

Intraspecific and interspecific aggression among Flame, Scarlet and Dusky Robins

Tabitha C.Y. Hui

School of Zoology, University of Tasmania, Sandy Bay TAS 7005, Australia (Current address: College of Marine and Environmental Sciences, James Cook University, Townsville QLD 4811, Australia)
Email: tabitha.hui@gmail.com

Abstract. Flame *Petroica phoenicea* and Scarlet Robins *Petroica boodang* are interspecifically territorial wherever they meet. However, aggressive interactions between Dusky Robins *Melanodryas vittata* and these two species are rare where they co-occur. Interspecific aggression among co-existing species may be due to competition for resources. In this study at Cloudy Bay, South Bruny Island, Tasmania, in August 2004–February 2005, I examined intraspecific and interspecific territoriality in Flame, Scarlet and Dusky Robins by observing displays of aggression within and between the three species. I also used song-playback experiments to test whether the robins could discriminate between conspecific and congeneric species. Flame and Scarlet Robins responded differentially to playback of each other's song, but did not respond to Dusky Robin calls. Aggression between Flame and Scarlet Robins may be because of competition for horizontal space or resources. Conversely, the lack of aggression between Dusky Robins and these two species may be because of their ability to exploit different resources even when they are in the same area.

Introduction

Most birds defend territories against conspecific individuals, but some species also defend territories against individuals of other, usually closely related species, competing for limited resources such as food, space or nest-sites (Orians & Willson 1964; Brown & Orians 1970; Cody 1985; Jankowski *et al.* 2010). Interspecific territoriality has been experimentally verified in several studies of bird species with large overlaps in resource use (e.g. Rice 1978; Garcia 1983; Greenberg & Ortiz 1994; Secondi *et al.* 2003). The aggression that mediates interspecific territoriality has been found to be highly directed, in the sense that any given species enforces territorial exclusivity against only one or two other species in a locality (Robinson & Terborgh 1995). These interactions typically occur in habitats that are suitable for all the interspecifically territorial species where they come into contact (Murray 1971, 1981; Hudman & Chandler 2002; Jankowski *et al.* 2010). Elsewhere, the territory of each member of the interacting species is typically surrounded by conspecific territories, negating any opportunity for interspecific interactions (Robinson & Terborgh 1995; Jankowski *et al.* 2010).

Flame *Petroica phoenicea*, Scarlet *Petroica boodang* and Dusky Robins *Melanodryas vittata* are insectivorous and obtain the greatest proportion of their prey by pouncing from a perch to the ground (Recher *et al.* 2002). These three species may thus compete with one another for resources such as food and foraging sites. Previous studies (Pescott 1968; Fleming 1980; Loyn 1980; Shields & Recher 1984; Robinson 1989; Hui & Rose 2010) suggest that Flame and Scarlet Robins are interspecifically territorial and defend mutually exclusive territories against each other. Dusky Robins, however, have often been observed foraging in close proximity to individuals of these two species with little or no aggression between them (Hui & Rose 2010). The Dusky Robin is much larger than the other two species (Dusky Robin 27 g, Flame and Scarlet Robins both 13 g; Higgins & Peter 2002) and may eat different prey and forage in a different microhabitat from them (Hui &

Rose 2010). This ecological segregation, otherwise known as competitive exclusion or niche partitioning, between the Dusky Robin and the other two species may reduce competitive pressures between them and allow their peaceful co-existence. Ecological segregation may not be possible between Flame and Scarlet Robins because they are too similar behaviourally, morphologically and taxonomically. In such circumstances, competing species may co-exist by partitioning the available terrain between them using interspecific territorial defence. Interspecific territoriality enables competing species to exclude each other from parts of the same area and ensures that territory holders will be able to obtain sufficient resources for survival, growth and reproduction (Catchpole 1973; Muñoz & Motta 2000; Jankowski *et al.* 2010).

