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HABITAT PARTITIONING AND INTERSPECIFIC TERRITORIALITY IN FLAME, SCARLET AND DUSKY ROBINS

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Flame *(Petroica phoenicea)*, Scarlet *(P. boodang)* and Dusky *(Melanodryas vittata)* Robins occasionally occur sympatrically in Tasmania. All three species are insectivorous, inhabit forests with an open understorey, and are ecologically similar. The question then arises as to how they are able to coexist. In this study, foraging behaviour, habitat selection and interspecific territoriality in the three species were examined. Flame and Scarlet Robins are known to be interspecifically territorial. We predicted that this is due to similarities in their use of resources, such that they cannot coexist in the same area. The Dusky Robin may be able to exploit different resources from Flame and Scarlet Robins, negating the need for territoriality between Dusky Robins and the other two species. Surprisingly, Scarlet Robins were more similar to Dusky Robins in their resource use than they were to Flame Robins, even though Flame and Scarlet Robins are congenerics. Although this should prevent Dusky Robins from sharing territories with Scarlet Robins, they actually had a greater territory overlap with Flame and Scarlet Robins, than these species had with each other. We suggest that Scarlet Robins compensate for the overlap by Dusky Robins by traversing a larger area in order to obtain sufficient resources.

INTRODUCTION

The question of coexistence of apparently ecologically similar species has been an important and dominant theme in community ecology throughout its history. This is because to understand the differing mechanisms that allow coexistence is to comprehend much of the natural control of biological diversity (MacArthur 1972; Cornell and Lawton 1992). Since the early work of Gause (1934), it has been generally accepted that when resources are limiting, two closely related species cannot coexist in the same area indefinitely if their ecological requirements are the same. Later refined by Hardin (1960) as the principle of ‘competitive exclusion’, this theory predicts that one species will be more efficient at exploiting a limited resource than the other, and by competing for the same limited environmental resources, will eventually displace the other. More realistically, there should be a limit to how similar two coexisting species can be (MacArthur and Levins 1967). In support of this theory, many ecologists have demonstrated that closely related species found coexisting in the same area are separated ecologically, or are otherwise occupying different niches (Lack 1971).

In nearly all guilds of animals studied, niche differentiation occurs on several dimensions and the number of dimensions increases with species richness (Schoener 1974, 1986). Niche differentiation is generally complementary; when species are similar in one dimension, they differ in another. Habitat is the most common niche parameter partitioned by animals, followed by food (Schoener 1986). Studies also support the hypothesis of temporal partitioning of rapidly renewable resources (Kotler *et al*. 1993, 1994; Ziv *et al*. 1993).

The Australasian robins (Petroicidae) comprise 38–46 species in 11–17 genera (Wolters 1975–1982; Sibley and Ahlquist 1990; Sibley and Monroe 1990). The majority of the Petroicidae are ground-foraging insectivores, which scan for prey from an elevated perch before pouncing. They occupy most wooded habitats, from coasts to uplands, including alpine regions and semi-arid habitats (Higgins and Peter 2002).

