Breeding biology of the red-capped robin

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Abstract

The breeding biology of the red-capped robin (*Petroica goodenovii*) (Petroicidae) was studied over two breeding seasons (2000–02) in Terrick Terrick National Park, Victoria. Breeding commenced in August and the last offspring fledged in January. Only females developed brood patches, built nests and incubated. However, both sexes fed the young. Clutch size ranged from one to three eggs, with a mean of 2.1, with clutches of three occurring relatively early in the season. For clutches of two, the period from laying of the first egg to hatching was 14 or 15 days, with a mean of 14.2. The time from hatching to fledging was 13–15 days, with a mean of 14. In all, 34% of nesting attempts successfully fledged offspring. On average, 0.62 fledglings were produced per nesting attempt, whilst 0.57 offspring reached independence. Nesting success peaked in October. Predation appears to be responsible for almost all nest failure, and predation rate varied over the season. Breeding pairs produced 0–3 broods per season (0–5 independent fledglings) and pairs that began nesting early in the season produced a greater number of independent offspring. Nestling weight was affected by both laying date and brood size. A comparative analysis within the Petroicidae, controlled for body size, revealed that species endemic to Australia have shorter incubation periods, and species from semi-arid and dry woodlands have longer incubation periods than other species. Findings from this study are discussed in relation to the breeding ecology of other members of the Petroicidae.

Introduction

Studies of the breeding ecology and behaviour of birds provide essential information to both evolutionary biologists and conservation managers. For the evolutionary biologist, the breeding characteristics of a species provide insights into the selection pressures that individuals of that species have faced over time. Additionally, as more data become available on the breeding ecology of previously unstudied species, it is possible to conduct more rigorous comparative tests to determine what factors are responsible for the differences in breeding parameters between species. For the conservation manager, realistic and effective modelling of risk management for a population requires that these breeding characteristics be accurately quantified.

Most research on the life-history of passerines has been conducted in the Northern Hemisphere, on species belonging to the Passerida (Rowley and Russell 1991). Less research has focussed on the Corvida, an ancient clade of passerines that evolved and radiated within Australasia (Sibley and Ahlquist 1990). In contrast to many birds of temperate regions in the Northern Hemisphere, Australian passerines (at least the sedentary and colonial species) are generally characterised by small clutches, long breeding seasons, multiple broods and extended parental care (Woinarski 1985; Rowley and Russell 1991; Russell 2000). It has been argued that these breeding characteristics are adaptations to aseasonal climatic conditions and year-round availability of food (Woinarski 1985; Rowley and Russell 1991), high rates of nest predation (Robinson 1990; Martin 1993), or reduced adult mortality (Martin *et al.* 2000). However, to make robust comparative tests of these hypotheses, further information is required on more Australian passerine species.

Recent studies have documented the detailed breeding biology of a growing number of Australo-Papuan robins (family Petroicidae). Of the 44 species in the family, 13 are

Australian endemics, 19 are confined to New Guinea, 7 occur in both Australia and New Guinea and a further 3 in New Zealand or its surrounding islands. Research has focused exclusively on species found within Australia and New Zealand. Of the six Australian species studied, nesting success has been reported to vary greatly. For instance, a study of the scarlet robin (*Petroica multicolor*) found that only 8% of eggs laid produced fledglings (Robinson 1990), whereas in a study of the grey-headed robin (*Heteromyias albispecularis*) 39% of eggs produced fledglings (Frith and Frith 2000). However, interpretation of variation in nesting success between species is difficult since substantial spatial variation can occur between different populations of the same species (Powlesland *et al.* 2000; Armstrong *et al.* 2000), as well as temporal variation within populations (Flack 1976; Powlesland 1983). There is little data allowing a comparison of variation in nesting success within species in Australian robins, although nesting success in the eastern yellow robin varies among populations (Marchant 1985; Zanette and Jenkins 2000). Intraspecific variation in nesting success also occurs in North Island robin (*Petroica australis longipes*) (Armstrong *et al.* 2000; Powlesland *et al.* 2000) and North Island tomtit (*Petroica macrocephala toitoi*) (Knegtmans and Powlesland 1999) populations in New Zealand exposed to differing levels of predation, and temporal variation has been observed in the South Island robin (*Petroica australis australis*) (Flack 1976; Powlesland 1983). In addition to being affected by differences in predation rates, nesting success may also vary according to differences in microclimate and parasite densities (Eeva *et al.* 1994).

The red-capped robin (*Petroica goodenovii*, Petroicidae) is one of five Australian 'red robins' (genus *Petroica*). Of these, the breeding biology of the scarlet and flame robin has been the focus of intensive research (Robinson 1990). There has also been a previous study on the breeding behaviour of the red-capped robin in the Southern Tablelands of New South Wales (Coventry 1988). Although informative, the breeding parameters described in that study may not be typical of red-capped robins for two reasons; firstly, the species does not normally occur in the area where the research was conducted and, secondly, the study involved observations from only three pairs (Coventry 1988). Here, I describe the breeding biology of a sedentary population of red-capped robins in Terrick Terrick National Park in the northern plains of Victoria. Furthermore, I conduct a comparative analysis of three life-history traits within the Petroicidae and compare the breeding characteristics of the red-capped robin with other species of this family.

Methods

Study area and species

The study was conducted at Terrick Terrick National Park (36°10′S, 144°13′E), located 45 km west of Echuca, Victoria. The woodland section of the park is approximately 2500 ha and consists of dry open woodland dominated by white cypress-pine (*Callitris glaucophylla*), and grey box (*Eucalyptus microcarpa*). Annual rainfall in the area is approximately 400 mm (LCC 1983). Areas of the park that are dominated by white cypress-pine woodlands appear to be saturated with red-capped robin breeding territories (Dowling *et al.* 2003*a*).

The red-capped robin is a territorial, socially monogamous passerine. It is sexually dichromatic, with yearling (in their first year) males moulting into adult plumage at the end of their first year. Yearling males also establish territories and yearlings of both sexes can breed successfully (Dowling *et al.* 2003*a*).

