of these terms). In contrast, under conditions of allopatry (spatial separation), each species'
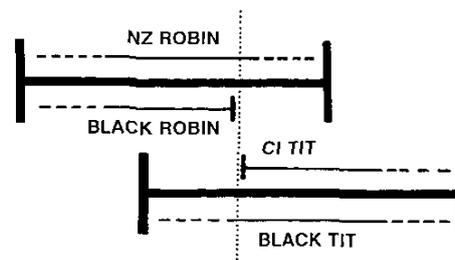
FIGURE 1 – Schematic representation of an arbitrary parameter of niche width for *Petroica* species under allopatry (NZ Robin, Black Tit) and sympatry (Black Robin, CI Tit). The speces are taxonomically similar and their fundamental niches (solid bar; the niche that can potentially be exploited) overlap. For all populations, the realised niche (thin solid line; the niche actually exploited by the population of interest) is narrower than the fundamental niche due to local environmental constraints (dashed lines). Under sympatry the presence of a competitor is represented as a barrier (vertical dotted line) that limits the realised niche in the area of ecological overlap.

realised niche will only be restricted by the particular characteristics of the island on which they reside, and should be closer to the fundamental niche.

In this study, we investigated the foraging behaviour of four island populations of *Petroica* species (Passeriformes: Petroicidae). *P. traversi* (Black Robin), and *P. macrocephala chathamensis* (Chatham Island (CI) Tit), were sympatric on South East (Rangatira) Island (176°10' W, 44°22' S). The two allopatric species were *P. australis australis*, (South Island Robin, here called NZ Robin) and *P. m. dannefaerdi*, the Snares (or Black) Tit. The NZ robin was studied on Nukuwaiata Island, one of the Chetwodes group at the entrance to Kenepuru Sound (174°06' E 40°56' S) and the Snares Tit was studied on Northeast Island, the main island of The Snares(166°36',E 48°02' S).

Fleming (1950a,b) described taxonomic relationships among these species and confirmed Reischek's (1889, in Fleming 1950a) view that the black Snares species was a tit rather than a robin. Although they will forage above the ground, New Zealand species of *Petroica* obtain much of their food from the ground (Fleming 1950a,b, Powlesland 1981, pers. obs., Butler & Merton 1992: figure 8). Tits spend more time foraging off the ground than do robins, they rarely perch on the ground whereas robins frequently do so, and they are smaller than robins (Fleming 1950a,b, Oliver 1954, Butler & Merton 1992, IGM & CH, unpublished data). Black Robins are between tits and NZ robins in size, but closer to tits (Table 1).

Historically, Chatham Island Tits and Black Robins were presumably sympatric on Rangatira Island. They were sympatric on Little Mangere Island in 1937 (Fleming 1939). Collection locations on museum specimen labels suggest that the two species were sympatric on Mangere and Pitt islands late last century, but it is not clear how geographically precise the label localities are. The sympatric populations studied here are the result of introductions of Black Robins to Rangatira Island from Mangere Island

TABLE 1 – Measurements (mm) of *Petroica* species on islands from Fleming (1950a,b) measured from museum specimens.

Taxon	Measurement			
	Tarsus	Wing	Culmen	Tail
Snares Tit (18)	25.5	78.9	12.3 (6)	61.6
Chatham Islands Tit (27)	25.6	74.7	11.5 (17)	56.9
Black Robin (21)	31.4	82.0	13.8 (13)	63.8
South Island Robin (54)	38.0	97.2	18.7 (20)	72.1

NOTE: Fleming gave means for each sex for tarsus, wing, and tail, but not for culmen. The total number of birds he measured are given in parentheses by the taxon, but it is possible that all measurements were not taken from every skin. Values given here are the arithmetic means of the means of the sexes, as an indication of mean size of that measurement for the species. Culmen means are from measurements of individual birds tabulated separately by Fleming (n given in parentheses).