In this study, intraspecific and interspecific territoriality in Flame, Scarlet and Dusky Robins was examined by observing displays of aggression within and between the three species. Song-playback experiments were used to test whether the robins could discriminate between not only conspecific neighbours and strangers, but also neighbours and strangers of the rival species competing for the same resources, as the threat posed by a congeneric intruder would be almost as much as that posed by a conspecific intruder. The objective of the study was to determine whether interspecific territoriality between Flame and Scarlet Robins and the apparent lack of such behaviours between Dusky Robins and these two species (Hui & Rose 2010) was related to competition for resources.

Study area and methods

Study area

Observations and playback experiments were conducted at Cloudy Bay, South Bruny Island, Tasmania (43°23'S, 147°14'E, 32–68 m above sea-level). The site covers ~400 ha on private land and contains a mixture of grazing pasture and wet sclerophyll forest, dominated by Messmate *Eucalyptus obliqua*. Data were collected from August 2004

to February 2005, which encompassed the 2004–2005 breeding season.

Robins were caught in a mist-net and banded with a numbered metal band provided by the Australian Bird and Bat Banding Schemes and a unique combination of colour bands to permit individual identification. Individual robins were observed opportunistically throughout the day. For all aggressive interactions observed between birds of different family groups or species, the species and locations of the territories of the aggressor, respondent and victor were noted. Aggressors were individuals that initiated disputes, respondents were birds that were attacked. Victors were considered to be individuals that remained at the site of the contest at the end of the interaction.

During aggressive encounters, the presence or absence of songs, calls, fights, display flights, displacements, chases and plumage displays was recorded. Displacements comprised the dislodging of a bird from its perch by an approaching robin. Plumage displays included 'puffing out' of breast feathers, increased exposure of white frontal-spot feathers, increased exposure of white wing-coverts and exposure of white outer tail-feathers.

Songs of all three species were recorded from the study site at Cloudy Bay and several other locations throughout Tasmania using a Sony® Minidisc digital recorder with a Sennheiser® K6 directional microphone and an amplifier. Suitable songs were digitised and analysed using the Canary 1.2 sound analysis package and unwanted noises (e.g. insects, other bird species) filtered out. Waveforms were occasionally amplified to ensure that all playback songs were broadcast at the same volume. A test disc, which consisted of trial songs lasting 3 minutes each, was then prepared.

In total, 12 groups of robins, four of each species, were played recordings of Flame, Scarlet and Dusky Robin neighbour and stranger songs. Each experiment on every group consisted of six trials with six different playback treatments: Flame neighbours and strangers, Scarlet neighbours and strangers and Dusky neighbours and strangers. A neighbour was an individual with a territory within 500 m of the subject group, whereas a stranger had a territory at a different site (i.e. ≥ 10 km away) (Hui & Rose 2010).

Playback experiments were conducted in the first 2 weeks of December 2004. This coincided with the late breeding season when juveniles were fully fledged and independent, though many stayed with the adults (Dusky Robins) or moved to the periphery of the adults' territories (Flame and Scarlet Robins). All trials were carried out

between 0500 and 1000 h, and were abandoned if it was windy or wet. Groups were tested randomly and the order in which each group received different song types was also randomised. Songs were broadcast from an amplified speaker connected to the minidisc player.

To avoid problems such as habituation to the speaker, non-independence of trials and biased responses to playback, only one trial per day was conducted per subject family. If a robin from another territory sang or approached the speaker, the trial was aborted. Responses during playback periods were recorded as follows: (1) number of songs, (2) number of calls and (3) number of flights. Two-way repeated measures Analysis of Variance (ANOVA) was used to test for variation between species and song categories (neighbour or stranger) for responses recorded during the playback period.

Results

A total of 16 interspecific encounters between the three robin species was observed. Of these, 11 were between Flame and Scarlet Robins, three were between Scarlet and Dusky Robins, and two were between Flame and Dusky Robins. Although both Flame and Scarlet Robins initiated Flame–Scarlet Robin encounters, Scarlet Robins initiated more (10 of 11 encounters), but Flame Robins won more (10 of 11 encounters) (Table 1). The three encounters between Scarlet and Dusky Robins were all initiated by Dusky Robins, which were always the victors (Table 1). Of the two encounters between Flame and Dusky Robins, one was initiated and won by the Flame Robin, and one was initiated and won by the Dusky Robin (Table 1).

