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WHY DO FLAME ROBINS *Petroica phoenicea* MIGRATE? A COMPARISON BETWEEN THE SOCIAL AND FEEDING ECOLOGIES OF THE FLAME ROBIN AND SCARLET ROBIN *P. multicolor*

DOUG ROBINSON

Department of Botany and Zoology, Monash University, Clayton, Vic. 3168
Present address: 28 Bath Street, Mornington, Vic. 3931

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Comparisons between the ecology of Flame and Scarlet Robins at a sympatric breeding site suggested that Flame Robins migrated during the winter months because of a decline in the availability of their major prey. During the nine months that Flame Robins were present at the breeding site, they foraged for flying insects twice as often as did Scarlet Robins. Scarlet Robins foraged more often for ground-dwelling prey. Flying insects are a very seasonal food resource, present mostly during the warmer months. Ground-dwelling arthropods remain relatively more common in winter. Thus, Flame Robins migrated from their breeding grounds once food abundance decreased and competition for remaining prey increased in the autumn months. Scarlet Robins were able to find sufficient food to remain at their breeding grounds throughout the year. Severe competition for territories in breeding habitat may have been a further selection pressure on Scarlet Robins to remain at their breeding grounds throughout the year, since territory turnover was low.

Morphological comparisons indicated that Flame Robins showed long-term adaptations to their winter environment and winter feeding behaviour (hop-gleaning on the ground). Such adaptations imply that migration may be an ancestral trait within this species rather than a recent event, and that Flame Robins have long moved between wintering and breeding grounds to exploit seasonally abundant supplies of food.

INTRODUCTION

In contrast to the temperate northern hemisphere, where 40–75 per cent of landbird species migrate *en masse* (Perrins and Birkhead 1983), landbird migration in Australia is poorly understood. Few Australian landbirds migrate large distances, or migrate in flocks (Ford 1989). Migrations by Australian landbirds instead tend to be 'diffuse' (Recher 1985), comprising short-distance or partial migrations (Ford 1989). Nonetheless, migration is a distinctive feature of many Australian bird communities (Nix 1976; Recher *et al.* 1983), and as many as 50 per cent of species in south-eastern Australia show regular movements between breeding and non-breeding environments (Nix 1976; Recher *et al.* 1983; Loyn 1985a).

Lack (1954) proposed that scarcity of food is the ultimate cause of migration among birds and that species which feed on seasonal resources are more likely to migrate than species whose foods are available all year round. He proposed furthermore that competition for food during winter caused intraspecific differences in migratory tendencies: thus, if they are smaller and weaker, females are more likely to migrate than males and young males are more likely to move than adults.

More recent models about the ecological causes of competition similarly consider food availability and competition for food to be the ultimate causes of migration, but stress the significance of social competition as a proximate cause. Migratory tendencies are predicted to vary between different age-classes, different sexes and different species because of competition for non-breeding season or breeding resources. Competition for resources during the non-breeding season may cause subordinate individuals or species to disperse to poorer quality habitats within their breeding range, or to migrate to separate wintering grounds (Cox 1968; Gauthreaux 1982; Ketterson and Nolan 1983). Competition for breeding season resources may cause those individuals most limited by resource availability to migrate only short distances, or to return to their breeding grounds as early as possible (Greenwood 1980; Myers 1981; Ketterson and Nolan 1983; Pienkowski and Evans 1985).

Physiological constraints are another possible cause of bird migration. Smaller-bodied individuals may be less able to withstand extended periods of fast than larger-bodied birds. Selection pressures may lead to the migration of smaller-bodied birds from breeding grounds where food becomes too scarce in winter, or to longer migrations by smaller birds (Myers 1981; Ketterson and Nolan 1983).

Flame Robins *Petroica phoenicea* and Scarlet Robins *P. multicolor* are closely-related species of flycatchers that are widespread through south-eastern Australia. Both species are found in forest and woodland environments but often are separated by interspecific differences in altitude or habitat selection during the breeding season. Scarlet Robins are more common at lower altitudes in drier woodland and forest environments. Flame Robins are one of the commonest breeding species at higher altitudes (800–1 700 m) (Loyn 1985b). At the end of the breeding season, the majority of Flame Robins migrate to lowland grasslands and pastures. Some birds may also migrate to the mainland from Tasmania (Campbell 1909; Dennett 1982). The majority of Scarlet Robins are sedentary (Huddy 1979; Bell and Ford 1987; Robinson 1990).

It seems clear why Flame Robins migrate from high-altitude breeding grounds for the winter, since their breeding grounds are often snow-covered between June and September and food is presumably scarce. Cold temperatures may also reduce individuals' chances of over-winter survival (e.g., Green 1959). It is not clear why Flame Robins migrate from lower-altitude sites (600–1 000 m), where sympatric populations of Scarlet Robins remain all year round. Here I compare the ecology of Flame and Scarlet Robins at a sympatric breeding ground in light of the above hypotheses to assess why Flame Robins migrate and Scarlet Robins do not.

STUDY AREA AND METHODS

Most of the study was done on the Southern Tablelands of New South Wales, at a 300 ha site near Nimmitabel (36°46′S, 149°22′E, 800–900 m asl). Because I could not locate populations of Flame Robins on the tablelands in winter, a separate Flame Robin population was observed during the non-breeding season at a site near Seaford, Victoria (38°06′S, 145°05′E, 10 m asl). Data were collected from July 1983 to May 1986.

The Nimmitabel study site comprised *Eucalyptus viminalis*, *E. pauciflora* forest and woodland, and some open grassland habitat. The forest and woodland habitats were used by robins all year round, and the grassland habitat was used during autumn and winter. The Seaford site was a 20 ha paddock covered mostly by short (<10 cm), introduced grass species and some patches of sedge *Juncus acutus* and Blackberry *Rubus fruticosus*. The paddock was bordered by a tea-tree *Leptospermum laevigatum* hedge and a row of 15 m high pines *Pinus radiata*.

Temperatures at both sites showed marked seasonal variation, and were cooler at Nimmitabel. Mean minimum temperatures at Nimmitabel fell below 0°C between May and September; mean minimum temperatures at Seaford were never lower than 4°C. Maximum temperatures were similar at both sites during most of the year and ranged from approximately 15°C in winter to 21–23°C in summer and autumn (Table 3). Rainfall was lowest in January, February and March, and tended to be high in spring; there were no other consistent patterns. Snow fell occasionally at Nimmitabel in every winter and spring; none was recorded at Seaford.