(where there were no tits) in 1983 (Butler & Merton 1992). We do not know to what extent earlier periods of sympatry and allopatry may have influenced the foraging behaviour of the two species. It seems unlikely that there would have been time for significant adaptive change during the most recent period of sympatry.

Because tits are smaller, we predicted that they would be more likely than robins to modify their foraging behaviour in the face of a competitor. We therefore further predicted that tits sympatric with robins would feed off the ground more, use foraging behaviours inappropriate to ground-feeding, and would be more likely to use peck sites (small branches, twigs and leaves) only available higher in the forest than tits allopatric with robins. We also predicted that allopatric tits would behave like robins to some extent, possibly exhibiting a broader foraging niche than under sympatry.

We found it more difficult to predict what robins would do under the same conditions. As primarily ground feeders, they may have fewer ecological options than tits; as the larger species they may be less constrained by the presence of tits. We therefore made no predictions for robins.

METHODS

Black Robins and CI Tits were studied (by IGM) on Rangatira I. from 29 March to 7 April, 1992; Snares Tits were studied (by PMS) from 3 to 21 March, 1993; NZ Robins were studied (by CH) from 21 to 23 May, 1993. Thus all populations were studied during the late summer or autumn, when a proportion of the population was presumably young birds and densities were high. Prevailing temperatures were similar at all three study areas because the most northerly island (Nukuwaiata) was visited latest in the season and the most southerly island (Snares) was visited earliest. Data were gathered only when the weather was reasonably dry and calm.

When searching for birds we carefully scanned the entire height range of forest in the vicinity. On Rangatira and the Snares the ground is relatively clear of vegetation because of the activities of breeding seabirds, and birds were observed easily at horizontal distances up to 30 m. The forest was denser at ground level on Nukuwaiata, presumably because seabirds are absent and feral farm animals were eradicated in the 1960s (E. Huddleston, pers. comm.). Subjective assessments indicated that the population densities of birds were reasonably similar, with CI and Snares tits being two to three times as abundant as Black and NZ robins.

Feeding behaviour was sampled at any time of day. Tits were sampled on Rangatira and Snares once only when encountered, and only one sample was taken from a bird encountered in the same general location on any day. Individual tits are unlikely to have been sampled more than a few times during the period of study. Forty-five samples were taken from male and 15 from female tits on Rangatira. The sex of Snares tits was not recorded. Black Robins were all individually identifiable and were sampled once or twice when encountered; samples were taken at least 2 min apart, and the individual was not sampled again that day. Sixty samples were taken from 36 individuals, with a maximum of three samples taken from any one bird. Each NZ Robin was sampled once or twice; samples were taken at least 2 min apart. The observer moved about the island and so individual birds were unlikely to have been encountered more than once. On Rangatira, robins and tits were sampled wherever they were encountered. Most samples were taken in the lowland forest near the hut, where both species frequent the same habitat.

Feeding behaviour was sampled essentially as described in McLean (1989) and Hunt & McLean (1993), but with some modifications. Once a bird was encountered and identified and (for robins) had ceased watching the observer, the time between its first peck at a site and the next peck was measured by stop watch. Details recorded for the second peck (by IGM and PMS) or the first peck (CH) included: i) peck site (ground, trunk, large branch >2.5 cm diameter, small branch <2.5 cm and >0.5 cm, twig <0.5 cm, leaf, air, notch, dead wood, seed head); ii) substrate (litter, bare ground, bark, dead wood, air, leaf, moss, seed head); iii) perch site (as for peck site); iv) feeding method (see below); v) height of peck site and vi) height of canopy above that site. The distance moved by the bird between the two pecks, and the time, were recorded.

Peck height (v) as a percentage of canopy height (vi) was used to calculate an index of feeding height in relation to local forest structure. An index of foraging – the moving rate, distance moved/inter-peck time – combined distance between peck sites and pecking rate. The inter-peck time interval provided a direct measure of the pecking rate.