Bird capture, measurement and observations

I monitored the nesting success and breeding behaviour of 50 breeding pairs of robins during the 2000–01 breeding season and 60 pairs during the 2001–02 season. Birds (*n* = 158) were caught in mist-nets and banded with a numbered metal band provided by the Australian Bird and Bat Banding Scheme and a unique combination of colour rings to permit individual identification. The length of the right tarsus, the right wing

(maximum chord: flattened, straightened wing) and the distance from the back of the head to the tip of the bill (head–bill length) was measured with callipers to 0.01 mm. The weight of each bird was measured to 0.1 g.

The breeding activity of birds in each territory was determined by following territorial females continuously for 20 min. This observation period was long enough to determine whether birds had begun nesting. Each territory was checked at least every three days to determine locations of colour-banded individuals, presence of nesting activity and stage of nesting. Once found, nests were checked every three days to determine their fate. The length, width (to 0.01 mm) and weight (to 0.1 g) of a small sample of eggs ($n = 14$) were measured, usually within the first three days of laying, and the remainder of eggs left undisturbed. A small number of nests ($n = 8$ in 2000–01, $n = 9$ in 2001–02) were inaccessible due to their position in the tree. At all other nests, each nestling was weighed once, to 0.1 g. Age was recorded, or calculated if unknown by comparing body traits such as body size, size of tarsi, presence of wing feather shafts, degree of body down and whether the eyes had opened with the data for the same traits in nestlings of known hatching date. Nestlings ($n = 240$) were banded with a metal band and a unique combination of three colour-bands, usually when they were ~6–8 days old.

The sex of each member of a breeding pair was determined by examining reliable plumage and behavioural differences between the birds. Adult males are black and white with red forehead and breast patches, whereas females are buff-grey. The sexes also differ behaviourally. Only females build nests, incubate eggs and brood offspring (DKD, unpublished data). When breeding pairs contained yearling males (in female-like plumage), the sex of each bird was later confirmed using a molecular technique described in Griffiths *et al.* (1998).

Every time a territory was visited, the location of each bird within the territory was recorded. Throughout the breeding season, the boundaries of each territory were mapped. Territory boundaries were defined for each breeding pair in each breeding season, using movements of birds within territories, and locations and results of territory disputes between territory neighbours. A simple index of territory size was calculated by multiplying the length of a territory at its longest margin by the width at its perpendicular margin.

Comparative analysis within the Petroicidae

I compiled breeding data for the Petroicidae, from the primary literature cited in Table 5, and texts on Australian (Boles 1988), New Guinean (Rand and Gilliard 1967; Peckover and Filewood 1976; Coates 1990) and New Zealand (Falla *et al.* 1981; Moon 1992; Heather and Robertson 1996) birds. Few data are available on the breeding biology of species endemic to New Guinea. Data presented for species common to both Australia and New Guinea are collected from Australian populations. I compiled data on body size, clutch size, egg volume (egg volume index = $\pi/6 \times$ length $\times$ width^2: Hoyt 1979) and length of incubation. The North Island (*P. australis longipes*) and South Island (*P. australis australis*) robin subspecies, and the North Island (*P. macrocephala toitoi*) and South Island (*P. macrocephala macrocephala*) tomtit subspecies, were treated as separate species for the statistical analysis because detailed breeding biology data were available for both, and they differ in clutch size, egg volume and duration of incubation. I tested two hypotheses: (1) species from different geographic regions have different breeding parameter values, and (2) species from different habitat types have different values. To test these hypotheses, I calculated the residuals from three separate linear regressions of clutch size, egg volume and incubation length on body size. The residuals of these regressions indicate measures of relative clutch size, relative egg volume and relative incubation length, controlled for size differences between species. To control for size differences, I used body size (mm) rather than mass (g) because more data were available for size and there is a strong linear relationship between the two measures ($r^2 = 0.900$, $n = 20$, $P < 0.001$). Data were available for 24 species in the analysis of clutch sizes and egg volumes, but for only 17 species in the analysis of incubation.

Multiple regression was used to test the relationship between the above three dependent variables versus geographical region and habitat preference. Geographical range was divided into three broad categories: (1) Australian endemics, (2) species found both in Australia and New Guinea, and (3) New Zealand and surrounding island endemics. Habitat was divided into four categories: (1) semi arid and dry open woodland, (2) *Eucalyptus* spp. forest, woodland, (3) wet sclerophyll forest and coastal forest, and (4) rainforest.

I did not control for phylogeny in these analyses because these data are lacking within the Petroicidae.

Analysis of nesting success

I defined a nesting attempt as any nest that was built regardless of whether eggs were eventually laid in it.

I calculated total nesting success in two ways. First, I included all nests that were found regardless of whether they were found during nest-building or incubation ($n = 277$). This estimate of nesting success may be biased if some nests failed during nest-building before I located them. Second, to account for this potential bias, I re-estimated population nesting success using only nests that were located prior to egg laying ($n = 174$). All other calculations of nesting success (e.g. mean nesting success of breeding pairs) are estimated from the total sample of nests ($n = 277$).

Although I calculated the percentage of nest failures that occurred during pre-laying, incubation, and nestling provisioning, it is probable that some nests classified as pre-laying had commenced incubation at the time of failure (and, to a lesser degree, some nests classified as containing eggs, may have contained nestlings) considering that nests were usually checked only once every three days.

Statistical analyses

Parametric tests were used to analyse the data after dependent variables were checked for normality. All tests are two-tailed, with a significance criterion of $P < 0.05$. When testing the date of first nesting for breeding females versus number of fledglings produced per season, I used data from only one randomly chosen breeding season for females that were present in both seasons, to ensure statistical independence.