Five to 20 days per month were spent in the field. Robins were caught by mist-netting and by clap-traps baited with mealworms. All birds caught were individually colour-banded, measured and released. The following measurements were taken for as many birds as possible:

(1) body weight (to the nearest 0.1 g);

(2) wing length (to the nearest 0.1 mm for flattened wing chord);

(3) tarsus length (to the nearest 0.01 mm from the intertarsal joint to the bottom of the lowest undivided scutellar segment);

(4) bill length (to the nearest 0.01 mm from the base of the frons to bill tip);

(5) bill width (to the nearest 0.01 mm from just anterior to each bird's nostrils);

(6) bill length/bill width (derived from the above two measurements made in the field).

Wing, tarsus and bill measurements were divided by the cube root of body weight to allow for allometric effects of weight on these measurements (Gaston 1974). Birds were sexed and aged using behavioural and biometric criteria. The rate of capture of birds caught was expressed as the number per net hour, a figure based on the number of active nets and the length of time that these were open.

Individual movements of robins were monitored during monthly visits to the territories of all known birds and by regular searches of habitat within and adjoining the study site. The locations of all robins sighted were plotted with reference to a 50 m by 50 m grid established throughout the study site. Between May and August, 1985, I searched grasslands and paddocks within a 30 km radius of Nimmitabel to try to locate wintering groups of Flame Robins. I also placed 'Request for Information' columns in all local media.

Foraging data were collected during 5–45 minute watches of focal birds, during which I recorded the method, substrate, height and plant species (if plant species used) for every observed foraging act. Methods were categorized as: *pouncing*, where a perched bird dropped to the ground to capture a prey item and returned to a perch; *hawking*, where a flying bird captured (or attempted to capture) a prey item in flight; *snatching*, where a bird flew from a perch to snatch a prey item from substrates such as foliage and bark; *gleaning*, where a stationary bird took prey items resting on substrates; and *hop-gleaning*, where birds hopped along the ground making repeated pecks at different prey items. Foraging heights were recorded to the nearest metre and later pooled into five different height classes: 0–1 m, 1–3 m, 3–5 m, 5–16 m and >20 m. Substrates were defined as: ground, air, branches, trunks, foliage, and logs and rocks.

Statistical analyses of foraging behaviour were done by scoring whether or not a particular individual used a particular feeding method, height class, substrate or plant species category during an observation period. Categories were scored only once per observation period. Chi-square tests were then used to compare the frequency with which individuals did or did not use a particular category of foraging behaviour. Population averages for every category of foraging behaviour were derived by summing each individual's percentage score for that category to obtain a population value and dividing that value by 'n', where n is the number of birds watched any month/season/year. Population averages for each category of foraging behaviour are presented throughout the paper.

During observations of focal birds, I recorded the time spent in foraging and the number of foraging acts made per observation period. Foraging time included the time spent alert at perches that was not spent in other activities (e.g., singing or aggressive behaviour). Foraging acts were all assumed to be equally successful, as prey sizes were too small to let me judge the success or failure of any observed act. I also recorded the frequency and duration of agonistic interactions during observation periods, from which I calculated seasonal durations and rates of aggressive interactions between robins.

A cursory assessment of Flame Robins' diets at Seaford was done by stomach-flushing a small sample of birds in May and June 1986. A 2 mm diameter tube attached to a 5 ml syringe was inserted into the robins' stomachs. Once the tube was in place, birds were injected with 2 ml of warm water, the tube was removed, and birds were held over a collecting funnel to regurgitate stomach contents. Stomach contents were preserved in 70 per cent ethyl alcohol and later examined under a stereo-microscope. Prey items were identified to order and measured to the nearest 0.1 mm.

All morphometric, feeding rate and interaction rate data were tested for homogeneity of variances prior to statistical analyses. Feeding rate and interaction rate data were subsequently log-transformed because variances of samples increased with increasing means. Morphometric, feeding rate and interaction rate data were compared by t-tests. Foraging data were compared by χ^2 tests. Five per cent significance levels are used throughout the paper, unless otherwise stated.

Because Flame Robins were absent from Nimmitabel between May and July, seasons were defined arbitrarily as: winter (May–July); spring (August–October); summer (November–January); autumn (February–April). These definitions of seasons are used throughout the paper.

'Brown birds' refers to female and first-year male Flame Robins pooled as one category, as the two groups were not clearly distinguishable in the field.

RESULTS

Morphometrics

Flame Robins were slightly but significantly heavier than Scarlet Robins of corresponding sex (Table 1). Flame Robin males had significantly longer wings, tarsi and bills than Scarlet Robin males, after correcting for size differences between the two species (see Methods). There were no significant differences between their bill widths (having corrected for size differences) nor the ratio of bill length/bill width. Male Flame Robins therefore had longer and finer bills than male Scarlet Robins. Female Flame Robins similarly had relatively narrower bills than female Scarlet Robins, and longer tarsi. Wing lengths, bill lengths and bill widths of female Scarlet and Flame Robins were not significantly different (Table 1).

TABLE 1

Morphometric comparisons between (a) all male Scarlet Robins and Flame Robins, (b) adult male robins and (c) female robins. Values represent mean ± SD and sample size. With the exceptions of body weight and culmen/width measurements, levels of significance are based on t-tests done on morphometric values divided by the cube root of body weight.

(a)

Measurement	Flame Robin (all males)	Scarlet Robin (all males)	P
weight	13.52 ± 0.82, 55	13.12 ± 0.76, 34	<0.05
wing length	78.46 ± 1.44, 55	74.40 ± 1.98, 33	<0.001
tarsus length	21.47 ± 0.75, 30	20.17 ± 0.89, 19	<0.001
culmen length	10.29 ± 0.50, 35	9.44 ± 1.88, 23	<0.05
bill width	3.58 ± 0.25, 19	3.65 ± 0.33, 11	n.s.
length/width	2.89 ± 0.21, 19	2.51 ± 0.81, 10	n.s.

(b)

Measurement	Flame Robin (adult males)	Scarlet Robin (adult males)	P
weight	13.30 ± 0.74, 33	12.99 ± 0.72, 16	n.s.
wing length	78.95 ± 1.53, 33	74.89 ± 2.00, 15	<0.001
tarsus length	21.35 ± 0.80, 17	20.12 ± 0.90, 10	<0.01
culmen length	10.03 ± 0.60, 23	9.21 ± 0.36, 14	<0.05
bill width	3.61 ± 0.25, 14	3.76 ± 0.36, 7	n.s.
length/width	2.86 ± 0.21, 14	2.39 ± 0.97, 7	n.s.