The sample was rejected and a new sample begun if: i) the bird was lost to view for more than 2 s between the two pecks, ii) the bird ceased feeding (e.g., watched the observer, or preened), iii) the bird flew more than 25 m. We remained still throughout the observation unless forced to move

to keep the bird in view, but movements were kept to a minimum. Binoculars were used to follow birds as required.

Each feeding sample included continuous variables (distance and time) and categorical variables (height, perch, and peck sites, substrate, feeding method). Height (strictly, height index, described above) was treated as a categorical variable because it was heavily skewed for all species. For statistical comparisons of foraging behaviour between species, continuous variables were analysed with parametric statistics with the results confirmed by equivalent nonparametric tests if variances were not equal. Nonparametric tests gave the same result in all comparisons and results are not reported. Categorical variables were analysed by χ^2 tests, with lumping of small cells when required. All data are presented, but results of χ^2 tests are only given (and any lumping explained) if the comparison was statistically significant ($p < 0.05$).

Allopatric populations are not constrained by the presence of an ecologically similar competitor and should exhibit a broader niche than an equivalent population in sympatry with a possible competitor. In comparing sympatric and allopatric populations, we therefore predicted that the mean for any variable should be intermediate for an allopatric population relative to two sympatric populations (Grant 1986), and that variance should be higher for allopatric populations than for sympatric populations. We used the coefficient of variation (Sokal & Rohlf 1973) to assess variance.

The predictions could be tested for continuous variables, but estimates of mean or variance are not available for categorical variables. We therefore calculated an index of similarity for each categorical variable, as follows: for the two robins, we subtracted the percent use of each category from the equivalent percent use by the sympatric tit (CI Tit); we did the same for the two tits, using the sympatric robin (Black Robin). The calculated values were added to give a dimensionless index of similarity for each variable that could be compared between species. For example, to compare peck sites for the two tits (Table 1) required six subtractions (tit-Black Robin) for each tit (one subtraction for each category) to give the values $32 + 27 + 3 + 2 + 1 + 2 = 67$ for Snares Tits and $23 + 9 + 2 + 0 + 7 + 7 = 48$ for CI Tits (negative signs ignored). With niche separation, the index should be higher for the sympatric population than for the allopatric population (in this example the reverse is found).

RESULTS

Six feeding methods were identified. *Glean*, a perched bird pecked at a sedentary prey item. *Pounce*, a bird flew a short distance to a new perch where it attacked a sedentary prey item seen from the first perch. *Rake*, a bird scratched or probed at the feeding site or turned over vegetation. *Snatch*, a bird saw a sedentary prey item from a perch and flew by, grabbing the prey as it passed. *Hawk*, flying prey taken on the wing. *Flush*, prey items disturbed and caused to fly or run by actions of the feeding bird.

Snatch and *pounce* were lumped for tits because they were characterised slightly differently by the observers. The critical difference between *pounce* and *snatch* was whether or not the bird remained at the peck site. Tits rarely

stayed at the peck site for more than about 1 s. IGM recorded pounce if the tit remained for more than 0.5 s and therefore recorded pounce quite frequently; PMS recorded pounce only once for Snares Tits because he recorded snatch even if the bird remained at the peck site for 1-2 s.

Trends in the data indicated that the two tit populations foraged in similar ways, as did the two robin populations, whereas tits and robins generally foraged in rather different ways. Overall, fewer significant differences were found for foraging by the two robins (different species) than for the two tits (same species).

Statistical analyses comparing variation in all four species were highly significant (p<0.01), primarily because of the differences between tits and robins, and these analyses are not presented here. Results are presented separately for tits and robins.

Tits

Birds in both tit populations pecked at the ground at similar frequencies, although they rarely perched on the ground and caught most prey by snatching or pouncing from large perches (Table 2). Snares Tits pecked more at the ground than CI Tits, but the difference was not significant (Table 1). The two tits used similar patterns of height; both populations pecked at above-ground sites in about the same height range (Figure 2).