I tested whether nestling weight was related to date or brood size. These data are presented in two ways. First, nestling weights and ages are averaged for each nest to control for within-brood effects. Mean nestling weight per nest was controlled for mean age at weighing by taking the residuals from the logarithmic regression of weight on age (relative nestling weight). Also, to control for perceived pseudoreplication caused by multiple nesting attempts by the same female being included in the analysis, I reanalysed these data, taking only one randomly selected nesting attempt for each female. I emphasise the first analysis, in which the individual nest is the unit of statistical analysis because I was interested in testing the effects of relative nestling weight on date, and this factor is specific to individual nesting attempts, not individual females.

In other tests in which an overall measure for the population was important, I included more than one nest per female per season.

Results

Territory sizes

Territory sizes ranged from 0.4 to 3 ha, with a mean of 1.22 ha (s.e = 0.08, $n = 49$) in 2000–01 and 1.19 ha (s.e. = 0.07, $n = 58$) in 2001–02.

Morphometric differences between sexes

There was a tendency for males to have longer tarsi than females ($F_{1,155} = 2.95$, $P = 0.09$) (Table 1), but there was no effect of age or interaction between sex and age (yearling or adult) on tarsus length. When age was removed from the model, males had significantly longer tarsi than females ($t = –2.09$, $n = 159$, $P = 0.04$). Males had longer wings than females ($F_{1,155} = 25.19$, $P < 0.001$) and adults (individuals older than 1 year) had longer wings than yearlings ($F_{1,155} = 31.14$, $P < 0.001$, sex*age interaction: n.s.). Males also had longer head–bill lengths than females ($F_{1,155} = 5.42$, $P = 0.02$), but there was no effect of age or interaction between sex and age on head–bill length (Table 1). Females that had commenced nesting activities possessed brood patches whereas males did not.

Table 1.   Mean sizes (±1 standard error) of body traits that differ between sexes or age classes
Measurements are in millimetres. Adults are individuals older than 1 year, yearlings are individuals younger than 1 year. Asterisks indicate probabilities: *, $P < 0.05$; ***, $P < 0.001$

	Right tarsus	Right wing length	Head–bill length
Females ($n = 71$)	17.18 ± 0.07	62.23 ± 0.20	27.94 ± 0.07
Males ($n = 104$)	17.36 ± 0.05*	63.84 ± 0.17***	28.19 ± 0.05*
Adults ($n = 137$)		63.55 ± 0.16***	
Yearlings ($n = 39$)		61.89 ± 0.23	

The body mass of individuals did not change throughout the season ($r^2 = 0.01$, $n = 159$, $P = 0.37$), but did vary with time of day ($r^2 = 0.09$, $n = 159$, $P < 0.01$), increasing slightly throughout the day. Combining sex and age classes, mean body mass was 8.85 g after removing outliers ($n = 155$, s.e. = 0.04). After controlling for time of day, females tended to be heavier than males and adults heavier than yearlings (sex: $F_{1,150} = 2.87$, $P = 0.09$; age: $F_{1,150} = 3.08$, $P = 0.08$; time: $F_{1,150} = 17.28$, $P < 0.01$), with no interaction between sex and age.

Breeding season

Red-capped robins bred for five months each year (Table 2). First eggs of each season were laid on 11 August 2000 and 21 August 2001 and the last nestlings fledged on 18 January 2001 and 8 January 2002 respectively. Birds were multibrooded, with new nests initiated from August to December.

Nest sites

All nests were built in forks of white cypress-pine ($n = 277$). The average diameter of the nest cup was 42.4 mm (s.e. = 0.52 mm, $n = 7$). Average height above the ground of nests was 6 m (s.e. = 0.13 m, $n = 277$, range = 1.5–15.5 m). In all, 91% of nests were built in forks, with either two or three supporting branches (mean number of branches = 2.67, s.e = 0.04, $n = 267$). Nests were often built on the main trunk (29%), and only rarely (4%) further than 2 m from the trunk (mean distance from trunk = 0.82 m, s.e. = 0.05, $n = 266$). The largest supporting branch had a variable diameter, ranging from 1.6 cm to as large as 35 cm when the nest was on the main trunk (mean = 7.18 cm, s.e. = 0.36, $n = 241$). The average diameter of all supporting branches ranged from 1.0 cm to 16.5 cm (mean = 4.23 cm, s.e. = 0.19, $n = 231$). New nests were always built in a different tree to the previous nest.

Nesting cycle

Both members of a breeding pair participated in nest-site selection. As observed in aviary-housed red-capped robins (Hutton 1991), the male initiated a nesting attempt by perching and rubbing his body in a forked branch and performing a continuous and distinctive trill until the female flew to the fork and examined it. Males may perform this display at a number of sites, but females appear to make the ultimate nest-site decision because only female robins built nests and incubated eggs. Male robins fed females during nest-building and incubation of the eggs. The male robin with food sang a quiet, abbreviated song to which the incubating female responded by flying off the nest and perching next to the male, whereupon he passed the food to the female. Occasionally, the

Table 2. Numbers of new nests initiated in each month of the 2000–01 and 2001–02 breeding seasons

Month	Nests 2000–01	Nests 2001–02	Total nests
August	14	22	36
September	36	39	75
October	26	34	60
November	40	30	70
December	22	14	36
Total nests	138	139	277

female was fed on the nest. Once eggs hatched, only females brooded the nestlings, but both sexes fed nestlings. Males arriving near the nest sang the same distinctive and soft, abbreviated song and females flew off the nests so that the male could feed the nestlings. Later in the nesting cycle, females also sporadically produced this call when they had food for the fledglings. Occasionally, male robins passed food to brooding females on the nest, who then passed the food items on to the nestlings.

Average egg dimensions were 16.00 mm (s.e. = 0.15, $n = 14$) × 12.71 mm (s.e. = 0.08, $n = 14$) and mean egg weight was 1.26 g (s.e. = 0.03, $n = 13$). Average clutch size was 2.1 eggs ($n = 104$, s.e. = 0.04) and ranged from one to three eggs, with 85.6% of clutches composed of two eggs and 12.5% of three eggs. Clutch size varied with month ($F_{4,94} = 6.8$, $P < 0.001$) (Fig. 1). All clutches of three eggs were laid in September, with the exception of one clutch that was laid in October. There was no effect of season or interaction between season and month on clutch size.