(c)

Measurement	Flame Robin (females)	Scarlet Robin (females)	P
weight	13.78 ± 1.32, 27	13.11 ± 0.72, 20	<0.05
wing length	74.31 ± 1.46, 28	73.16 ± 1.80, 19	n.s.
tarsus length	21.55 ± 0.53, 13	19.88 ± 1.12, 11	<0.001
culmen length	10.10 ± 0.49, 14	9.77 ± 0.58, 12	n.s.
bill width	3.46 ± 0.21, 8	3.29 ± 1.48, 7	n.s.
length/width	2.95 ± 0.30, 8	2.51 ± 0.21, 6	<0.01

Social ecology of the Flame Robin

Most Flame Robins were present at Nimmitabel for approximately nine months of the year between August and April. Adult males were the first birds to return and the last birds to depart, and were present from the last week of July/first week of August until early May. The median arrival date of adult male robins was 5 August; the median arrival date of first-year males was 14 August. There may have been some separation between the arrival dates of adult and first-year female Flame Robins, but sample sizes of banded birds were too small to test the difference. The first two females to return to Nimmitabel in 1985 had both bred there the previous year.

Males on average returned to Nimmitabel a week earlier than female robins, but arrival dates of the two sexes overlapped considerably. The median arrival date of females was 15 August; male's median arrival date was 8 August. Individuals of each sex continued to arrive and settle at Nimmitabel until mid September.

September was one of the two peak periods of Flame Robin movement through the study site (Fig. 1) as birds returned to their breeding grounds. Most Flame Robins caught at Nimmitabel during September did not establish territories there, and disappeared within a few days. Birds that settled were very site-faithful. Eighty-three per cent of males and 67 per cent of females that settled on territories at Nimmitabel returned for a second breeding season, most of them returning to the previous season's territory.

Flame Robins defended territories from August to the end of the breeding season (January or February). Most subsequently abandoned their territories, at least until completion of the annual moult, and joined groups of first-year Flame Robins that were wandering through the study site. Some Flame Robins became partly territorial once more in March and April. These birds spent at least a few hours a day on their former territories, but abandoned them during the middle of the day or during cold weather.

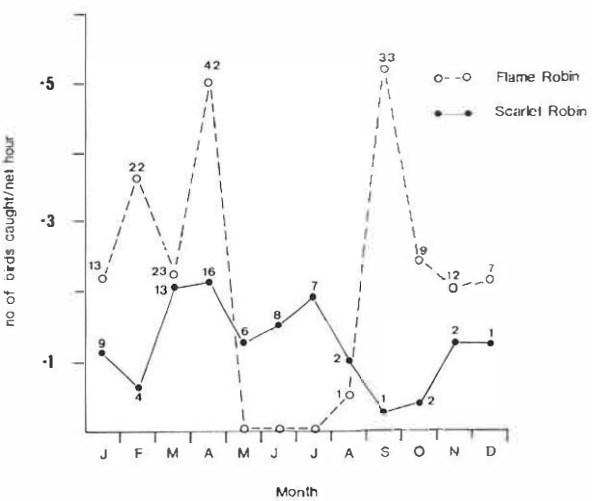

Figure 1. *Capture rates of Scarlet and Flame Robins at Nimmitabel for all years combined. Results are expressed as the number of birds caught per net hour. Numbers above symbols show actual number of birds caught in that month.*

During late summer and autumn there was an influx of immigrant Flame Robins to the study area (Fig. 1), most of which were brown birds (66%) or juveniles (29%). This influx of robins into the study area significantly increased the rate of aggressive interactions between Flame Robins (FL FL in Fig. 2). The interaction rate between Flame Robins and Scarlet Robins also increased (FL SC in Fig. 2), although the increase was not significant ($t_{169} = 1.52$, $P > 0.05$). The largest numbers of Flame Robins moved through the study area in April (Fig. 1). By mid May, no Flame Robins remained at Nimmitabel, their departure coinciding with decreases in minimum temperatures in April and May.

Flame Robins in winter were non-territorial and foraged in small groups together. Groups included females, adult males and first-year males. Pair-bonds were not evident. Twenty-seven per cent of adult males and 13 per cent of brown birds were resighted at the same locality one or more years after banding at Seaford. Four of the nine robins banded in brown plumage and subsequently retrapped at Seaford had acquired adult male plumage. The remaining five birds were retrapped in brown plumage and considered to be females. Thus, females, adult males and first-year males all showed site fidelity to their wintering grounds in successive years.

Winter searches of grassland areas within 30 km of Nimmitabel failed to locate any colour-banded Flame Robins and managed to locate only three Flame Robins in all. Media requests for information also failed to produce records of colour-banded Flame Robins from the Bega or Bombala districts of New South Wales.

Social ecology of the Scarlet Robin

Seventy-three per cent of the Scarlet Robins occupying territories at Nimmitabel were resident birds which defended territories throughout the year. Residents were nearly all adults (82%, n = 22), and tended to occupy territories in the forest habitat (95%, n = 22). High adult survivorship and intense competition for suitable breeding habitat led to low annual rates of territory turnover in the forest habitat: nine of 11 territories occupied during the 1984–85 breeding season were retained by the same males in the 1985–86 breeding season (Fig. 3).

The remaining 27 per cent of territorial Scarlet Robins were present only during the non-breeding season. In late summer and autumn there was an influx of Scarlet Robins into the study site (Fig. 1), leading to an increase in the rate of intraspecific aggressive interactions (SC SC in Fig. 2). Some of the immigrants stayed and established non-breeding season territories; the rest departed after a few days to one month (Robinson 1990). Heavier birds appeared more likely to stay than lighter birds, although sample sizes were too small for statistical comparisons. First-year males that stayed weighed on average 13.4 ± 0.8 g (n = 9). First-year males that departed weighed 12.7 ± 0.1 g (n = 4). Seventy-one per cent of the males caught from January to April (n = 21) were first-year birds, as were five of eight females which I was able to age. No Scarlet Robins moved through the study site at the end of winter or in early spring (Fig. 1).