When off the ground, both tits perched on and pecked at mostly trunks and large branches, although CI Tits used them less than Snares Tits, mainly because CI Tits pecked more at the ground (Table 2). Snares Tits pecked significantly more at bare ground and bark, whereas CI Tits pecked more at litter and leaves (bark and dead wood combined, air and leaf combined, $\chi^2_3 = 53.2$, p<0.001). The difference in use of bare ground and litter was probably because there was more bare ground on the Snares (where Sooty Shearwaters *Puffinus griseus* are very abundant) than on Rangatira. No other differences were significant.

Most tits foraged by pouncing or snatching; Snares Tits occasionally gleaned. The differences were almost significant ($\chi^2_2 = 5.46$, p = 0.07, Table 2).

Tits in the two populations foraged at very similar rates ($t_{155} = 0.08$, NS, Table 3), but the distance and time between pecks differed significantly (distance: $t_{126} = 3.15$, p<0.01; time: $t_{150} = 2.63$, p<0.01). Snares Tits travelled farther and took longer between pecks than CI Tits. These differences cancelled out in the calculation of foraging rate.

Robins

Most pecks by both robin species were at the ground (Table 2). They perched on the ground much less frequently before attacking prey, mainly because pounces and snatches involved attacking a prey item from a distance, usually from a perch off the ground. Both robins pecked most at litter.

When off the ground, NZ Robins fed slightly higher than Black Robins (Figure 2), but differences in height were minor. When above the ground, both robins perched more on large than small perches (Table 2). Both species
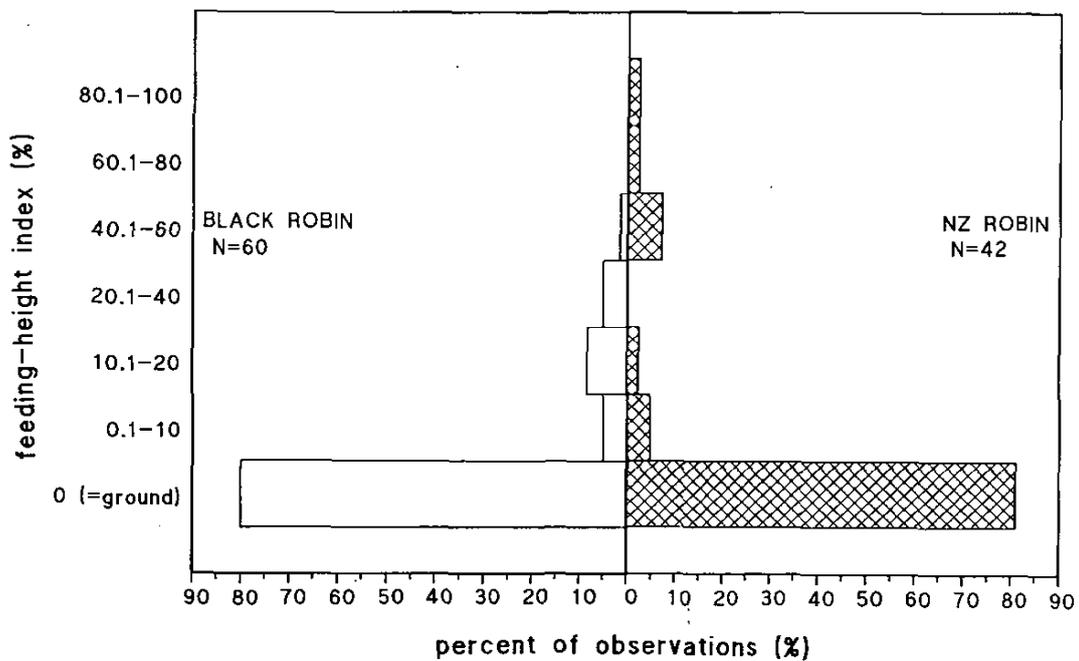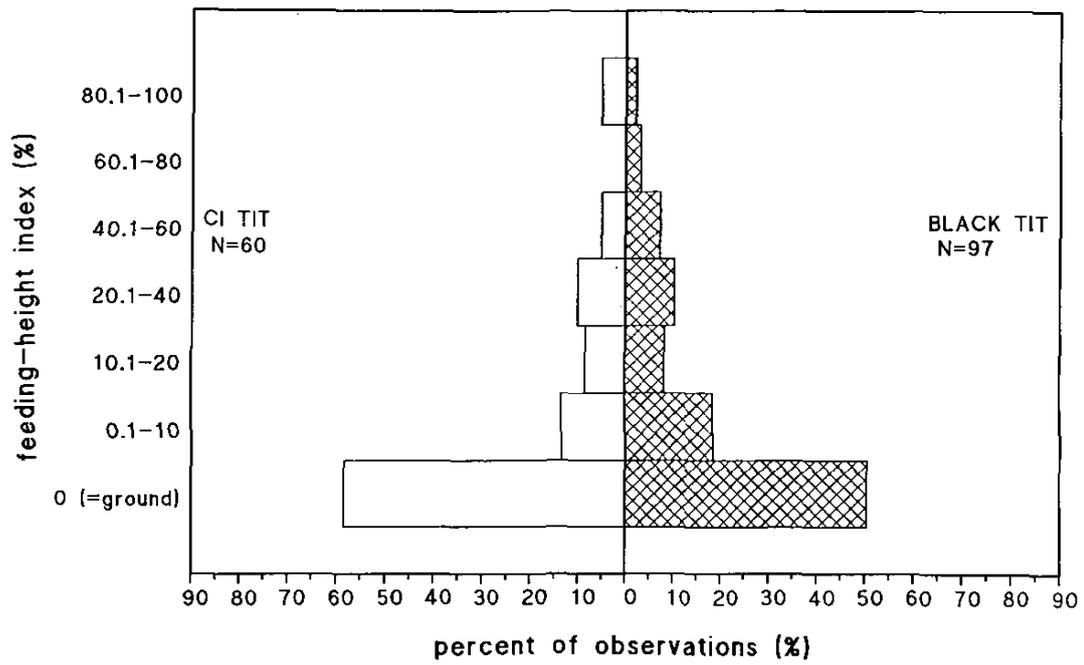
FIGURE 2 – Feeding-height indices, calculated for the peck height as a proportion of the canopy height above the peck site, for island populations of *Petroica* species. *CI* = Chatham Islands, NZ = New Zealand.