Four species of robins occur in Tasmania. Of these, three species were studied: the Flame Robin (*Petroica phoenicea*), Scarlet Robin (*P. boodang*) and Dusky Robin (*Melanodryas vittata*), which occasionally occur sympatrically in Tasmanian eucalypt forests and woodlands with an open understorey. The Pink Robin (*P. rodinogaster*) usually occurs in wetter and denser forests than the other three species. Flame and Scarlet Robins are of similar size and appearance (males are red-breasted, females are mostly brown), averaging about 13 grams. Overlap between these two species’ use of vertical foraging space on the Australian mainland is high (Robinson 1992) and they have similar mating systems and similar degrees of parental care (Robinson 1989). Flame Robins are migratory over much of their range and disperse to lower altitudes and more open habitats in the non-breeding season (Blakers *et al.* 1984). Scarlet Robins are mostly sedentary (Blakers *et al.* 1984; Bell and Ford 1987), although some individuals may migrate (Recher *et al.* 1983; Emison *et al.* 1987). The Dusky Robin is one of the largest robins in Australasia, averaging about 27 grams. It is endemic to Tasmania and the Bass Strait islands. Unlike Flame and Scarlet Robins, Dusky Robins do not display any sexual dimorphism, lack any bright plumage and are brown with a distinctive dark eye stripe. All three species are insectivorous and obtain the greatest proportion of their prey by pouncing from a perch to the ground (Recher *et al.* 2002). Flame, Scarlet and Dusky Robins may thus compete with each other for resources such as food and perch sites. Competition between two similar species may be so keen that they cannot coexist in the same area of the habitat at the same time. Flame and Scarlet Robins are known to be interspecifically territorial and defend mutually exclusive territories against one another (Pescott 1968; Fleming 1980; Loyn 1980; Shields and Recher 1984; Robinson 1989). Interspecific territorial behaviour is well known among birds (Orians and Willson 1964; Cody 1974; Murray 1981) and occurs most frequently between ecologically similar species competing for limited resources such as food, space or nest sites (Orians and Willson 1964; Brown and Orians 1970; Cody 1985). We thus predicted that interspecific territoriality between Flame and Scarlet Robins is due to similarities in their use of resources, such that they cannot obtain sufficient resources if they coexist in the same area. No detailed studies on the Dusky Robin have been published so far, but it was predicted that its larger size would have enabled it to exploit larger prey than Flame and Scarlet Robins, negating the need for territoriality between Dusky Robins and the other two species. While a few studies have focused on the foraging ecology and habitat use of robins, none have explored the relationship between resource overlap and horizontal segregation by a group of similar species. In this study, therefore, comparative aspects of territoriality, use of space and foraging behaviour in Flame, Scarlet and Dusky Robins were examined. Our objectives were to determine: (1) the degree of horizontal segregation (interspecific territoriality) and resource overlap between Flame, Scarlet and Dusky Robins, and (2) whether interspecific territoriality is due to similarities in resource use.

MATERIALS AND METHODS

Study Area

This study was conducted at Cloudy Bay, South Bruny Island, Tasmania (43°23’S, 147°14’E, 32–68 m asl). Mean maximum temperatures ranged from 11°C in July to 19°C in February. Mean minimum temperatures ranged from 6°C in July to 12°C in February. Mean annual rainfall was about 950 millimetres. The site covered approximately 400 hectares on private land and contained a mixture of grazing pasture for cattle, hay fields, gardens surrounding human dwellings and wet sclerophyll forest dominated by *Eucalyptus obliqua*. Other tree species present in the canopy layer included *E. viminalis* and *E. globulus*. Canopy height ranged from 25–35 metres. The understorey consisted mainly of *Acacia melanoxylon, A.dealbata, Astroloma humifusum, Banksia marginata, Coprosma quadrifida, Daviesia ulicifolia, Epacris myrtifolia, Leptospermum scoparium* and *Melaleuca gibbosa*. The ground was covered in *Pteridium esculentum*, leaf litter and fallen timber in forested areas, and native grasses (mainly *Austrodanthonia* sp.) of various heights in different fields. Grazing pastures were tightly grazed with the heights of grasses rarely exceeding 15 centimetres. The heights of grasses in hay fields ranged from 60–80 centimetres until the fields were harvested in January. Data were collected from August 2004 to February 2005. This encompassed the 2004/05 breeding season.

Habitat Use

Focal-animal sampling (Altmann 1974) was used to quantify each species’ habitat preferences and foraging behaviour. Robins were caught by mist net and banded with a numbered metal band provided by the Australian Bird and Bat Banding Scheme and a unique combination of colour bands to permit individual identification. Individual robins were observed opportunistically throughout the day for a maximum of 15 minutes or until the bird disappeared from sight, whichever occurred first. This was done to avoid sampling a single bird for too long. Only one observation period was made per bird per day to ensure independence of results. If there was more than one robin present, the robins were observed one at a time. During each observation period, the focal individual was followed and a continuous description of its height and perch substrate recorded with a tape recorder. Tape recordings were later transcribed and the amount of time spent in each microhabitat category was recorded to the nearest second. Perch substrates were categorised as ‘ground’, ‘branch’, ‘trunk’, or ‘man-made structure’ (such as sheds, fences, laundry lines and tables). The height of the focal bird above the ground was estimated to the nearest metre and pooled into four categories: 0–1.0 metres, 1.1–3.0 metres, 3.1–6.0 metres and greater than 6.0 metres. These categories broadly represented a ground layer, shrub layer, short tree/sapling layer and canopy layer respectively.