Eggs were laid on consecutive days. For clutches of two, the interval between laying of the first egg and hatching was 14 or 15 days (mean = 14.2, s.e. = 0.13, $n = 9$). Hatching appears to be synchronous ($n = 5$). Nestlings fledged 13–15 days after hatching (mean = 14 days, s.e. = 0.11, $n = 20$) and nestling growth followed a characteristic logarithmic function, described by the function weight = $2.18(\text{age})^{0.61}$ ($n = 235$, $r^2 = 0.728$).

After fledging of the young, parents fed the offspring for at least three weeks. Each parent tended to feed one fledgling initially (for broods of two). However, females often began re-nesting 2–3 weeks after their offspring fledged, and males would then feed both fledglings. Parents usually stopped provisioning and began to chase begging fledglings ~3–4 weeks after fledging (although they appeared to be more tolerant of their juveniles remaining on their territories late in the breeding season when nesting activity had stopped).

Although two pairs managed to successfully raise three broods in a season, the most common number of broods produced per pair was one (Table 3).
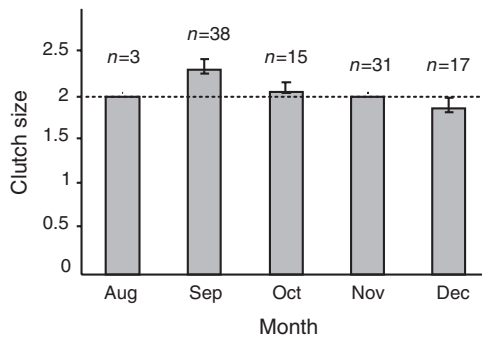

Fig. 1. Mean clutch size per month. Data are pooled from both breeding seasons. Bars indicate standard error, and sample size for each month is shown above each column. Horizontal dotted line indicates modal clutch size.

Table 3. Number of successful broods produced per pair in both the 2000–01 and 2001–02 breeding seasons

Broods produced	2000–01	2001–02	Combined seasons
0	19	15	34
1	20	35	55
2	12	5	17
3	2	0	2

Nesting success

In total, 34% of all nests found (n = 277) were successful (i.e. resulting in at least one fledgling reaching nutritional independence: 37.0% in 2000–01, 31.7% in 2001–02). Of the nests first located during nest-building (n = 174), 28% were successful (31.6% in 2000–01, 24.5% in 2001–02). Of eggs laid (n = 474), 33% resulted in independent fledglings (Table 4). On average, each pair made 2.56 nesting attempts per season (range = 1–7), of which 0.88 nests per pair (range = 0–3) were successful. On average, each pair produced 1.6 fledglings (range = 0–5) and 1.45 (range = 0–5) independent young per season (Table 4). In total, 0.62 fledglings were produced per nesting attempt (0.70 in 2000–01, 0.56 in 2001–02), and only 0.57 fledglings per attempt reached independence (0.60 in 2000–01, 0.54 in 2001–02).

Females that initiated their first nesting attempt earlier in the season produced more nests per season (r^2 = 0.29, n = 66, P < 0.001), as well as a greater number of nests that successfully fledged offspring (r^2 = 0.19, n = 67, P < 0.001), and produced a greater number of fledglings that reached independence (r^2 = 0.15, n = 67, P < 0.01) (Fig. 2).

The proportion of successful nests, producing at least one fledgling reaching independence, was lowest at the start of each season (August), peaked in October and declined again towards the end of the season (month: $F_{4,269}$ = 3.05, P < 0.05; season: n.s.; season*month: n.s.) (Fig. 3).

Predation accounted for most nest failures. In three nests the eggs were abandoned, in another two nests the eggs were unfertilised, and in two nests the nestlings were found dead in the nest. In all other cases, nest contents were missing and the nest was usually either damaged or totally destroyed, indicating predation as the likely cause of nest failure. The estimated predation rate across both seasons was 65% (Season 1: 61%; Season 2: 69%).

Table 4. Nesting success of red-capped robins within the study population

Total number of nests initiated, eggs, nestlings, fledglings and independent young produced within the study population over both breeding seasons (2000–01, 2001–02), and the mean per season for each pair are shown. Values in parentheses indicate standard errors of the mean

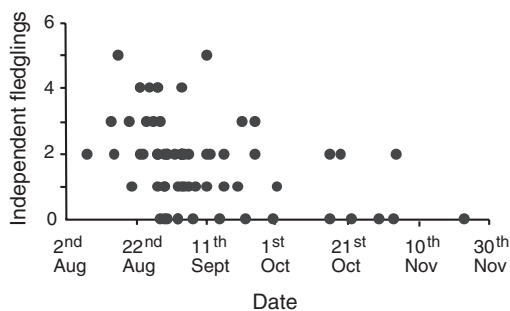|	Population total	Mean per pair (n = 108)
Nesting attempts	277	2.56 (0.14)
Eggs	474	4.39 (0.25)
Nestlings	296	2.74 (0.17)
Fledglings	173	1.60 (0.13)
Independent young	157	1.45 (0.12)

Fig. 2. The number of fledglings that were successfully raised to independence for each breeding female per year, and the date at which each female initiated her first nesting attempt of the season.
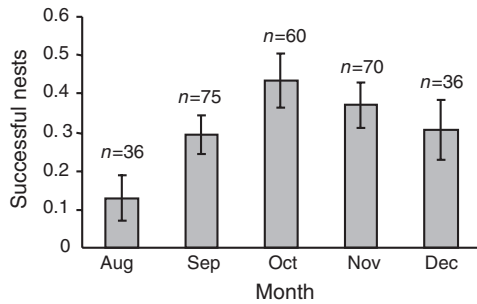
Fig. 3. Mean proportion of nests initiated in each month that subsequently fledged offspring that reached independence. Bars indicate standard error, and sample size for each month is shown above each column.
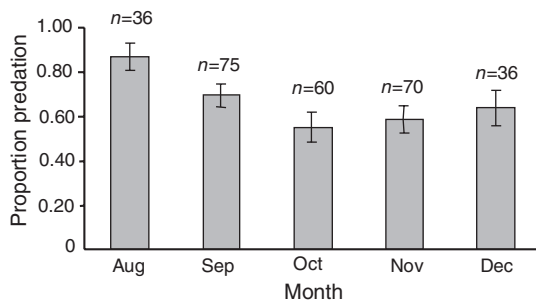

Fig. 4. The proportion of nesting attempts initiated each month that succumbed to predation. Bars indicate standard error, and sample size for each month is shown above each column.

