

## LIFE IN THE SLOW LANE: REPRODUCTIVE LIFE HISTORY OF THE WHITE-BROWED SCRUBWREN, AN AUSTRALIAN ENDEMIC

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**ABSTRACT.**—An understanding of geographic and phylogenetic variation in passerine life histories is hampered by the scarcity of studies from the Southern Hemisphere. We documented the breeding biology of the White-browed Scrubwren (*Sericornis frontalis*), an Australia endemic in the Pardalotidae (parvorder Corvida). Like other members of the Pardalotidae, scrubwrens had a long laying interval (two days), a long incubation period (declining from 21 to 17 days through the season), and a long period of postfledging parental care (6 to 7 weeks). Scrubwrens appeared to be typical of the Australian Corvida in having a small clutch size (three eggs) and a long breeding season (5.4 months), and they also had a long interval between breeding attempts (10 days after a failed attempt, 21 days after a successful attempt). Scrubwrens were multibrooded, often raising two broods successfully and occasionally raising three broods. The breeding biology of scrubwrens adds further support to claims of a distinct life-history strategy for members of the Corvida but also reinforces evidence that some "Corvida" life-history traits more specifically are those of the Pardalotidae. Received 17 November 1998, accepted 18 October 1999.

MOST STUDIES of the breeding biology of passerines have been carried out in the Northern Hemisphere, primarily on members of the parvorder Passerida (sensu Sibley and Ahlquist 1990). This biases our understanding of passerine biology because these species are not representative of passerines as a whole. For example, the Australian Corvida have smaller clutch sizes than passerines that breed at similar latitudes in the Northern Hemisphere and Passerida that are resident in Australia (Yom-Tov 1987, 1994; Rowley and Russell 1991). It has also been claimed that members of the "old endemic" Corvida of Australia have a syndrome of slow reproduction, with small clutch sizes, prolonged periods of parental care at all stages of nesting, and long breeding seasons (Ford 1989, Rowley and Russell 1991). Nevertheless, other than clutch size, most features of the breeding biology of these species are not well known, and comparisons of many life-history attributes are inconclusive owing to the lack of data from the Southern Hemisphere (Martin 1996).

Although the 49 species in the Pardalotidae that are resident in Australia appear to epitomize the syndrome of slow reproduction, only a

few species have been studied (e.g. *Acanthiza pusilla*, *A. reguloides*, and *A. lineata* [Bell and Ford 1986]; *A. chrysorrhoa* [Ford 1963]; *Sericornis frontalis* [Ambrose and Davies 1989]; *Pardalotus* spp. [Woinarski and Bulman 1985]). Even for these species, sample sizes often are small, and quantitative data do not cover the whole breeding cycle. Indeed, for each of these species, little is known about postfledging care, duration of the breeding season, and number of breeding attempts per season made by individual females.

Here, we provide a quantitative description of the breeding biology of a population of the White-browed Scrubwren (*Sericornis frontalis*), a sedentary, cooperatively breeding species in the Pardalotidae that is common in southern and eastern Australia. Ours is the first detailed study of the breeding cycle and breeding season of any member of the genus and is based on data gathered from a color-marked population over five years. Our goal is to provide a detailed account of the breeding cycle of a member of this speciose family of Australian birds as a first step toward disentangling the effects of environment and phylogeny on the life history of passerines.

### METHODS

*Study species.*—The White-browed Scrubwren is a small (ca. 11 to 15 g) passerine that is endemic to

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mainland Australia (Christidis and Boles 1994). It is one of six members of the genus endemic to Australia. White-browed Scrubwrens are largely sedentary as adults (Brown et al. 1990, Wilson 1994) and breed in diverse habitats from coastal rainforest to alpine heath (Blakers et al. 1984). Scrubwrens feed primarily on arthropods on the ground or in low shrubs, but they also search under bark or in foliage, sometimes in tree canopies (Keast 1978, Ambrose 1985, Cale 1994). The nest is domed with a side entrance and usually is well hidden under leaf-litter or vegetation, on or near the ground. White-browed Scrubwrens are known to breed cooperatively (Bell 1982, Ambrose and Davies 1989), including our study population (see below).