Foraging Behaviour

For every foraging attempt made by a focal individual, the method used and the substrate from which the prey was taken were recorded. Foraging attempts, rather than foraging successes, were recorded because prey items were usually small and it was not always possible to determine whether foraging attempts were successful. Foraging methods were classified as *pouncing*, where a perched bird drops to the ground to capture a prey item; *hawking*, where a bird flies out from a perch and captures prey in the air; *snatching*, where a perched bird flies to take prey items resting on substrates such as foliage and branches without landing on the substrate (this category includes taking prey items whilst hovering); *gleaning*, where a perched bird takes prey resting on substrates; and *ground-feed*, where a bird hops along the ground making repeated pecks at different prey items. Ground-feeding and gleaning are similar foraging methods, but differ in where they take place. Substrates considered were ‘ground’, ‘air’, ‘branch’, ‘trunk’ and ‘foliage’.

Size and Overlap of Territories

To determine territory size and placement, a GPS (Global Positioning System) device was used to record the initial geographical position of each located bird. Only the positions of adult birds were recorded, as juveniles do not hold territories (Robinson 1990). The territories of breeding pairs of robins were combined in the analysis of territory size and overlap.

Territory sizes were calculated using the fixed-Kernel (KE) method with a least squares cross-validation (LSCV) smoothing parameter (Harris *et al.* 1990; Powell 2000). A 95 per cent isopleth was used to estimate KE territory. Data were analysed using the software programs Animal Movement (Hooge and Eichenlaub 1997) and Home Range Extension (HRE) (Rodgers and Carr 2001) in ArcView 3.3. Territory analyses may have contained statistically auto-correlated data. However, fixes were thought to be biologically independent because a time period of 24 hours was more than enough to allow any robin to traverse its entire territory. Following Powell (1987) and Goodrich and Buskirk (1998), the assumption was made that potential problems of serial auto-correlation were minimal because individual movements were likely to depend upon past experience and knowledge of resources within the territory. Schoener's (1981) and Swihart and Slade's (1985) indices were used to test the independence of observations made. No significant deviations from the expected values were found when both these indices were applied to the observed points.

To determine the amount of horizontal overlap tolerated within and between species, the areas of overlap of any Flame, Scarlet and Dusky Robin territories on each territory were calculated. All overlap values were converted to percentages of the total areas of the respective territories. This process produced a pair of average values for each species pair, e.g. percentage overlaps of Flame Robin territories on Scarlet Robin territories and Scarlet Robin territories on Flame Robin territories.

Statistical Analyses

All statistical analyses were carried out using SPSS 11.0. Proportional data were transformed using the Freeman and Tukey (1950) equation:

$$P' = \text{arcsine}\sqrt{\text{proportion}}$$

This was used as much of the data were at extreme ends of the data range, i.e. near 0 or 100 per cent.

Principal Components Analysis (PCA) was used to compare species based on combined values of perch substrate (ground, branch, trunk, man-made structure) and height (0–1.0 m, 1.1–3.0 m, 3.1–6.0 m, > 6.0 m) categories. The resulting principal components which best represented the inter-relations among the set of variables were then extracted and analysed using Multivariate Analysis of Variance (MANOVA) to investigate habitat use differences between species. Preliminary assumption testing was conducted to check for normality, linearity, univariate and multivariate outliers, homogeneity of variance-covariance matrices and multicollinearity, with no serious violations noted. Tukey's HSD (honestly significant differenced) test was then used to determine where significant differences between species lay. Chi-square tests for independence were used to explore the relationships between species, foraging methods and prey substrates. One-way ANOVAs were conducted to determine the differences in territory size between species. Pairwise comparisons between species were then made using Tukey's HSD test.

RESULTS

A total of 69, 100 and 91 individual observation periods were recorded for 19, 31 and 26 Flame, Scarlet and Dusky Robins respectively. Observations ranged in duration from 9 seconds to 900 seconds (mean ± s.e. = 130.8 ± 8.6 s). These observations were made on 13, 14 and 11 family groups of Flame, Scarlet and Dusky Robins respectively. Each family group had an average of three to four birds (typically two adults and one or two juveniles). Robins were considered to be part of the same family group if they were in close proximity to each other (less than 10 m) and were not engaged in antagonistic interactions with each other. Fourteen robins (one Flame, six Scarlet and seven Dusky) were mist-netted and banded. Robins which could not be banded were identified using a combination of plumage patterns, colour intensity, developmental stage and number of young, and position in relation to banded birds.