TABLE 2 – Foraging characteristics for *Petroica* species on islands - categorical variables as percentages of sample sizes. NZ, New Zealand; Tr, trunk; LB large branch; SB, small branch.

Peck site	n	Ground	Tr/LB	SB	Twig	Leaf	Air
Snares Tit	99	48	43	3	2	2	2
Chatham Island Tit	60	57	25	2	0	12	7
Black Robin	60	80	16	0	0	0	0
NZ Robin	42	81	19	0	0	0	0

Perch site		Ground	Tr/LB	SB .	Twig
Snares Tit	99	8	45	44	2
Chatham Island Tit	60	3	48	42	7
Black Robin	60	32	50	18	0
NZ Robin	42	38	55	5	2

Peck substrate		Litter	Bare ground.	Bark	Dead wood	Air	Leaf
Snares Tit	99	7	42	44	2	2	2
Chatham Island Tit	60	48	17	10	7	5	13
Black Robin	60	77	3	12	0	3	5
NZ Robin	42	74	10	14	2	0	0

Feeding method		Glean	Pounce	Snatch	Rake	Hawk	Flush
Snares Tit	99	12	84		0	4	0
Chatham Island Tit	60	2	93		0	5	0
Black Robin	60	27	57	3	8	0	5
NZ Robin	42	26	19	10	45	0	0

mainly pecked at trunks and large branches when off the ground. None of the between-species comparisons was significant.