Nest-predation rate varied according to month ($F_{4,269} = 3.483$, $P < 0.01$) (Fig. 4), but there was no effect of season or interaction between month and season.

Most nest failures occurred before hatching ($\chi^2 = 19$, d.f. = 2, $P < 0.01$), either before laying (22%) or during incubation (47.8%). Nests failed during provisioning of nestlings in 30.2% of cases.

Nestling weight

I calculated relative nestling weights by averaging weights and ages of nestlings from the same nest and then calculating the residuals of a logarithmic regression (function $y = 2.293x^{0.581}$, $r^2 = 0.734$, $n = 114$) of nestling weight (y) on age (x). Nestlings that are heavier than expected for their age have positive residuals while those that are lighter than expected have negative residuals. The relative weight of nestlings increased throughout the season ($r^2 = 0.115$, $n = 114$; date: $P < 0.001$) (Fig. 5), and was not related to time of day
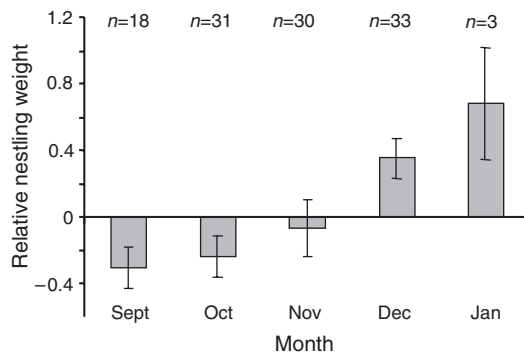

Fig. 5. Mean relative nestling weight (mean weight per nest) for each month. Relative nestling weights are the residuals of the logarithmic regression of mean nestling weight per nest versus mean nestling age. Bars indicate standard error, and sample size for each month is shown above each column.
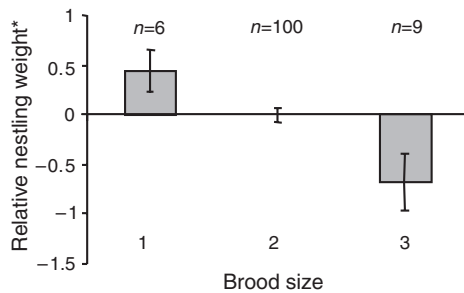
Fig. 6. Mean relative nestling weight (mean weight per nest) for differing brood sizes. *In this figure, relative nestling weight is further controlled for date of weighing by taking the residuals of the linear regression of relative nestling weight versus date ($r^2 = 0.125$, $n = 115$, $P < 0.001$). Bars indicate standard error, and sample size for each month is shown above each column.

($P = 0.944$). Controlling for date, relative brood weight decreased with brood size (ANCOVA: brood size: $F_{2,111} = 5.273$, $P < 0.01$; date: $F_{1,111} = 11.296$, $P < 0.01$) (Fig. 6). If perceived pseudoreplication, caused by multiple nesting attempts by the same female being included in the analysis, is removed by taking only one randomly selected nesting attempt for each female, the direction of these trends remain (function: $y = 2.280x^{0.576}$, $r^2 = 0.729$, $n = 74$; relative nestling weight v. date and time: $r^2 = 0.044$, $n = 74$; date $P < 0.05$, time $P = 0.769$; nestling weight v. brood size controlled for date: brood size $F_{2,70} = 2.218$, $P = 0.117$; date $F_{1,70} = 3.245$, $P = 0.076$).

Courtship behaviour

Hutton (1991) described characteristic circular flights that males kept in aviaries made around a perched female during courtship. I observed the same behaviour in the wild population I studied.

Pair fidelity, dispersal and survival

Pair-bonds were not always maintained within and between breeding seasons. At least nine new breeding pairs were formed during the 2000–01 breeding season and four new pairs during the 2001–02 season containing birds that had been paired with other individuals earlier in the season. Most commonly, females abandoned a territory and paired with a nearby male ($n = 6$). On two occasions males switched territories, pairing with a new female. There were four cases of sequential polyandry, where females abandoned their male partners while fledglings were still being provisioned and paired with a new male, leaving their previous partner to rear the fledglings. I was unable to determine exactly how quickly the females swapped territories/males after fledging their initial young. In one instance, I observed a female with her new partner ~14 days after fledging offspring in her initial territory, and the other females were observed with their new partners 18–24 days after fledging offspring in their previous territories.

At the beginning of the 2001–02 breeding season, 30 of 48 (62.5%) banded males that had held territories during the previous season remained within the study area compared with 13 of 42 (31%) females. Only six breeding pairs (of 42 identifiable pairs) from the 2000–2001 season remained together in the study area during the subsequent 2001–02 season. Retention rates for birds of each sex within the study area at the start of 2002–03 season were similar to each other: males 27 of 60 (45%), females 18 of 43 (41.9%). Five breeding pairs (of 43) from the 2001–02 season remained together during the 2002–03 season. Ten males and three females that were present as adults (at least one year old) in October 2000 were still in the study area in October 2002, indicating that longevity can be at least three years.