Differences in Habitat Use Between Flame, Scarlet and Dusky Robins

The eight habitat variables were subjected to PCA. Prior to performing PCA the suitability of data for factor analysis was assessed. Inspection of the correlation matrix revealed the presence of many coefficients of 0.3 and above. The Bartlett's Test of Sphericity (Bartlett 1954) reached statistical significance, supporting the factorability of the correlation matrix.

PCA revealed the presence of four components with eigen values exceeding 1, explaining 33.0 per cent, 18.7 per cent, 15.3 per cent and 14.0 per cent of the variance respectively. Using Catell's (1966) scree test, we decided to retain these four components for further investigation. These four components accounted for 81.0 per cent of the variation between species, suggesting four dimensions were sufficient to represent the relationships between variables accurately (Table 1).

TABLE 1

Correlations of the eight habitat variables with the four extracted principal components

Habitat variables	Principal Component			
	1	2	3	4
Branches	-0.888			
0-1 m	0.819			0.316
Man-made	0.686			-0.671
Ground	0.633			0.573
1-3 m		-0.892		
3-6 m	-0.388	0.659	0.512	
> 6 m	-0.342		-0.777	
Trunks			0.440	0.326

A one-way between-groups MANOVA was performed to investigate species differences in habitat use. The four principal components, which best described the variation in the habitat data set were used. There was a significant difference between species based on the combined dependent variables ($F_{8,510}$=4.85, p<0.001, Pillai's Trace=0.14, partial eta squared=0.07). When the results for the dependent variables were considered separately, the only differences to reach statistical significance using a Bonferroni adjusted alpha level of 0.0125 were PC1 ($F_{2,257}$=4.47, p=0.012, partial eta squared=0.03) and PC3 ($F_{2,257}$=8.37, p<0.001, partial eta squared=0.06).

For PC1, post hoc comparisons using Tukey's HSD test indicated that the mean score for Flame Robins was more negative than that for Scarlet Robins (p=0.011). Dusky Robins did not differ significantly from either Flame (p=0.072) or Scarlet Robins (p=0.749). This means that Scarlet Robins spent significantly greater proportions of their time on the ground and on man-made structures (mostly fences) than Flame Robins. Flame Robins spent more time in branches and less time below one metre compared to Scarlet Robins (Figure 1).

Tukey's HSD test indicated that Flame and Dusky Robins differed significantly on PC3 (p<0.001), with Dusky Robins having the more positive mean score. No significant differences were found between Scarlet Robins and the other two species on this component (Flame p=0.072, Dusky p=0.088). This implies that Dusky Robins spent significantly greater proportions of time at 3–6 metres and smaller proportions of time above six metres compared to Flame Robins (Figure 2).

Foraging Behaviour

A total of 402 foraging observations were gathered: 128 from Flame Robins, 171 from Scarlet Robins and 103 from Dusky Robins. Data from the five foraging methods and five prey substrate categories were combined to ensure that the minimum expected cell frequency was greater than five (χ^2 test assumption). This was possible as some of the foraging methods (pounce, ground feed and hawk) actually describe the substrates from which the prey is taken. Six new variables describing both foraging methods and prey substrates were obtained: pouncing, ground feeding, hawking, and foraging on branches, trunks and foliage. The last three categories were formed by adding together the number of foraging attempts made by snatching and gleaning from branches, trunks and foliage.

Flame, Scarlet and Dusky Robins employed significantly different foraging methods and prey substrates (χ^2=31.50, d.f.=10, p<0.001). All three species foraged predominantly by pouncing (Figure 3). Their use of other foraging techniques, however, varied substantially. Flame Robins ground fed more often than the other two species (Figure 3). Hawking was the method employed least frequently by Dusky Robins. Flame and Scarlet Robins hawked more often than Dusky Robins (Figure 3). The three species made about equal proportions of their foraging attempts on branches (Figure 3). Scarlet and Dusky Robins foraged more often on trunks than Flame Robins. In fact, foraging on trunks was the second most frequently used technique by Scarlet and Dusky Robins (Figure 3). Scarlet Robins obtained more of their prey from foliage than Flame and Dusky Robins. Flame and Dusky Robins did not forage much in foliage (Figure 3).