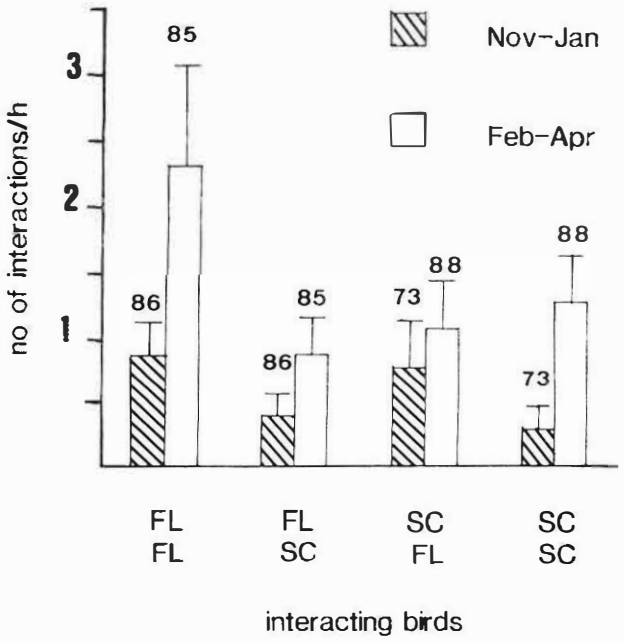

Figure 2. *Frequency of intraspecific and interspecific disputes between Scarlet and Flame Robins. The species listed first in the captions below the x-axis represents the species being observed. The bars show the average hourly rate of interaction between individuals. The vertical lines represent one standard error. Sample sizes (number of observation periods) are given above the bars for each species of robin.*

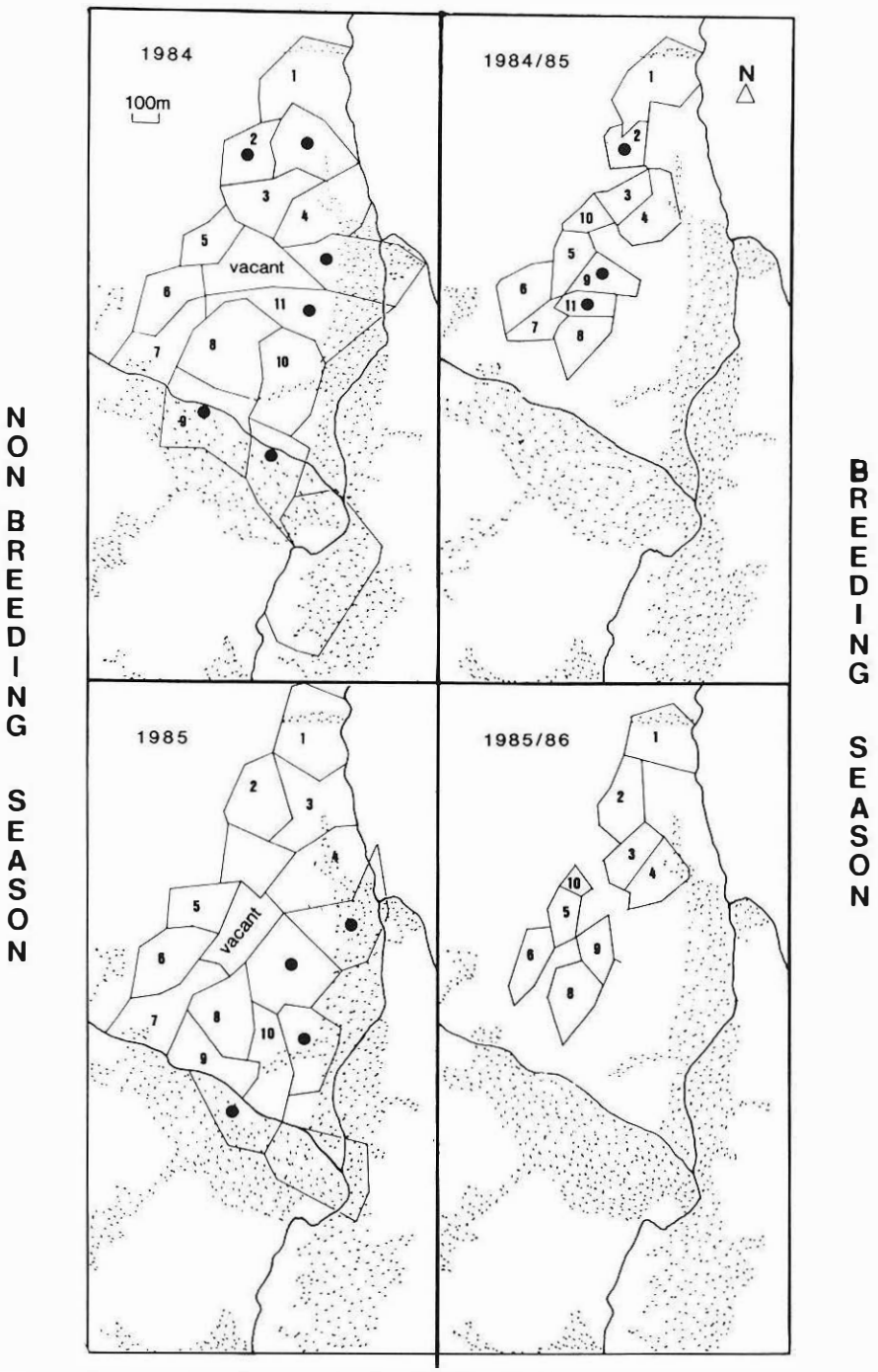

Figure 3. *Distribution of Scarlet Robins' territories at Nimmitabel during the breeding and non-breeding seasons. Stippled areas indicate grassland habitat. Large black dots indicate those territories occupied by first-year males. The numbers represent the identity of individual pairs that were recorded from Nimmitabel during the non-breeding and breeding seasons. Pairs are given the same number in both years.*

TABLE 2

Territory sizes and percentage grassland of territories occupied by year-round resident (Res.) and wintering (Vis.) pairs of Scarlet Robin during the breeding season (S) and non-breeding season (W). Values represent mean ± SD and sample size. The 'P' column denotes levels of significance for comparisons between territory sizes and per cent grassland of territories occupied by winter visitors and resident birds during the non-breeding season (upper figure), and territory sizes and per cent grassland of territories occupied by resident birds in winter and summer (lower figure).