Territorial behaviour

One adult male was actively forced off his territory permanently by an intruding adult male during September 2000. The territory dispute resulted in both males fighting, grappling with each other on the ground. The intruding male won the territory. In most cases, I was unable to conclude whether birds that disappeared from the study site had died or dispersed. However, it is likely that birds that disappear occasionally disperse elsewhere because I found that three adult females that had been present at the site in 2000–01 returned briefly to occupy territory vacancies in 2001–02 before disappearing again. Additionally, an adult female that was paired with a yearling male in 2000 dispersed and paired with an adult male three territories away from its own when the female that was paired with that male died. Since the female had to move over two territories to reach her new male, this suggests that females probably leave their territories to actively search for other 'better' vacancies.

Male robins displayed distinctive escalation behaviour during territorial disputes. Males seeking to establish territory boundaries, create a new territory or seek a female partner would incessantly sing a distinctive, 'insect-like' territory song. Sometimes a disputed boundary resulted in two males perching close together on a horizontal branch. Constantly staring at each other, they performed a 'stand off' on the perch, with one male advancing a short distance (up to 40 cm), while the other male retreated a similar distance. Both males moved back and forth on the perch for some time, before one flew off. The retreating bird performed a 'submission' flight, whereby he flew in a direct line to a nearby tree within his own, undisputed territory. This flight was characterised by fast movement of the wings but low speed, so it seemed the bird was almost hovering. Ultimately, an unresolved territorial dispute results in a chase and physical confrontation.

Nest defence

Both sexes display the same distraction display behaviour described in other petroicid robins (Marchant 1985; Sullivan 1993; Frith and Frith 2000; Fitri and Ford 2003) when their brood or young fledglings are threatened. Birds made distinctive alarm calls when the nest was approached, and often either parent flew towards the nest, spread its wings aloft and hopped around before fluttering to the ground below. On the ground, the bird continued to hold its wings up as it hopped about.

Horsfield's bronze cuckoos (*Chrysococcyx basalis*) were present at the study site during 15–28 August 2000 and 14–21 August 2001. Male robins reacted aggressively to the presence of these cuckoos by chasing them out of their territories on long, direct flights while making a distinctive shrill call, and mobbing and attacking persistent cuckoos. I found no parasitised robin nests.

Comparative analysis within the Petroicidae

Within the Petroicidae, clutch size was negatively related to body size ($r^2 = 0.206$, $n = 24$, $P < 0.05$) (Fig. 7*a*), egg volume was positively related to body size ($r^2 = 0.761$, $n = 24$, $P < 0.001$) (Fig. 7*b*) as was length of incubation ($r^2 = 0.334$, $n = 17$, $P < 0.05$) (Fig. 7*c*).

Controlling for body size, petroicid species endemic to Australia had shorter incubation periods than those found in other geographical regions. Species found in semi-arid and dry woodlands had longer incubation periods than those living in other habitats ($r^2 = 0.813$, $n = 17$; region $P < 0.001$, habitat $P < 0.01$) (Fig. 8). Neither relative clutch size nor relative egg volume were related to the geographical region or habitat preference of each species.
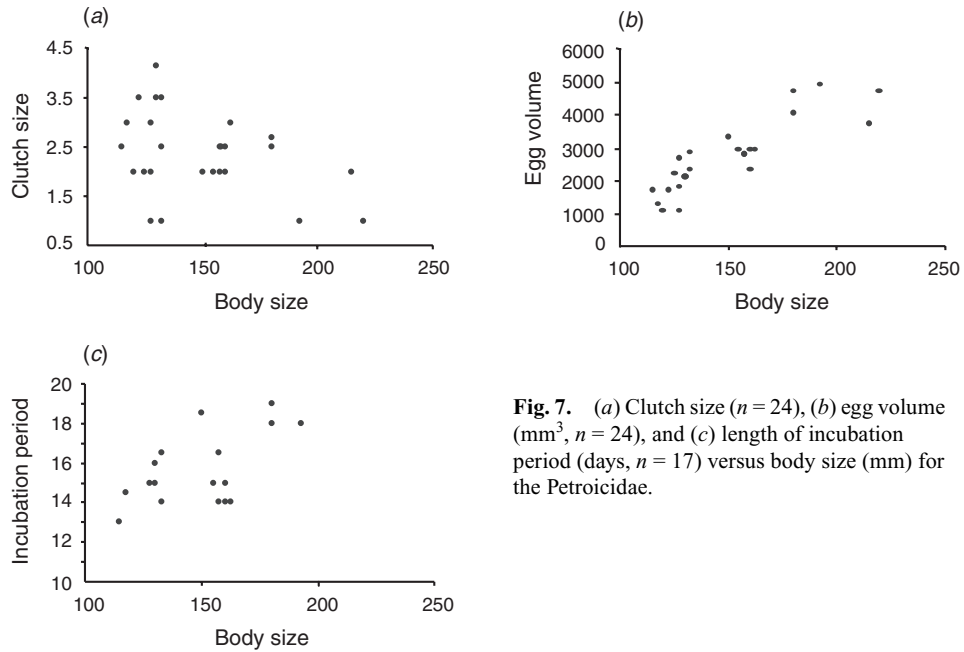
Fig. 7. (*a*) Clutch size (*n* = 24), (*b*) egg volume (mm^3, *n* = 24), and (*c*) length of incubation period (days, *n* = 17) versus body size (mm) for the Petroicidae.
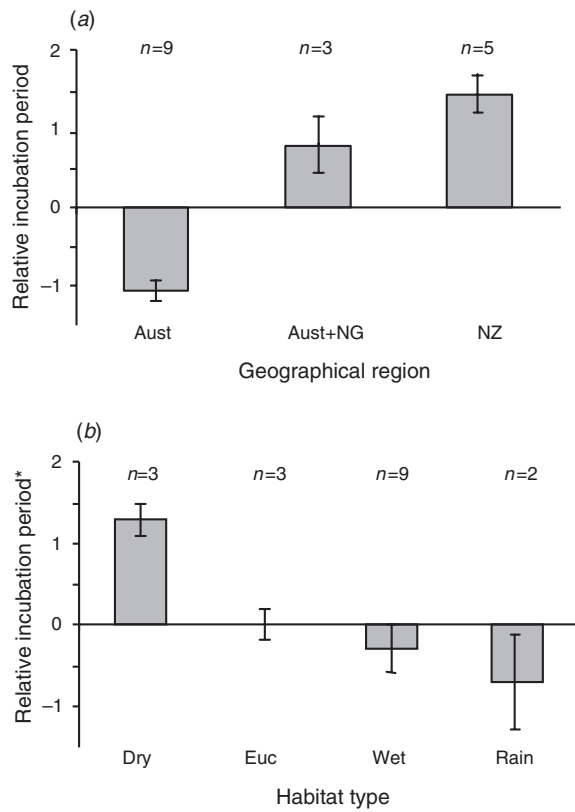