Territory Sizes

The mean territory size was calculated to be 6.93 hectares for Flame Robins, 11.66 hectares for Scarlet Robins and 8.35 hectares for Dusky Robins (n=13, 14 and 11 respectively). The differences are significant ($F_{2,35}$=9.86, p<0.001). Tukey's HSD tests showed that Scarlet Robin territories were significantly larger than both Flame (p<0.001) and Dusky Robin territories (p=0.017). No significant differences were found between the territory sizes of Flame and Dusky Robins (p=0.450) (Figure 4).

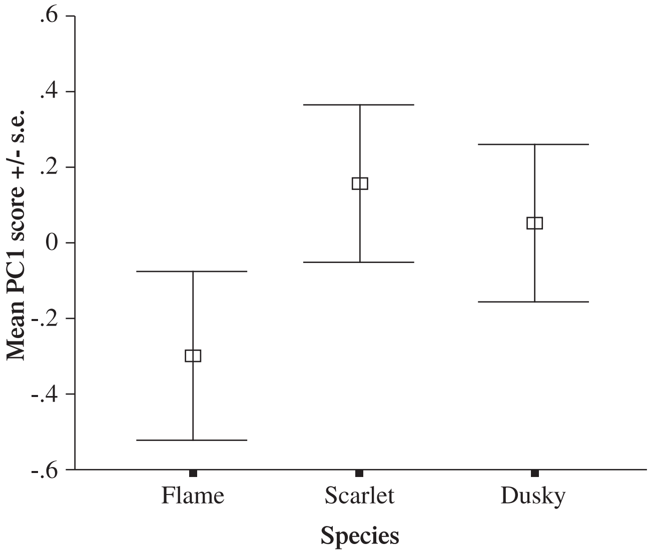

Figure 1. *Mean PC1 scores for each species. More positive scores on PC1 indicate greater proportions of time spent below one metre and on man-made structures and less time spent in branches. Scarlet Robins spent significantly greater proportions of their time on the ground and on man-made structures (mostly fences) than Flame Robins. Flame Robins spent more time in branches and less time below one metre compared to Scarlet Robins.*

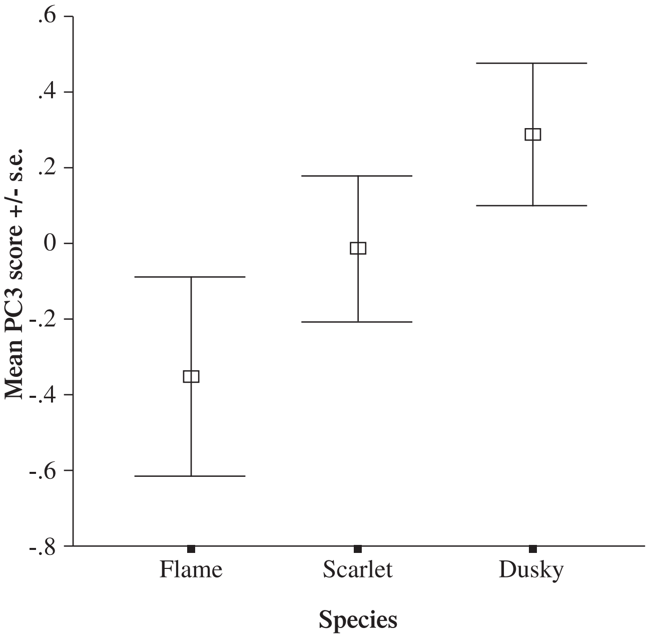

Figure 2. *Mean PC3 scores for each species. More positive scores on PC3 indicate greater proportions of time spent at 3–6 metres and on trunks and less time spent above 6 metres. Dusky Robins spent significantly greater proportions of time at 3–6 metres and less time above 6 metres compared to Flame Robins.*