			Territory size (ha)	P	Per cent grassland	P
1984	Vis.	W	9.9 ± 5.2, 4	n.s.	54.5 ± 36.8, 4	n.s.
1984	Res.	W	7.0 ± 2.4, 11		15.9 ± 21.9, 11	
1984	Res.	S	3.2 ± 1.5, 11	<0.001	0.3 ± 1.2, 11	<0.05
1985	Vis.	W	8.5 ± 2.2, 4	n.s.	64.0 ± 44.2, 4	<0.05
1985	Res.	W	6.1 ± 1.5, 9		5.0 ± 6.2, 9	
1985	Res.	S	3.2 ± 1.3, 9	<0.001	1.5 ± 3.2, 9	n.s.
84/85	Vis.	W	9.3 ± 3.9, 8	<0.05	59.3 ± 38.0, 8	<0.01
84/85	Res.	W	6.6 ± 2.1, 20		11.0 ± 17.3, 20	
84/85	Res.	S	3.2 ± 1.4, 20	<0.001	0.9 ± 2.4, 20	<0.05

Scarlet Robins present at Nimmitabel during only autumn and winter were nearly all first-year birds (75%, n = 8), and mostly established territories in the grassland habitat (75%, n = 8, Fig. 3). Grassland robins showed little site fidelity. Four of the five first-year pairs which settled in grassland habitat disappeared at the start of the breeding season without attempting to breed, and did not return the following year. The fifth pair moved 600 m from its grassland territory to a breeding season territory in forest habitat (pair 9, Fig. 3). By contrast, 60 per cent of first-year pairs that established territories in the forest habitat (n = 5) did not disappear at the start of the breeding season and retained their territories during the breeding season and following years. First-year males that established territories in forest habitat tended to be heavier (13.7 ± 0.5 g, n = 5) than first-year males that established territories in grassland habitat (13.1 ± 1.1 g, n = 4), although sample sizes were too small to make statistical comparisons. Breeding season movements of Scarlet Robins that disappeared from either the grassland or forest habitats at the end of winter remain unknown.

Scarlet Robins which remained at Nimmitabel throughout the year defended significantly larger territories during the non-breeding season than during the breeding season (Table 2). They also showed a significant habitat shift during the non-breeding season, and included more grassland habitat within their defended space (Table 2). Two pairs (pairs 9 and 10) moved distances of more than 500 m between separate breeding-season and non-breeding-season territories (Fig. 3). Non-breeding-season territories averaged 6.6 ha and comprised 11 per cent grassland habitat. Breeding-season territories measured 3.2 ha and comprised less than 1 per cent grassland habitat. Territory sizes of robins present only during the non-breeding season were larger still: they averaged 9.3 ha, and comprised 59 per cent grassland habitat (Table 2). The largest territory held by a wintering pair of Scarlet Robins measured 17.7 ha and comprised 78 per cent grassland habitat.

Feeding ecology

Males of each species spent from between 60 and 90 per cent of their daily time budgets foraging for food, spending most time foraging in winter and spring when average temperatures were lowest (Table 3). There were no significant interspecific differences between their foraging time budgets, although Flame Robins in summer appeared to spend more time foraging than did Scarlet Robins ($P < 0.10$).

Their foraging behaviour showed extensive overlap, especially in autumn (overlap = 84%) and spring (overlap = 85%) (Robinson 1992). Overlap was highest for use of vertical space, and lowest for use of foraging methods (Robinson

TABLE 3

Time spent foraging by male robins in every season as per cent of daylight hours. Percentage values are underlined. Numbers in brackets represent the number of hours observation. Average seasonal temperatures (°C) at Nimmitabel and at Seaford (in brackets) are also given. Note that seasons are defined here as in the methods section: autumn (February–April); winter (May–July); spring (August–October); summer (November–January).

Season	Scarlet Robin feeding time	Flame Robin feeding time	Maximum temperature	Minimum temperature
Autumn	75.0 (30.6)	66.5 (25.5)	21.3 (23.2)	6.7 (12.2)
Winter	89.9 (18.7)	92.0 (21.5)	15.2 (15.8)	−3.0 (5.5)
Spring	81.3 (16.9)	83.3 (23.0)	16.4 (16.5)	0.9 (7.7)
Summer	60.9 (21.9)	74.3 (22.0)	21.5 (22.6)	6.6 (12.0)

TABLE 4

Foraging data for Scarlet and Flame Robins at Nimmitabel during the nine months (August–April) pooled, in autumn (February–April) and winter (May–July). The winter data for Flame Robins are for the Seaford site. Figures in columns represent average percentage values for each species' population (see Methods for more detailed description). Number of feeding records and number of birds observed are given below each subheading.

	Nine months		Autumn		Winter	
	Scarlet Robin	Flame Robin	Scarlet Robin	Flame Robin	Scarlet Robin	Flame Robin
Method						
No. of records	4 926	5 228	2 187	1 469	2 201	1 220
No. of birds	324	323	130	103	105	81
pounce	44.6	33.9	32.5	20.7	71.4	16.8
hawk	16.0	33.2	18.7	35.0	2.8	9.6
snatch	37.0	22.7	44.2	32.4	24.3	1.4
glean	2.0	2.3	3.8	3.9	1.0	0.1
hop-glean	0.4	7.9	0.8	8.0	0.5	72.1
Substrate						
No of records	4 502	5 099	1 920	1 469	1 856	1 220
No of birds	324	323	130	103	105	81
ground	48.5	41.8	36.5	27.3	86.2	89.0
air	17.7	34.2	21.0	35.0	3.3	9.5
branch	10.4	5.2	14.4	9.4	1.9	0.8
trunk	13.0	9.3	17.1	16.6	1.6	0.1
foliage	8.8	6.0	9.3	8.6	5.1	0.6
logs/rocks	1.6	3.5	1.7	3.1	1.9	0.0
Height						
No of records	4 763	5 140	2 082	1 469	2 146	1 220
No of birds	324	323	130	103	105	81
0–1 m	56.3	61.6	47.9	50.4	82.5	96.5
1–3 m	13.1	14.3	17.4	18.9	6.8	1.9
3–5 m	7.9	7.5	10.7	9.6	4.0	0.2
5–16 m	21.0	13.6	22.5	15.2	5.4	1.4
16–30 m	1.7	3.0	1.5	5.9	1.3	0.0

1992). Nonetheless, there were significant differences between average values recorded for Flame Robins' and Scarlet Robins' feeding methods, foraging substrates, feeding heights and use of plant species (Robinson 1989). Flame Robins hawked for flying prey twice as often as did Scarlet Robins. They also hop-gleaned more often than Scarlet Robins (Table 4). Scarlet Robins pounced for ground-dwelling prey and snatched for prey resting on branches, trunks and foliage of trees and shrubs more often than Flame Robins (Table 4). These differences remained in autumn (Table 4), when home ranges of each species began to overlap (Robinson 1990). Niche breadth values for each species ranged from between 0.40 to 1.56, and were lowest in winter and highest in autumn and summer (Robinson 1989). Niche breadth values for Flame Robin were broad and similar to those for Scarlet Robin in every season but winter. Flame Robins in winter were specialist ground-feeders (90% of foraging records, Table 4), which foraged almost exclusively at heights of 0–1 m (Table 4). Their niche breadth was lowest in that season (Robinson 1989).