The two robins used significantly different feeding methods: Black Robins pounced more and NZ Robins raked more (flush and snatch combined for analysis; $\chi^2{}_3 = 22.8$, p<0.001, Table 2). Only Black Robins were seen to flush prey.

Robins foraged at similar rates ($t_{100} = 1.22$, NS, Table 3), moved similar distances ($t_{100} = 0.69$, NS), and for similar time intervals ($t_{100} = 1.46$, NS) between pecks.

Niche width characteristics

Means and coefficients of variation for the continuous variables did not indicate that allopatric populations were either intermediate to, or foraged in more variable ways, than sympatric populations (Table 3). Of the four comparisons where the allopatric population mean was predicted to be intermediate to the sympatric population means (for distance and time), three were not intermediate. Coefficients of variation, predicted to be smaller for

sympatric than allopatric populations, were larger in three of the four comparisons available.

Ten indices of similarity were available for categorical variables, five from comparison of robins, and five from tits. An index for an allopatric population should have been lower than the equivalent index for a sympatric population. The values are not presented, but were calculated from the data in Table 2. Seven of the ten comparisons were in the wrong direction, indicating that allopatric populations were not foraging in ways intermediate to sympatric populations.

DISCUSSION

The only support for our prediction that Chatham Island Tits would tend to feed above ground because of the presence of Black Robins on the ground, was the difference in substrate use by the two tits. Chatham Island Tits pecked at leaves more often than did Snares Tits. However, most of the significant difference in substrate use was in the use of bare ground or bark (mostly on trunks lying on the ground) by Snares Tits, and litter by Chatham Islands Tits, and so does not support our predictions. In general, we conclude that there was little evidence for niche separation in the sympatric populations.

The two robins and the two tits each foraged in very similar ways and the two robins differed in fewer significant ways than did the two tits. The minor differences between species pairs within both tits and robins are easily explained by uncontrolled factors such as habitat differences between the islands, latitudinal, or seasonal effects. It is also possible that the Black Robins introduced to Rangatira I. had not yet reached densities where competition with tits influenced the behaviour of either species. However, the Black Robins used somewhat tit-like feeding methods, which suggested that some aspects of Black Robin feeding were intermediate between those of tits and NZ Robins. The Black Robin is smaller than the NZ Robin, but a more extensive study would be required to clarify the issue.

This is the first ecological confirmation of Fleming's (1950a,b) taxonomy of the Chathams and Snares *Petroica* S. Of greatest interest are the Black Tit and the Black Robin, which have been supposed in the past to be very closely related (reviewed in Fleming 1950a). In skin measurements in (Fleming 1950b, fig. 19, summarised here in Table 1) the two species are more similar to each other in wing and tail lengths than either is to most other *Petroica* populations. However, the Snares birds are clearly grouped with the tits by tarsus length, whereas the Black Robin, smaller overall than NZ Robins, has retained a relatively long tarsus. The behavioural and habitat-use patterns reported here, particularly the similarity between Black and NZ Robins, suggest that the robin and tit styles of foraging are clearly separable and represent a conservative evolutionary feature of the group.

TABLE 3 – Foraging characteristics for *Petroica* species on islands - continuous variables. Moving rate calculated from perch-perch distance and time variables, hence no coefficient of variation (CV) calculated for moving rate.

		Variable				
		Moving rate (m/min)	Perch-perch distance (m)		Perch-perch time (s)	
	n	Mean±SD	Mean±SD	CV	Mean±SD	CV
Snares Tit	97	15.2±14.85	6.3±7.85	124.6	22.8±19.38	85.0
Chatham Island Tit	60	15.0±12.69	3.0±2.55	85.0	15.7±14.48	92.2
Black Robin	60	5.7±3.27	1.9±2.47	130.0	19.3±16.43	85.1
NZ Robin	42	7.1±7.7	2.1±1.29	61.4	24.2±16.71	69.0

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