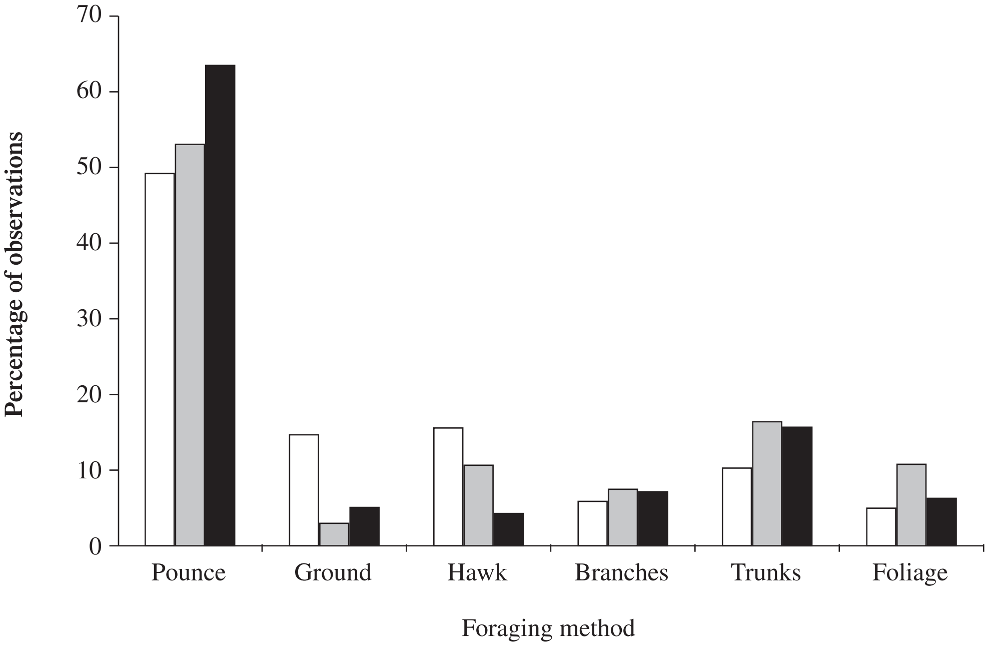

Figure 3. *Percentage of observations in each foraging category for Flame (open bars), Scarlet (grey bars) and Dusky (solid bars) Robins. All three species foraged predominantly by pouncing.*

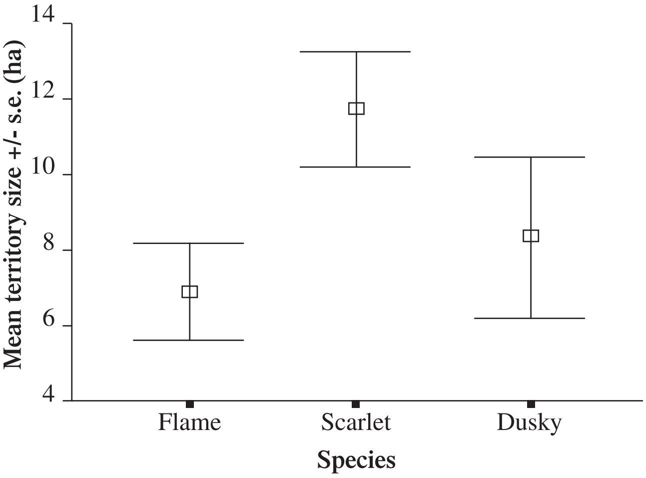

Figure 4. *Mean territory sizes of pairs of the three species of robin. Scarlet Robins had significantly larger territories than both Flame and Dusky Robins.*

Territory Overlaps

Overall, the mean percentage overlaps between Flame and Dusky Robins, and Scarlet and Dusky Robins were higher than that between Flame and Scarlet Robins. Scarlet Robins tolerated about equal proportions of overlap from both Flame Robins and other Scarlet Robins. Flame Robins, on the other hand, tolerated much less overlap from other Flame Robins than Scarlet Robins (Figure 5). Despite the lack of obvious territorial behaviour in Dusky Robins, overlap between Dusky Robins was relatively low (Figure 5). Overlaps between Scarlet and Dusky Robins were always higher than those between Flame and Dusky Robins (Figure 5).