Both species showed significant seasonal variation in the rates at which they foraged for food (Scarlet Robin: $F_{3,428} = 20.1$, $P < 0.001$; Flame Robin: $F_{3,401} = 79.5$, $P. < 0.001$), foraging at a more rapid rate in winter and spring (Fig. 4), when abundance of prey and temperatures were lowest. Scarlet Robins showed comparatively small increases in their foraging rate, on average making 57 foraging acts/h in autumn and 71 acts/h in winter. Flame Robins on average made 64 foraging acts/h in autumn and 244 acts/h in winter — a fourfold seasonal difference. Scarlet Robins made significantly fewer foraging acts/h than Flame Robins in every month except February, March and April. Differences between the two species' feeding rates were especially large in winter (Fig. 4).

Assuming that each species needed similar amounts of food to survive, Scarlet Robins were evidently able to obtain it from fewer foraging acts than Flame Robins (Fig. 4). This difference between the two species' foraging behaviour implied that Scarlet Robins were taking larger prey items than Flame Robins, or caught food more successfully.

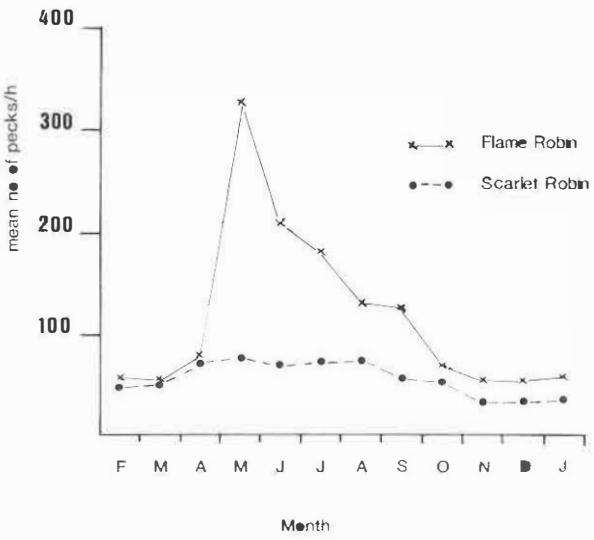

Figure 4. *Monthly variation in the feeding rates of Flame and Scarlet Robins. Values represent the average number of foraging acts recorded per hour.*

Field observations suggested that Flame Robins took many small prey items when hop-gleaning. Thus, the percentage of time spent hop-gleaning by Flame Robins was significantly correlated with the average number of foraging acts/h made per month ($r = 0.85$, $n = 12$, $P. < 0.01$). No significant, positive correlations were obtained between the average number of foraging acts/h made per month and the percentage of time spent pouncing, hawking or snatching. Furthermore, for the 15 Flame Robins sampled at Seaford in winter, the largest prey item measured just 10.0 mm, while most prey measured between 2.5 and 5.4 mm (Table 5). Small beetles, caterpillars, flies and ants were the commonest prey items recorded from the Flame Robins' stomachs (Table 5). Other studies of Flame Robins' stomach contents have also found beetles and ants to be common prey items in winter (Cleland 1911; Lea and Gray 1935; Favaloro 1953).

Interspecific comparisons between the frequency with which each species demolished prey items prior to eating them provided another means of estimating the size of prey taken by birds — assuming that only large prey needed to be demolished. 'Demolishing' here refers to the distinctive action of repeatedly hitting prey against

a solid substrate to rupture the prey item's exoskeleton. Scarlet Robins and Flame Robins each demolished less than 3 per cent of prey items in any season (Table 6). Both species nonetheless showed significant seasonal variation in the frequency with which they demolished prey (Table 6). Scarlet Robins demolished prey most often in winter, while Flame Robins demolished prey least often in winter ($\chi^2 = 104.9$, $P < 0.001$). Prey-demolishing was recorded twice as often for Scarlet Robin as it was for Flame Robin (Table 6).

TABLE 5

Stomach contents of Flame Robins at Seaford. Data based on samples obtained from 15 stomach-flushed birds in 1986. Frequency refers to the percentage of samples in which each arthropod group was recorded. Composition refers to the abundance of each arthropod group in the robins' diets, as a percentage of the total number of arthopods found in the 15 birds' stomach contents. Prey size values represent mean size ± SD and sample size for whole specimens obtained in the samples.

Prey item	Frequency (n = 15)	Composition (n = 165)	Prey size (mm)
Beetles (Coleoptera)	100	49.7	2.5 ± 1.1, 11
Flies (Diptera)	73	17.6	3.1 ± 0.5, 4
Caterpillars (Lepidoptera)	73	9.7	5.4 ± 2.7, 8
Ants (Hymenoptera)	67	20.6	2.5 ± 0.7, 3
Spiders (Arachnida)	13	1.2	
Wasp (Hymenoptera)	7	0.6	
Beetle larva (Coleoptera)	7	0.6	4.4 ± 0.0, 1

TABLE 6

Seasonal frequency with which robins demolished prey. N represents the number of recorded prey attacks for each species in any season. The percentage values represent the percentage of prey attacks accompanied by demolishing of prey.

Season	Scarlet Robin N	Scarlet Robin %	Flame Robin N	Flame Robin %
Autumn	2 246	2.1	1 774	1.8
Winter	2 213	2.3	6 389	0.2
Spring	1 812	0.3	3 139	0.5
Summer	838	0.5	1 372	0.4
χ^2	36.5, $P < 0.001$		74.0, $P < 0.001$	

DISCUSSION

Scarlet Robin dispersal

Seasonal patterns of settlement by some Scarlet Robins at Nimmitabel resembled the dispersal patterns of migrants. Grassland birds arrived in late summer and autumn, stayed for the non-breeding season, and disappeared at the end of winter. However, no grassland robins returned to their wintering grounds the following year, in one case, at least, because the male had established a territory in breeding habitat. Nor was there an influx of Scarlet Robins into the study area in spring to indicate a return movement by migrating birds to their breeding grounds. Furthermore, first-year Scarlet Robins which settled in forest habitat did not disappear at the end of winter but retained their territories for the breeding season and subsequent winter.