We studied a color-banded population of *S. f. frontalis* in and adjacent to the Australian National Botanic Gardens (35°16'S, 149°06'E) in Canberra from 1992 to 1996. The Gardens occupy an area of 40 ha, 27 ha of which are planted exclusively with Australian native plants. Most of the remaining 13 ha are natural woodlands that are contiguous with a large area of natural habitat in which scrubwrens breed. Although breeding extended beyond the end of December in each season, we refer to the season by the year in which breeding began.

White-browed Scrubwrens are resident throughout the year, and during the breeding season we visited territories at least three times a week to document reproductive attempts. Between 35 and 48 breeding groups were present in any one breeding season. Scrubwrens typically bred in pairs (46% of groups) or in trios consisting of a socially dominant pair and a subordinate male (44%), although 10% of the groups had more than one subordinate male (Magrath and Whittingham 1997). Only the female builds the nest and incubates, but both members of the dominant pair, and often the subordinate males, provision the nestlings (Magrath and Whittingham 1997). Neither group size nor provisioning by subordinate males had a detectable effect on the duration of any stage of the reproductive cycle, the interval between nesting attempts, or the reproductive success of the group (Magrath and Yezerinac 1997).

*Field methods.*—We determined the sex of birds in the field from the color of the lores (males black, females brown; Rogers et al. 1986). We detected no "brown-lored males," which might occur in *S. f. maculatus* (Ambrose and Davies 1989). Nests usually were found by watching building females, following females back to the nest during incubation, or following adults that were feeding nestlings. Most nests were on or near the ground. If a nest was found before laying in 1992, it was checked daily to determine the date of laying of each egg in the clutch. In subsequent years, we checked nests only to determine the date on which the first egg was laid (the "laying date"). If the nest was not found until after eggs had been laid, the laying date was estimated from the

hatching date and regression of incubation period on laying date (see below).

The incubation period was defined as the period from the laying of the last egg in the clutch until the completion of hatching. The date of hatching was determined from daily visits to nests toward the end of the incubation period. We did not flush females from nests during this period, so we were unable to inspect the contents on each visit and therefore also used the appearance and size of young nestlings to estimate the day of hatching (Magrath and Yezerinac 1997). We gave each nestling a unique combination of color bands when it was 9 or 10 days old.

To quantify the duration of postfledging parental care, we watched 30 focal fledglings in 15 broods several times a week for 15 min during 1993 and recorded whether they were fed by an adult during this period. Watches usually were conducted on different days, but a few fledglings were watched twice per day, separated by several hours. The date of termination of parental care was taken to be the midpoint from the last watch in which we saw the young being fed and the first watch of a sequence of at least three watches in which we did not see it being fed. These two dates were a median of three days apart (range 0 to 11).

*Data analyses.*—We analyzed data with SPSS (Norris 1995). We used parametric statistics whenever assumptions of the analyses appeared to be met or the data could be transformed to meet those assumptions. Data that were transformed for analyses were back-transformed for presentation in the text. When we had data (e.g. clutch size, incubation, and nestling periods) from more than one nest of a female in a given year, we randomly selected a single attempt to maintain statistical independence. Sample sizes varied among analyses because nests were found at different times during the breeding cycle and because many nests failed before fledging (see Magrath and Yezerinac 1997). Analyses of timing of breeding and number of attempts per season were restricted to females that we followed sufficiently closely to detect each nesting attempt.

As an index of the length of the breeding season, we calculated the number of "equally good months for breeding" following MacArthur (1964:394). This entailed entering the proportion of clutches initiated in each month into the Shannon-Wiener diversity formula and then taking the antilog of the diversity value.

## RESULTS

*Clutch size and laying interval.*—Most scrubwren clutches contained three eggs (93.6% of 171), although nine clutches had two eggs, one had one egg, and one had four eggs, giving a mean clutch size of 2.94 eggs. We did not mark

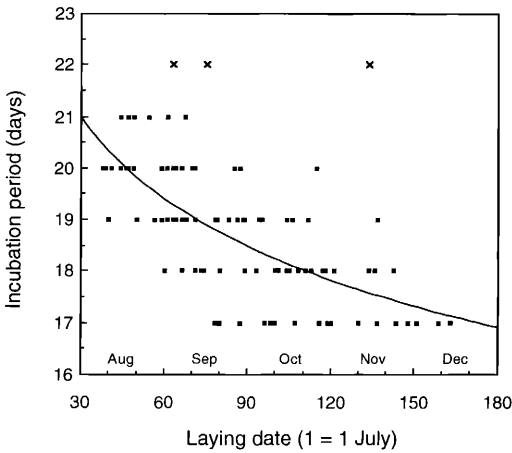


FIG. 1. Seasonal change in the incubation period of White-browed Scrubwrens with laying date ( $y = 28.7 - 5.24[\log_{10}x]$ ,  $n = 92$ ,  $r^2 = 0.51$ ,  $P < 0.0001$ ). The three outliers shown as crosses were not included in the regression.