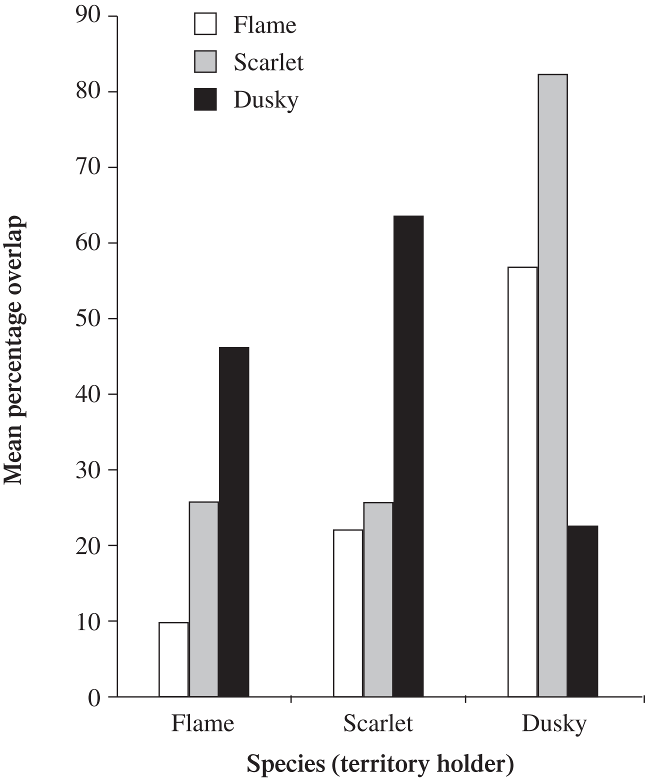

Figure 5. *Mean percentage territory overlaps between different pairs of species. Overall, the mean percentage overlaps between Flame and Dusky Robins, and, Scarlet and Dusky Robins were higher than that between Flame and Scarlet Robins.*

DISCUSSION

Three processes play a role in the stable coexistence of species living in sympatry: (1) different habitat selection, (2) different resource utilisation and (3) interspecific territoriality (Sedlacek *et al.* 2004). Different habitat selection would result in territories with different habitat compositions (Cody 1985). Coexistence based on different resource utilisation or interspecific territoriality would lead to territories with the same (or similar) habitat composition, overlapping in the first case and exclusive (or almost exclusive) in the latter (Lack 1971; Wiens 1989). As more closely related species, such as Flame and Scarlet Robins, tend to use the same types of resources, habitat and resource partitioning may not be possible between them. This leaves interspecific territoriality as the only option for coexistence within the same habitat. Indeed, Flame and Scarlet Robins are known to defend interspecific territories wherever they occur sympatrically (Pescott 1968; Fleming 1980; Loyn 1980; Shields and Recher 1984; Robinson 1989). Similar observations have been made among morphologically and ecologically similar species, e.g. Buffleheads (*Bucephala albeola*) and Barrow's (*B. islandica*) Goldeneyes (Thompson and Ankney 2002). Interspecific territoriality allows different species to use the same types of resources in different parts of the same habitat. More distantly related species (in this study, the Dusky Robin) have morphological differences that may allow them to exploit different resources and/or habitat types. Dusky Robins were thus expected to have significantly different habitat and foraging preferences from Flame and Scarlet Robins.

Overall, significant differences were found between the species based on habitat use. Pairwise comparisons revealed that the differences were between Flame and Dusky Robins, and Flame and Scarlet Robins. Despite the similarities in habitat preferences and foraging behaviour between Scarlet and Dusky Robins, both species had largely overlapping territories. The results thus paint an interesting picture of sympatry, in that they appear to contradict standard explanations for sympatry in ecologically similar species.

How are Scarlet and Dusky Robins able to coexist in the same area with such similar habitat usage and foraging behaviour? It is possible that both species are able to obtain enough resources within their territories, even though they are overlapping. The Scarlet Robin is the smallest of the three species, yet it has the largest territories in this study. This suggests that it compensates for the overlap by the other two species by traversing a larger area in order to obtain sufficient resources. Dusky Robins, while being much larger than Flame and Scarlet Robins, have much smaller territories than Scarlet Robins. The Dusky Robin's larger size, typical of island endemics when compared to similar species on the mainland, may enable it to occupy a wider ecological niche and employ more generalist foraging techniques than Flame and Scarlet Robins. For example, even though all three species of robin used the same foraging techniques in roughly similar proportions, Dusky Robins may be consuming larger prey in addition to the smaller prey types that are available to Flame and Scarlet Robins. Thus, Dusky Robins may be able to obtain sufficient resources even though their territories overlap and are much smaller than the Scarlet Robins' territories.