Ten intraspecific encounters were observed. Two were between Flame Robins and eight were between Scarlet Robins. No intraspecific encounters were observed between Dusky Robins. In all interspecific and intraspecific encounters, the victor was the territory holder.

Flame and Scarlet Robins behaved similarly during encounters. Flame Robins gave slightly more fights, flights, plumage displays, calls and chases than did Scarlet Robins (Table 2). Scarlet Robins displaced more often than Flame Robins, but gave the same number of songs during encounters (Table 2). Dusky Robins did not

Table 1. Interspecific encounters between Flame, Scarlet and Dusky Robins, Cloudy Bay, South Bruny Island, Tasmania, August 2004–February 2005. Parentheses indicate the number of encounters.

<i>Species involved</i>	<i>Aggressor</i>	<i>Victor</i>
Flame-Scarlet (11)	Scarlet (10), Flame (1)	Flame (10) Scarlet (1)
Scarlet-Dusky (3)	Dusky (3), Scarlet (0)	Dusky (3) Scarlet (0)
Flame-Dusky (2)	Flame (1); Dusky (1)	Flame (1) Dusky (1)

Table 2. Number of aggressive behaviours displayed by each species of robin—Flame, Scarlet and Dusky—during each encounter, Cloudy Bay, South Bruny Island, Tasmania, August 2004–February 2005. Parentheses indicate the number of encounters (both intraspecific and interspecific) involving that species. Results are shown as mean \pm standard error.

	<i>Flame (15)</i>	<i>Scarlet (22)</i>	<i>Dusky (5)</i>
Fights	1.62 \pm 0.17	1.55 \pm 0.13	0
Flights	1.58 \pm 0.13	1.50 \pm 0.13	2.00 \pm 0.00
Plumage displays	1.67 \pm 0.22	1.55 \pm 0.13	0
Songs	1.25 \pm 0.12	1.25 \pm 0.11	0
Calls	1.42 \pm 0.23	1.40 \pm 0.13	0
Displacements	1.58 \pm 0.23	1.60 \pm 0.13	1.40 \pm 0.14
Chases	1.42 \pm 0.23	1.30 \pm 0.12	1.60 \pm 0.14

fight, display plumage, nor call or sing during encounters (Table 2). However, they flew and chased more often during encounters than did the other two species (Table 2). Interestingly, female Scarlet Robin participated in 7 of the 22 encounters involving Scarlet Robins. They mostly followed their mates around and gave aggressive *chuck-chuck-chuck* calls and occasional chases. In one encounter with a Flame Robin, the juvenile male of a pair of Scarlet Robins also participated by chasing the Flame Robin and singing. Adult female and juvenile Flame Robins did not participate in any of the encounters observed. Most encounters involving Flame and Scarlet Robins lasted c. 2–3 minutes. Unlike encounters involving Flame and Scarlet Robins, encounters between Dusky Robins and the other two species were mild (no fights, plumage displays or vocal behaviours), very brief (a few seconds) and were not directional (no attempt was made to force the loser from the vicinity of the site of contest).

For the playback experiments, only the responses of male Flame and Scarlet Robins were statistically analysed as females responded in only two trials. The females' responses consisted of calls and flights. Juvenile Flame and Scarlet Robins did not respond in any of the trials. The responses of Dusky Robins were not analysed as they responded in only two trials. Both these responses were recorded during playback of Dusky Robin strangers' songs. In one trial, the subject family responded by giving

double whistle calls, but left soon after while the song was still being played. In the other trial, the subject family responded by giving alarm calls, and also left while the song was still being played.