These differences between the dispersal patterns of individual Scarlet Robins suggest that the autumn and winter influx of Scarlet Robins represented dispersal by subordinate, mostly first-year robins into secondary habitats, rather than migration. Moreover, the dispersal patterns of individual birds seemed to be correlated, at least partly, with their social status and body size. Adult males occupied most of the territories in breeding habitat and remained at Nimmitabel throughout the year. Birds that occupied territories in breeding habitat did not disperse, remaining at Nimmitabel throughout the year. Scarlet Robins unable to establish territories in the forest habitat established non-breeding-season territories in grassland habitat. Scarlet Robins that did not establish territories in grassland habitat disappeared from the study area. Grassland robins and robins that disappeared without establishing territories were nearly all first-year birds. Heavy first-year males were more likely than light birds to establish territories in breeding habitat. The lightest birds tended to disappear from Nimmitabel without establishing long-term territories there.

Therefore, competition for breeding season resources appeared to be critical in determining individual Scarlet Robins' dispersal patterns during the non-breeding season. Competition for territories in breeding habitat indeed may have been so severe that territory-holders remained at

Nimmitabel throughout the year rather than risk the loss of their territories and the chance to breed (cf. Haartman 1968; Fretwell 1980).

Dispersal of subordinate birds into secondary habitats may explain the winter influx of Scarlet Robins recorded from various localities in eastern Australia (Cohn 1926; Leach 1928; Lamm and Calaby 1950; Watson 1955; Rowley 1961). Other records of wintering robins may represent local movement by resident birds into grassland habitats adjoining their breeding territories, rather than migration (Fig. 3). Still other records of movements by Scarlet Robins suggest that some Scarlet Robins migrate. Scarlet Robins were recorded as passage visitors at Thredbo, New South Wales, in autumn and spring (Gall and Longmore 1978), implying that birds were migrating between breeding and wintering grounds. Further banding studies are required to examine the fidelity of Scarlet Robins to sites where they occur only in winter.

Why do Flame Robins migrate?

Discussion about why Flame Robins migrate is necessarily speculative, as no population has yet been located at both its breeding and wintering grounds, a problem confounding most studies of migrants (Ketterson and Nolan 1983; Pienkowski and Evans 1985; Bell 1986). The discussion is also speculative because the hypotheses outlined in the introduction are not mutually exclusive. Individuals may migrate from their breeding grounds because of lack of food, smaller body size, subordinate status, less intense competition for breeding resources, or all of these factors (Myers 1981; Ketterson and Nolan 1983; Pienkowski and Evans 1985). An understanding of the ultimate and proximate causes affecting migration by Flame Robins and other Australian migrants requires much more information than now exists (Bell 1986). It nevertheless seems worthwhile to consider Flame Robins' dispersal patterns within the framework of existing migration hypotheses, if only to generate testable hypotheses for further research.

The critical assumption of the body-size hypothesis is that larger-bodied individuals can better withstand extended periods of fast than smaller-bodied individuals, because of their larger reserves of fat (Calder 1974; Myers 1981; Ketterson and Nolan 1983). Accordingly, it is the smaller-bodied individuals, because of their larger reserves of fat (Calder 1974; Myers 1981; Ketterson and Nolan 1983). Accordingly, it is the smaller-bodied Scarlet Robin which should have migrated from Nimmitabel if body size was an important selective force on robins' migratory behaviour. Scarlet Robins instead remained at Nimmitabel throughout the year while the larger Flame Robins migrated. It is unlikely, however, that physiological constraints on body size were important selective pressures on either species' dispersal patterns, since conditions were not severe enough to cause prolonged periods of fast. Food was available throughout the year, albeit at lower densities in the non-breeding season (data from Recher *et al.* 1983), and snow cover rarely lasted for more than a few days. The body size hypothesis therefore may be rejected, although body size may be implicated as a cause of migration because of its correlation with social status (Gauthreaux 1982; Ketterson and Nolan 1983).

Differences between the diets of Flame Robins and Scarlet Robins and the comparative abundance of arthropods taken by them instead represent the most likely causes of migration by Flame Robins. Flame Robins at Nimmitabel foraged for flying insects twice as often as did Scarlet Robins. Scarlet Robins took more arthropods from the ground and bark substrates. Comparable differences between the feeding behaviour of the two species have been reported from elsewhere (Fleming 1980; Recher and Holmes 1985), although the differences were smaller than recorded from Nimmitabel.

While the biomass and abundance of all arthropods tend to decrease in winter, ground-dwelling arthropods remain relatively more common in winter than arthopods on other substrates, and especially more common than flying insects (Recher *et al.* 1983). Flying insects show major seasonal variation in their abundance and biomass. They are usually adults which emerge after ambient temperatures rise above a critical threshold (Hughes 1975) and the spring flush of new plant growth (Nix 1976). They disappear or die as temperatures decrease again, leaving their larvae to develop slowly during the cooler months (Hughes 1975). Flying insects are consequently a very seasonal food resource, their numbers and biomass lowest in June, July and August and highest in summer (Huddy 1979; Recher *et al.* 1983; Bell 1985; Cameron 1985).

Numbers and biomass of ground-dwelling invertebrates also are highest in summer. However, their winter biomass in south-eastern Australia remains many times greater than the winter biomass of flying insects. Recher *et al.* (1983) found that numbers of flying insects in south-eastern New South Wales ranged from between 70–160 insects/sticky trap in summer to 0–40 insects/sticky trap in winter. Their biomass decreased from an average of 0.7 g/trap in January to 0.1 g/trap in June and July. The biomass of ground-dwelling invertebrates decreased from an average of 70 g/trap in January to 5–25 g/trap in June and July. Whereas the average size of flying insects decreases in winter (Huddy 1979; Pyke 1983; Cameron 1985), the average size of ground-dwelling invertebrates may even increase in winter, because of the emergence of insect larvae, earthworms and millipedes (Ashton 1975; Huddy 1979).

Scarlet Robins thus exploited a food resource that was relatively more common in winter than other foods (Ford 1989) by pouncing for comparatively large, ground-dwelling prey. They compensate for the winter decrease in prey abundance by foraging over larger areas, foraging more often in grassland habitat (Table 2) and increasing the time per day that they foraged (Table 3).

Flame Robins also pounced for ground-dwelling prey throughout the year (Table 4), but foraged significantly more often for flying insects than did Scarlet Robins. When numbers of flying insects decreased at their breeding grounds, following a sharp decrease in overnight temperatures in April and May, the Flame Robins migrated. In winter, they became specialist ground-feeders in grassland environments on tiny, ground-dwelling prey.