It is also possible that perch and foraging substrate variables were measured at too broad a scale to reveal significant differences between the three species. Although the ground was treated as a singular substrate in this study, it may be split into categories such as leaf litter, bare ground, grass or herbs. However, as most ground-pouncing birds use a wide range of substrates (Antos and Bennett 2006), the use of ground substrates is unlikely to be an important separator of co-existing ground-foraging species (Recher *et al.* 2002). Likewise, the three species may have differed in their use of plant species for foraging and perching, but as the composition of insectivorous bird assemblages is largely determined by the structure of the vegetation rather than by the plant species present (Gilmore 1985), plant species were not examined in detail in this study.

Overlap can be high in some resource dimensions, but when all resource dimensions are considered together, the overlap between species may be relatively low (Calver and Wooller 1981). For this reason, Cody (1974) emphasised the need to consider all resource dimensions together when investigating the competitive relationships among coexisting species. As an extension of this idea, a more thorough study of resource use among the three robin species may have resulted in clearer patterns of niche partitioning being found. Specifically, a greater number of niche measurements might have revealed the greater similarities in resource use between Flame and Scarlet Robins, and the greater differences between these two species and the Dusky Robin predicted at the beginning of this study.

Horizontal segregation between Flame and Scarlet Robins appears to be the result of different habitat preferences. Flame and Scarlet Robins were differentiated in terms of height and perch substrates. Scarlet Robins spent greater proportions of time on man-made structures, below one metre and on the ground. Flame Robins spent more time on branches and above one metre. The Scarlet Robins' microhabitat preferences were probably linked to the location of their territories. Most of them had territories incorporating human dwellings where open ground and man-made structures were common. Fences, in particular, were frequently used by Scarlet Robins and as these were mostly below one metre high, the correlation between their use of man-made structures and preference for being in the 0–1 metre stratum is expected. Differences in habitat selection between these two species have also been found on mainland Australia. Historically, Flame and Scarlet Robins were both widespread throughout the forests of southeastern Australia, but usually occurred in different habitats (Loyn 1985). Flame Robins bred at higher altitudes and in moister environments than Scarlet Robins, and Scarlet Robins occurred in drier woodland and forest environments (Loyn 1985; Emison *et al.* 1987; Robinson 1992). Flame and Scarlet Robins may have only recently come into contact as a result of a reduction in their preferred habitats caused by land clearance activities (Loyn 1985). Comparisons in this study may therefore have been drawn between two species, which do not usually occur together, revealing their significantly different habitat preferences.

However, Flame Robins are believed to be dominant over Scarlet Robins at the start of the breeding season when territories are being established (Robinson 1989). If so, the Scarlet Robins in this study could have been forced into suboptimal habitat. That Scarlet Robins may have been forced into suboptimal habitat is supported by observations of them moving into territories vacated by migrating Flame Robins at the end of the breeding season (T.C.Y. H., unpub. data). The differences in habitat use found between the two species may therefore be the result of differences in habitat type. If Scarlet Robins repeatedly lose in interspecific encounters with Flame Robins, there can be no benefit in them being interspecifically territorial. Scarlet Robins will have to adapt to the habitat they are forced into, or face exclusion from areas where Flame Robins are present. Thus, if human activities such as logging and burning result in the creation of more heterogeneous habitats such that it becomes more common for Flame and Scarlet Robins to meet, there will be greater selective pressure for Scarlet Robins to adapt to suboptimal habitat as a greater proportion of the Scarlet Robin population will be in contact with Flame Robins. Conversely, if large areas of forest and woodland are left unmodified such that it is rare that Flame and Scarlet Robins coexist in the same area, there will be little selective pressure for Scarlet Robins to adapt to suboptimal habitat as only a fraction of the Scarlet Robin population will be in contact with Flame Robins. Under such circumstances, interspecific territoriality could persist in the few areas where Flame and Scarlet Robins occur together.

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