Two-way repeated measures ANOVAs were conducted to explore the impact of species (Flame or Scarlet Robin song) and song type (neighbour or stranger) on the responses of subject Flame ($n = 4$) and Scarlet Robins ($n = 4$). Individual ANOVAs were conducted for each species (Flame or Scarlet Robin subjects) and response type (number of songs, number of calls, number of flights). Preliminary assumption testing was conducted to check for normality and homogeneity of variances with no serious violations noted. Flame and Scarlet Robins responded to conspecific and congeneric playback of song, but never responded to Dusky Robin song. There was a significant interaction effect of species and song type on the number of songs given by Flame Robins ($F_{1,3} = 13.21, P = 0.036$). The mean number of songs given by Flame Robins was highest towards playback of Flame strangers' songs and lowest towards Scarlet neighbours' songs (Figure 1). There were significant main effects of song type on the number of flights given by Flame Robins ($F_{1,3} = 96.00, P = 0.002$) and the number of calls given by Scarlet Robins ($F_{1,3} = 11.52, P = 0.043$). Flame Robins gave more flights during playback of strangers' songs than neighbours' songs, and Scarlet Robins gave more calls during playback of strangers'

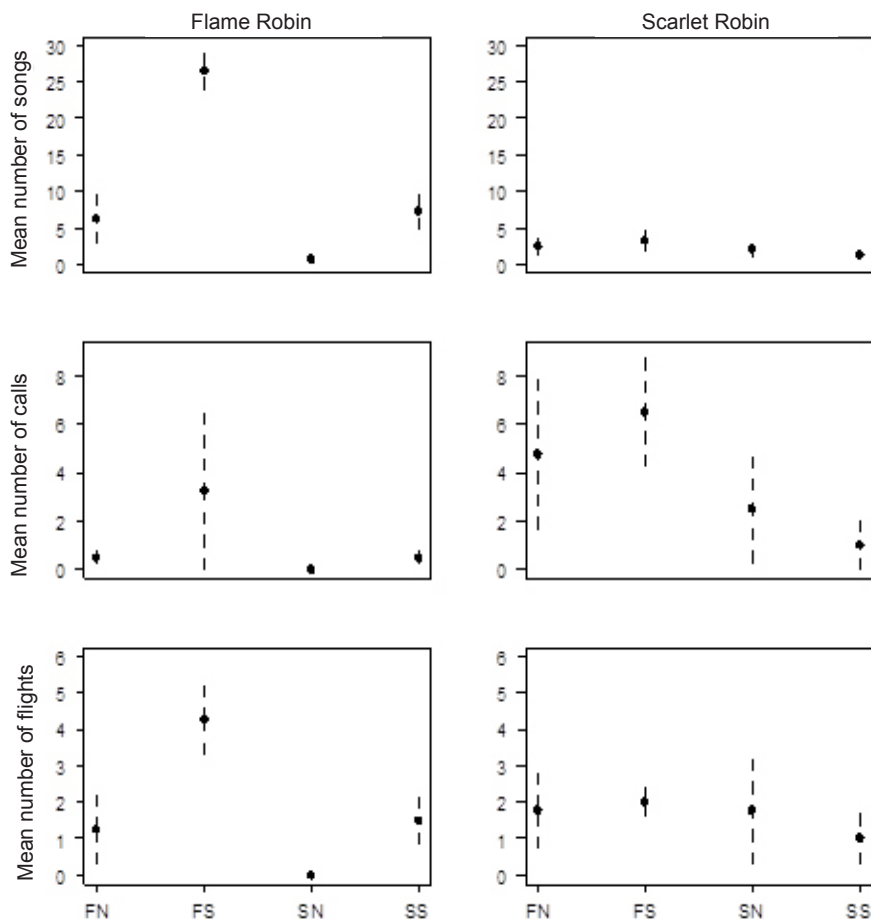


Figure 1. Responses of Flame and Scarlet Robins to playback of Flame and Scarlet neighbours' and strangers' songs, Cloudy Bay, South Bruny Island, Tasmania, August 2004–February 2005. Song types: FN = Flame neighbour, FS = Flame stranger, SN = Scarlet neighbour, SS = Scarlet stranger. Circles and error bars indicate mean \pm standard error.

songs than neighbours' songs (Figure 1). No significant effects ($P > 0.05$) of species or song type on the number of calls given by Flame Robins and the number of songs and flights given by Scarlet Robins were found (Figure 1). None of the robins tested were singing or calling before the start of the trials, so all responses were assumed to be the result of song playback rather than other factors such as aggressive interactions between the subjects and other birds.