eggs during laying, so it is probable that some clutches of less than three eggs resulted from egg loss during laying or incubation. Eggs were laid at two-day intervals in all 35 cases where the interval was known accurately. The 35 intervals include 13 cases of first to second egg and 22 cases of second to third egg. These data come from 27 clutches laid by 21 different females.

*Incubation period.*—The mean incubation period was  $18.8 \pm$  SD of 1.3 days ( $n = 95$ ), ranging from 17 to 22 days. Excluding the three cases of a 22-day incubation period (outliers) gives a mean value of  $18.7 \pm 1.2$  days. Only clutches of three were used to calculate incubation periods.

A dramatic decline in the length of the incubation period (from 21 to 17 days) occurred over the course of the breeding season (Fig. 1). We detected no difference between years in the mean incubation period or in the slope of decline (ANOVA, including date as a covariate, year effect after dropping interaction term,  $F = 0.5$ ,  $df = 4$  and 86,  $P = 0.80$ ; year  $\times$  date interaction,  $F = 1.9$ ,  $df = 4$  and 82,  $P = 0.12$ ; outliers identified in Fig. 1 were excluded from analyses).

The seasonal decline in incubation period illustrated in Figure 1 may have resulted from females with different incubation abilities laying at different dates (each female is represent-

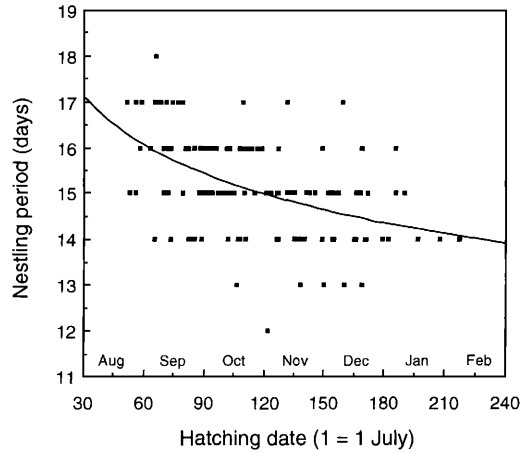


FIG. 2. Seasonal change in the nestling period of White-browed Scrubwrens with hatching date ( $y = 22.4 - 3.55[\log_{10}x]$ ,  $n = 124$ ,  $r^2 = 0.23$ ,  $P < 0.001$ ).

ed in the sample only once per year), or to some seasonal factor that affected each individual female. We addressed this issue by examining the slope of the regression of incubation period on date (log transformed) for individual females for whom we had measures of the incubation period for different clutches within a season. The mean slope of the regression was  $-5.0 \pm$  SE of 0.6, which is significantly less than zero ( $t = 8.4$ ,  $df = 34$ ,  $P < 0.001$ ) but is not significantly different from the population regression slope of  $-5.2$  ( $t = 0.4$ ,  $df = 34$ ,  $P = 0.70$ ). Thus, the seasonal decline in length of the incubation period affected individual females and was not a consequence of different females laying at different dates.

*Nestling period.*—Eggs in a clutch hatched roughly synchronously. In 37 out of 45 broods (82%), all nestlings had hatched between inspections of nest contents on sequential days; in the remaining 8 broods, all nestlings had hatched by the next day. This implies that hatching usually takes place over a few hours, or perhaps that it occurs overnight.

The mean nestling period was  $15.1 \pm$  SD of 1.1 days ( $n = 124$ , range 12 to 18 days). The nestling period declined through the breeding season (Fig. 2), and neither the mean nor the pattern of seasonal decline differed among years (year, after dropping interaction term,  $F = 1.3$ ,  $df = 4$  and 118,  $P = 0.30$ ; year  $\times$  date interaction,  $F = 1.5$ ,  $df = 4$  and 114,  $P = 0.20$ ).