Morphological differences between Scarlet and Flame Robins suggested that differences between the two species' diets and foraging behaviour were not merely artifacts of the sampling period or site, but long-term adaptations by each species to different environments and different prey types. Thus, Flame Robins had significantly longer tarsi than Scarlet Robins, presumably an adaptation to their ground-feeding behaviour in winter, as ground-feeders tend to have longer tarsi than congeners which feed from other substrates (Fretwell 1969; Gaston 1974). Flame Robins also had longer bills than Scarlet Robins and may have been able to capture more mobile prey, since the bill tips of longer-billed birds close faster than those of shorter-billed birds (Ashmole 1968). However, Flame Robins' comparatively longer, more slender bills may have restricted the size of the prey they could effectively capture and demolish, since the force exerted by beaks near their tip is inversely related to length (Ashmole 1968; Lederer 1975), and increases with increasing width (Lederer 1975). Hence, Flame Robins may have been less able than Scarlet Robins to exert sufficient force at their bill tips to capture large prey. The comparatively shorter, broader bill of the Scarlet Robin may have assisted it to capture larger prey items than those taken by Flame Robins.

Observations at Nimmitabel were consistent with Cox's (1968) hypothesis that intraspecific and interspecific competition for resources in winter may cause the elimination of competitively inferior species from their breeding range during the non-breeding season. As shown in Figure 2, the frequency of aggressive disputes between robins increased in autumn, as mostly young individuals of each species moved through the study area. This influx of birds may have caused increasing competition for food, especially among Flame Robins, since their numbers were considerably higher than those of Scarlet Robins. Such competition is predicted to be severest in late autumn and winter as numbers of aerial insects decrease. Interspecific competition by Scarlet Robins for ground-dwelling invertebrates may then further induce Flame Robins to migrate. However, this hypothesis needs more information to test whether or not Flame Robins do disperse from their breeding range in response to increasing competition for food from conspecific and congeneric individuals, and whether Scarlet and Flame Robins feed on different prey types. Further studies of Flame Robin migration also need to consider intraspecific variation between individuals' dispersal patterns, for instance: do birds of different age-classes and sexes from the one breeding population migrate to the same wintering ground, or do some birds migrate further; why do adult males depart earlier from and return earlier to their breeding grounds than females or first-year males; why do some Flame Robins migrate further than others, for example across Bass Strait, while others remain near their breeding grounds?

Studies of bird communities overseas suggest that migratory species tend to feed on seasonally limited, patchy food resources, whereas residents feed on more stable resources (Herrera 1978; Fretwell 1980; Lack 1986). Several studies have also shown that aerial feeders are near-obligate migrants while ground-pouncers are usually sedentary (Herrera 1978; Lack 1986). This separation between ground-feeding residents and aerial-feeding migrants appears to be true of insectivorous birds in eastern Australia. Loyn (1985a) commented that the only birds remaining in Mountain Ash *E. regnans* forest during winter were litter-feeders, birds feeding on bark substrates and some honeyeaters; aerial feeders and foliage-feeders departed. Huddy (1979) and Cameron (1985) found that flycatchers with more specialized feeding strategies, notably hawking and foliage-snatching species, migrated from their study areas, while the more generalized, ground-feeding species remained.

A similar distinction was apparent between the dispersal patterns of Flame Robins and Scarlet Robins at Nimmitabel. The more aerial-feeding Flame Robin migrated from the study area for at least three months during the non-breeding season, most likely to grasslands at lower altitudes. The ground-pouncing Scarlet Robin remained at Nimmitabel throughout the year. The Flame Robin therefore may be considered an opportunistic species which moves between wintering and breeding grounds to exploit seasonally abundant food resources at the two sites. Morphological adaptations to the winter environment suggest that selection pressures during the non-breeding season have influenced the Flame Robin's evolution (see Fretwell 1969), and further imply that migration by Flame Robins may be an ancestral trait of this species.

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BOOK REVIEWS

New Zealand's Extinct Birds.
Brian Gill and Paul Martinson, 1991. Random Century New Zealand Ltd. Auckland. 210 × 280 mm, hardback. 109 pages. NZ$49.95.

A large format book which is easy to read with 25 attractive colour plates from paintings by Paul Martinson, and well produced.

There are 57 known extinct New Zealand birds. Some were extinct before the arrival of humans and undoubtedly more fossil remains will be found. A unique terrestrial fauna evolved in the absence of competition for food and predation by mammals. A feature was the many species of flightless birds which included the now extinct moas, species of which are the largest known flightless birds, and their extinct avian predator, the New Zealand Eagle which is the largest known eagle.

Polynesians and native rats arrived 1 000 years ago, forest clearance began and a third had been removed by the time European settlement began in 1840. Polynesians ate the fauna, as did the native rats, and killed birds for their plumage.

Thirty-two species were extinct before Europeans arrived and deforestation was accelerated together with changing the habitat by agricultural practices. Also, other rats, mice, cats, ferrets, stoats and weasles were introduced, and a further nine species and several subspecies have since become extinct. Aspects of the biology of some of the extinct species, such as moas, can be described because preserved stomach contents have been found.

The book is interesting and an excellent background reading for the exciting work of a new generation of New Zealand ornithologists bent on saving further species from extinction.

M. D. Murray

Acta XX Congressus Internationalis Ornithologica.
New Zealand Ornithological Trust Board, Wellington. 160 × 240 mm, soft back, vols I–IV, 2 568 pages. U.S.$300, NZ$500.

These volumes record the activities of the 20th Congress held in Christchurch, New Zealand in December 1991.

Papers are given in full, and include seven plenary lectures, listed below, and several from 48 symposia. Clearly this massive contribution to ornithological knowledge cannot be reviewed in detail in a small space. Pleasing is the scattering of contributions from the host country, New Zealand, and impressive are the recent studies. These demonstrate that mammalian predators can be eliminated from small islands and thus enable the establishment of focal populations of endangered species, that forest browsers such as possums can be eradicated from islands with consequent rapidly apparent benefits, and that biological manipulations can do much to save species from immediate extinction.

The plenary lectures were: *Phylogeny and classification of birds from DNA comparisons*, C. G. Sibley; *An ornithological glimpse into New Zealand's pre-human past*, I. A. E. Atkinson and P. R. Millener; *Recent avifaunal changes and the history of ornithology in New Zealand*, B. D. Bell; *Communal breeding along the changing face of theory*, J. L. Craig; *Applied ornithology: putting theory and practice together*, E. H. Butcher; *Respiration of avian embryos at high altitude*, C. Carey; *Ecological and physiological constraints on reproduction in albatrosses*, J. P. Croxall.

M. D. Murray