Discussion

Interspecific encounters were observed between all three species studied, though much more frequently between Flame and Scarlet Robins. Encounters also tended to be more aggressive between Flame and Scarlet Robins, with both species displaying all seven aggressive behaviours recorded. Dusky Robins, on the other hand, only gave flights, chases and displacements during encounters. Although they did not display any vocal aggressive behaviours, they flew and chased more often during encounters than did Flame and Scarlet Robins.

The results of the playback experiments support previous observations (Pescott 1968; Fleming 1980; Loyn 1980; Shields & Recher 1984; Robinson 1989; Hui & Rose 2010) that Flame and Scarlet Robins are interspecifically aggressive. Flame and Scarlet Robins responded to playback of each other's song, even though their songs are clearly different. However, they did not respond to the calls of Dusky Robins, which are also very different from Flame and Scarlet Robins' songs. This shows that the aggression between Flame and Scarlet Robins is highly directed and specific. The results also show that these species distinguish between both conspecific and congeneric neighbours and strangers. Flame Robins gave more flights and Scarlet Robins gave more calls during playback of strangers' songs than neighbours' songs. Dusky Robins did not respond to playback of Flame and Scarlet Robins' songs and responded only twice to playback of conspecific songs.

In many species, interspecific aggression is associated with interspecific competition (Robinson 1993; Garcia & Arroyo 2002). Species that show high overlap in choice of habitat and foraging niche often evolve a system of mutually exclusive territories to secure resources (Moynihan 1968; Cody 1969, 1973, 1974, 1978; Robinson & Terborgh 1995). Although interspecific aggression is costly in terms of time and energy spent on territorial defence, it may be adaptive in species that overlap broadly in resource use as it leads to better distinction of territory boundaries between the species and thus reduces the level of interspecific competition (Bourski & Forstmeier 2000; Reif *et al.* 2015).

Based on this theory that interspecific territoriality is caused by competition for the same resources, Scarlet and Dusky Robins would be expected to be more aggressive and territorial towards each other than to Flame Robins, as they show the greatest overlap in habitat use and foraging techniques (Hui & Rose 2010). However, Dusky Robins seldom engaged in aggressive interactions with Flame and Scarlet Robins. This may be because of the Dusky Robin's ability to exploit different resources from Scarlet Robins even when they are in the same area (Hui & Rose 2010) or defend their territories and resources

using non-vocal means. Birds often sing, call and display plumage to deter intruders, but Dusky Robins did not. This does not mean, however, that they are not territorial as they did displace, fly over and chase other birds. It is possible that these behaviours are enough to deter intruders from entering Dusky Robin territories or potential competitors for resources.

It is interesting that Flame and Scarlet Robins continue to be interspecifically territorial when they already utilise different resources (Hui & Rose 2010). 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, then Scarlet Robins could have been forced into suboptimal habitat. The differences in resource utilisation found between the two species may therefore be the result of differences in habitat type. The dominance of Flame Robins over Scarlet Robins is supported by my observations of encounters between the two species. Although Scarlet Robins initiated aggressive interactions more often than Flame Robins, Flame Robins won the majority of these encounters. If Scarlet Robins repeatedly lose to Flame Robins, there will be little benefit in their remaining interspecifically territorial and this behaviour should eventually cease. However, if Flame and Scarlet Robins seldom come into contact with each other, then interspecific territoriality could persist in the few regions where they do.

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