The decline in the nestling period through

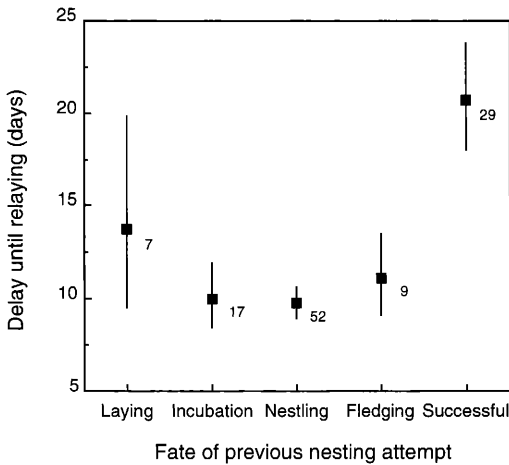


FIG. 3. Interval between breeding attempts of White-browed Scrubwrens according to the fate of the previous nesting attempt. The delay to relaying is the number of days from fledging or failure of the first nest until the laying of the first egg in the next clutch. Laying, incubation, nestling, and fledging refer to when the nest failed; successful nests produced one or more young that survived at least one week after fledging. Values are  $\bar{x}$  with 95% CI; numbers are sample sizes.

the season occurred for sequential broods of 31 females, not merely for the population as a whole. The mean slope of the regression for individual females was  $-2.6 \pm \text{SE of } 0.7$ , which is significantly less than zero ( $t = 3.6$ ,  $df = 30$ ,  $P = 0.001$ ) but is not significantly different from the population regression slope of  $-3.6$  ( $t = 1.4$ ,  $df = 30$ ,  $P = 0.20$ ). One extreme outlier was dropped from these analyses (a deformed nestling that had a long nestling period compared with nestlings in an earlier brood).

*Interval between nesting attempts.*—The interval between the termination of a nesting attempt and the initiation of laying of the next clutch in the same season was longer if a nest was successful ( $\bar{x} = 21$  days) than if it had failed ( $\bar{x} = 10$  to 14 days depending on time of failure;  $F = 26.1$ ,  $df = 4$  and 109,  $P < 0.001$ ; Fig. 3). We defined a successful nest as one in which at least one young survived for at least one week after leaving the nest. The interval appeared to be longer if the nest failed during laying ( $\bar{x} = 14$  days) than at a later stage ( $\bar{x} = 10$  to 11 days), but the difference was not significant (Student-Newman-Keuls multiple range

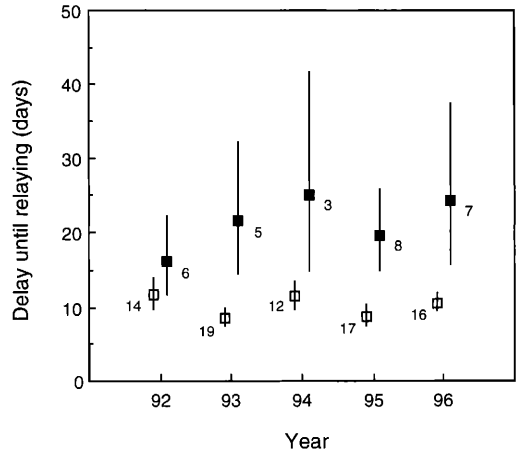


FIG. 4. Yearly variation in the interval between breeding attempts of White-browed Scrubwrens. The delay to relaying is the number of days from fledging or failure of the first nest until the laying of the first egg in the next clutch. Filled squares = delay after successful attempts; unfilled squares = delay after failed attempts. Values are  $\bar{x}$  with 95% CI; numbers are sample sizes.

test,  $P > 0.05$ ), perhaps because of small sample sizes.

The shortest interval until relaying, which did not appear in the random sample above, was two days after the fledging of a successful brood. This was the only interval shorter than five days that we recorded during the study ( $n = 173$ , including multiple samples from individual females within years), and in this case the female completed building the new nest before her young had fledged.

Variability in the delay until relaying was higher if the initial nest was successful than if it failed, and the mean delay varied among years. If the nest was successful, the delay until relaying ranged from 12 to 43 days, with an interquartile range of 11 days ( $n = 29$ ); if a nest failed, the delay ranged from 5 to 22 days, with an interquartile range of 4 days ( $n = 78$ ; 7 nests that failed during laying were excluded). An analysis of variance controlling for the fate of the previous nest (failed or successful) revealed no seasonal trend in the interval until relaying ( $F = 1.4$ ,  $df = 1$  and 100,  $P = 0.20$ ), but there was a small difference among years ( $F = 2.9$ ,  $df = 4$  and 100,  $P = 0.03$ ; Fig. 4).