Fig. 8. (*a*) Relative incubation period (residuals of incubation period on body size) for three geographical regions: petroicid species endemic to Australia, those present in Australia and New Guinea, and species endemic to New Zealand and its surrounding islands. (*b*) Relative incubation period* (further controlled for geographical region) for four habitat types: Dry (semi-arid and dry woodland), Euc (*Eucalyptus* spp. forest and woodland), Wet (wet sclerophyll forest and coastal forest), and Rain (rainforest).

Discussion

The red-capped robin has breeding traits characteristic of many other Australian Corvida. These include small clutches, long breeding seasons, multiple broods, potentially high adult survival (Woinarski 1985; Rowley and Russell 1991) and extended parental care (Rowley and Russell 1991; Russell 2000) relative to members of the Passerida. This slow reproductive rate spread over a long breeding season and multiple breeding seasons is suggested to be an adaptation to a stable, favourable climate (Woinarski 1985; Rowley and Russell 1991) and a strategy in response to high predation rates (Robinson 1990; Martin 1993).

Life-history comparisons among the Petroicidae

Body size

Similar to allometric relationships reported by Yom-Tov (1987) and Trevelyan and Read (1989), body size was negatively related to clutch size and positively related to incubation length and egg volume in the Petroicidae.

Possible influence of nest predation and food abundance on incubation period

Predation is potentially an important selective pressure on growth rates in altricial birds. Species exposed to greater predation should have shorter incubation periods in the nest (Skutch 1976). Recently, growth rates of nestling birds have been shown to vary with nest predation pressure (Bosque and Bosque 1995; Martin 1995). Controlling for differences in body mass, Bosque and Bosque (1995) determined that open-nesting species native to islands that lack native mammalian and reptilian predators have longer incubation and nestling periods than related species from continental areas that contain predators.

Although sample sizes within each group were small, I found that petroicid species that are endemic to Australia have shorter incubation periods than those of other regions, and also that species found in semi-arid and dry woodlands have longer incubation periods than those living in other habitats. Nest predation rates appear to be high in both the Australian (Robinson 1990; Zanette and Jenkins 2000; this study) and New Zealand (King 1984; Powlesland *et al.* 2000) Petroicidae. However, high rates of nest predation in New Zealand are attributable to recently introduced mammals (King 1984; Powlesland *et al.* 2000), and are thus a recent selection pressure for New Zealand species. In contrast, Australian Petroicidae have evolved in the presence of many native nest predators (Trevelyan and Read 1989) and may have responded by evolving shorter incubation periods. Further research is required to test whether this trend occurs in other bird families that have species distributed in Australia and New Zealand. However, a previous analysis of reproductive strategies between terrestrial Australian and New Zealand birds found no differences in incubation period between the two geographical regions (Trevelyan and Read 1989).

It is difficult to explain why petroicid species from semi-arid and dry woodlands appear to have longer incubation periods than species from other habitats. No data are available on differences in predation pressures across habitat types. An alternative explanation is that differences in food abundance may be related to differences in incubation periods (Bosque and Bosque 1995) between geographical regions and habitat types. Woinarski (1985) hypothesised that the life-histories of Australian land and freshwater birds have evolved in response to a stable, year-round food supply and suggested that this factor is responsible for the differences in life-histories of Australian birds to those of the Northern Hemisphere. If food is more scarce in semi-arid and dry habitats, females may spend more time searching for food rather than incubating their clutch, and thus incubation periods may be longer.

Nesting success

Nesting success varies markedly among the Petroicidae (Table 5). However, it is difficult to compare differences in nesting success between species because there is often spatial (Armstrong *et al.* 2000; Powlesland *et al.* 2000) and temporal variation (Powlesland 1983; Flack 1976) within species. Within the Petroicidae, much of this variation may be explained by differing predator exposure (Table 5). Nest predation has a large impact on the nesting success of the North Island robin. When mammalian predators were controlled before the onset of the breeding season, nesting success was much higher than when there was no predator control (Powlesland *et al.* 2000). Nesting success was also relatively high in a separate population free from exotic mammalian predators (Armstrong *et al.* 2000). Predator control similarly increased nesting success of the North Island tomtit (Knegtmans and Powlesland 1999).

It is unknown how much variation in nesting success occurs within species in Australian Petroicidae because there have rarely been multiple studies on the same species within Australia. Nesting success of eastern yellow robins differed in two separate studies of different populations (Marchant 1985; Zanette and Jenkins 2000). A previous study of the breeding biology of the red-capped robin reported higher nesting success than did this study. However, a small sample size was used in that study (*n* = 3 pairs, 11 nests), and it was conducted in an area where the species does not normally occur (Coventry 1988).

The red-capped robin has a wide distribution, inland of the Great Dividing Range, in dry woodlands of Australia. Its range extends from central Victoria to central Queensland, and from the east to west coasts of Australia and Rottnest Island (Blakers *et al.* 1984). Predator diversity and abundance, and food abundance, probably differs across this distribution and, thus, it is probable that nesting success will also differ.

Weight of nestlings

Nestlings in December and January were relatively heavier than those produced in earlier months, and nestlings from larger broods were lighter. There are several possible explanations for this pattern between nestling weight and time of year. It is possibly related to food abundance over the season. Food resources fluctuate throughout the breeding season of Australian birds (Recher *et al.* 1983; Woinarski and Cullen 1984; Bell 1985), although these fluctuations are generally less pronounced than those experienced by Northern Hemisphere species where there is a shorter peak in food resources (Lack 1954; Woinarski 1985). Alternatively, parents may invest more resources in nestlings later in the season because it is their last opportunity to produce fledglings for the season. Furthermore, summer months may allow breeding females more time to forage and feed nestlings because nestlings may not need as much brooding during warmer temperatures and there are more daylight hours to forage during summer. Warmer temperatures may also lower the metabolic expense of thermoregulation for nestlings, resulting in greater weight gain.

Although the weight of nestlings varied with brood size and date, starvation of nestlings appeared to be rare (*n* = 2 broods). Instead, predation was the major determinant of nesting success. Although predation appears to be the primary cause of nest failure at the study site, I was not able to identify the predators responsible. Potential predators include other passerines such as ravens, non-passerines such as raptors and owls, as well as monitors (*Varanus* spp.) and native and introduced mammals.

Table 5. Summary of nesting success for the Petroicidae

Species	Total eggs	% eggs producing fledglings (independent young)	Fledglings (independent young) per pair	Fledglings per nest	% successful nests – raising at least one fledgling	Reference
Flame robin	189	22	1.2	–	25	Robinson (1990)
Red-capped robin	13	54	1.2	0.88	63	Coventry (1988)
Red-capped robin	474	36 (33)	1.6 (1.45)	0.57	34[A] (28[B])	This study
Scarlet robin	115	8	0.39	–	10.3	Robinson (1990)
Hooded robin	46	20	0.7	0.35	19	Fitri and Ford (2003)
Eastern yellow robin[C]	172	27	–	0.6	32	Marchant (1985)
Eastern yellow robin[D]	67	45	–	1.1	30	Marchant (1985)
Eastern yellow robin	267 nests	–	–	–	19	Zanette and Jenkins (2000)
Grey-headed robin	–	39	–	0.7	53	Frith and Frith (2000)
Chatham Island robin[E]	418	39 (31)	1.4 (1.1)	–	–	Butler and Merton (1992)
North Island robin[F]	–	–	3.8, *1.5*	–	75, *30*	Powlesland *et al.* (2000)
North Island robin[G]	–	–	0.4	–	11	Powlesland *et al.* (2000)
North Island robin[H]	–	–	2.5	–	51	Armstrong *et al.* (2000)
South Island robin[I]	405	26	2.5 [3[J]]	–	–	Powlesland (1983)
North Island tomtit	45	–	–	3.3	73.3 [45.4[K], 6.9[L]]	Knegtmans and Powlesland (1999)
South Island tomtit	–	–	–	4	31.3	Kearton (1979) in Knegtmans and Powlesland (1999)

[A]Successful nests in the present study are those that produced at least one fledgling reaching independence.
[B]Successful nests only including nests found during nest building.
[C]No auxiliary helpers.
[D]Auxiliary helpers.
[E]These statistics are for years 1989–92, when management of population ceased.
[F]Mammalian predators at study site controlled prior to breeding season; italicised values indicate breeding success one year after predator control in population.
[G]No predator control prior to breeding season.
[H]No exotic mammalian predators at study site.
[I]Study from 1977 to 1979,
[J]Flack (1976), study from 1971 to 1976 at same study site as used by Powlesland (1983).
[K]Nest Record Scheme cards of Ornithological Society of New Zealand (Knegtmans and Powlesland 1999).
[L]Brown (1997).

Turnover of breeding birds within the population

There is some evidence of a higher turnover of breeding females than males in the study population. At the beginning of the 2001–02 breeding season, there had been a greater rate of female dispersal and/or mortality than male dispersal/mortality for birds that had held territories during the previous season. This trend was less apparent during the following season.

Pair fidelity

The results of this study indicate that although the species is socially monogamous at any given time, long-term monogamous association between the sexes is uncommon. Furthermore, paternity analysis using DNA microsatellite markers (Dowling *et al.* 2003*b*) has revealed high rates of extra-pair matings in this population (23% of all nestlings [$n = 227$] are sired by extra-pair males, 37% of broods [$n = 113$] contain extra-pair young: DKD, unpublished data), whereby females mate with males other than their social partners.

Both Armstrong *et al.* (2000) and Powlesland *et al.* (2000) observed sequential polyandry in the North Island robin, where females paired and bred with a new male while their previous mates cared for the fledglings of the previous clutch. I observed this same behaviour on four separate occasions in the red-capped robin. Depending on whether a territory vacancy exists elsewhere, a female can abandon her previous partner to care for the fledglings of the previous clutch himself, and mate with a different male. It appears that males can successfully complete raising fledglings to independence themselves (in two cases both fledglings survived to independence, and in the other two cases one fledgling survived to independence). A female may potentially swap partners if she considers her new partner is of better individual 'quality'. Additionally, females may possibly maximise their reproductive output through sequential polyandry if it allows them to produce more successful broods per season. This depends on whether it is more time efficient to move to a vacant territory/male after fledging the initial young or to re-nest in the same territory. Regardless of time efficiency, a female that moves to a vacant territory, containing no fledglings, and re-mates with a new partner will potentially receive increased food provisioning during nesting because the new partner will not have the competing demands of provisioning both fledglings and her.

In contrast, it is possible for males to increase their reproductive output through extra-pair fertilisations, whereby they mate with females other than their social partners.

Conclusion

This study provides the first detailed account of the breeding biology of the red-capped robin. The results conform to those of other petroicid robins and more generally to other Australian Corvida. Although multibrooded, it has low annual productivity (on average, fewer than two fledglings per pair in a year). The major cause of this low productivity in the red-capped robin, together with the other Petroicidae and many other Australian Corvida, appears to be nest predation, indicating that nest predation is probably a major selective pressure in the life-history evolution of Australian passerines.

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