*Care of fledglings.*—Young were fed by adults for a mean of  $46 \pm \text{SD of } 5.7$  days after leaving the nest (range 32.5 to 57.5). All but 4 of the 30

TABLE 1. Number of clutches laid and number of successful broods\* raised per female per season in White-browed Scrubwrens.

| Number                   | 1992 | 1993 | 1994 | 1995 | 1996 | Total (%) |
|--------------------------|------|------|------|------|------|-----------|
| <b>Clutches laid</b>     |      |      |      |      |      |           |
| 0                        | 0    | 1    | 4    | 0    | 0    | 5 (3.4)   |
| 1                        | 5    | 1    | 6    | 2    | 2    | 16 (11.0) |
| 2                        | 4    | 8    | 12   | 10   | 7    | 41 (28.1) |
| 3                        | 16   | 12   | 5    | 10   | 13   | 56 (38.4) |
| 4                        | 5    | 7    | 1    | 5    | 4    | 22 (15.1) |
| 5                        | 0    | 1    | 0    | 0    | 0    | 1 (0.7)   |
| 6                        | 1    | 0    | 0    | 2    | 2    | 5 (3.4)   |
| <b>Successful broods</b> |      |      |      |      |      |           |
| 0                        | 9    | 6    | 17   | 9    | 9    | 50 (34.2) |
| 1                        | 7    | 17   | 11   | 15   | 12   | 62 (42.5) |
| 2                        | 12   | 7    | 0    | 5    | 7    | 31 (21.2) |
| 3                        | 3    | 0    | 0    | 0    | 0    | 3 (2.1)   |
| Total                    | 31   | 30   | 28   | 29   | 28   | 146       |

\* Successful broods were those in which at least one young survived until a week after fledging.

cases were between 39 and 51 days. These analyses were based on a mean of 25 watches (6.25 h) on each of 30 juveniles in 15 broods.

**Breeding seasons.**—Scrubwrens initiated clutches from July until January of the following year, with 96% of clutches being initiated from August to December. Thus, the breeding season extended from the austral winter (June to August) until summer (December to February). MacArthur's (1964) index of the length of the breeding season was 5.4 months.

Scrubwrens laid up to six clutches during the breeding season and raised up to three broods successfully (Table 1). The number of clutches laid, and particularly the number of nests producing surviving fledglings, differed among years (number laid,  $\chi^2 = 22.0$ ,  $df = 8$ ,  $P = 0.005$ ; successful broods,  $\chi^2 = 32.5$ ,  $df = 8$ ,  $P = 0.0001$ ; adjacent cells pooled to keep expected frequencies above five). In particular, most of the females had no successful breeding attempts in 1994, the year with the shortest breeding season (see below).

The median length of the breeding season for females that laid at least one clutch varied among years, ranging from 42 days in 1994 to 90 days in 1996, with a maximum for an individual of 183 days in 1996 (Kruskal-Wallis test,  $\chi^2 = 20.3$ ,  $df = 4$ ,  $P = 0.0004$ ; Fig. 5). Including only females that laid at least two clutches, the median length of the breeding season ranged

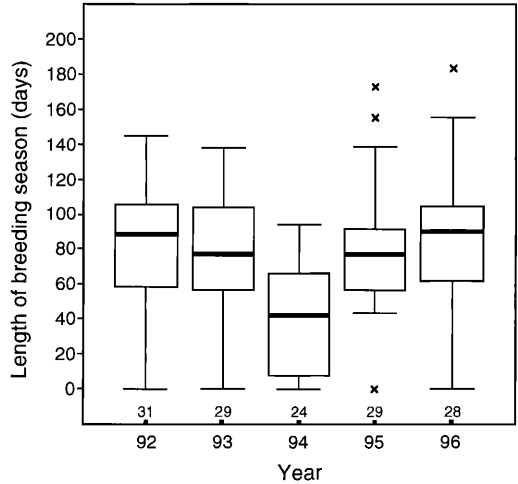


FIG. 5. Duration of the breeding season for individual female White-browed Scrubwrens in each year. Data are summarized by boxplots in which heavy bars denote medians, boxes denote interquartile ranges, and vertical lines denote the range of values within 1.5 interquartile ranges of the top and bottom of the boxes; crosses are extreme values. Numbers inside figure are sample sizes.

from 56.5 days in 1994 to 101 days in 1992 ( $\chi^2 = 20.0$ ,  $df = 4$ ,  $P = 0.0005$ ).

DISCUSSION

White-browed Scrubwrens show all of the features that have been suggested to distinguish the "old endemic" passerines of Australia from the passerines of north temperate regions (Ford 1989, Rowley and Russell 1991). They have small, relatively constant clutches, long breeding seasons coupled with multi-brooding, and a long period of dependency after leaving the nest. Like the few other members of the Pardalotidae that have been studied, White-browed Scrubwrens lay their eggs at two-day intervals and have long incubation periods.

**Clutch size.**—Scrubwrens usually laid a three-egg clutch, which is typical of the old endemic passerines (Woinarski 1985, 1989; Yom-Tov 1987). It is not known why these birds have small clutch sizes. Yom-Tov (1987) suggested that small clutches evolved when Australia was covered by rainforest and were retained in the lineage despite increased aridity, or that small clutch size is adaptive in environments with erratic rainfall. In contrast, Woinarski (1985) fa-

vored Ashmole's hypothesis that small clutch size results from an aseasonal environment in which mild winters allow high survival and there is no major peak of food in spring, resulting in fewer resources per capita for breeding (Ashmole 1963, Ricklefs 1980, Ford 1989).

Ashmole's hypothesis may be relevant to Australian birds, but little is known about the seasonality of resources for insectivorous birds. Some authors state that the winter decline in foliage arthropods in the evergreen forests of temperate Australia is relatively minor (Woinarski and Cullen 1984, Ford 1989, Ford and Recher 1991), whereas others emphasize seasonal changes (Recher et al. 1991, 1996). Most information relates to eucalypt foliage, in which arthropod abundance in spring is no more than twice that in winter (Recher et al. 1996). This increase presumably is far lower than in deciduous forests and suggests that food is not superabundant during breeding. No study, however, has assessed seasonal changes in arthropod abundance across years, and none has specifically measured variation in the major food items of scrubwrens.

Indirect evidence suggests that scrubwrens suffer relatively minor seasonal changes in food availability. First, several species of insectivorous passerines forage more often on the ground in winter than in summer, suggesting that foraging on the ground becomes more profitable in winter, at least compared with above-ground sites (Ford et al. 1990, Cale 1994). These findings suggest that scrubwrens, which are ground-feeding specialists that can also feed above ground, are likely to suffer relatively minor seasonal variation in food availability. Second, scrubwrens in the study population are sedentary and had an annual mortality of only 15 to 20% (Magrath and Yezerinac 1997), suggesting that conditions in winter were not severe.

Although the small, fairly constant clutch sizes of endemic Australian passerines are consistent with Ashmole's hypothesis, there still needs to be quantification of seasonal conditions for breeding and an assessment of hypotheses for the evolution of clutch size unrelated to the direct effect of food supply (Winkler and Walters 1983, Murphy and Haukioja 1986). For example, the role of nest predation and the life-history correlates of clutch size have not been adequately assessed, and the

only experimental manipulation of clutch size yielded equivocal results (Poiani 1993). In particular, starvation appears to be rare among nestling passerines in Australia in general (Ford 1989) and in scrubwrens in particular (Magrath and Yezerinac 1997), suggesting that food supply during the nestling period is not a proximate limit on clutch size, thereby challenging the aseasonality hypothesis.

*Laying interval.*—It has often been stated that the typical laying interval in passerines is one day (Lack 1968, Welty and Baptista 1988). This misleading statement reflects a phylogenetic bias in detailed studies of passerine breeding biology. Two-day laying intervals are the norm in the Tyranni (Skutch 1976, Astheimer 1985, Ricklefs 1993), and they occur in several families of the Corvida (Courtney and Marchant 1971). Moreover, two-day laying intervals appear to be universal in the Pardalotidae and the Ptilonorhynchidae (Marchant 1986, Frith 1994), they occur in some members of the Corvini and the Artamini, and they are suspected to occur in *Climacteris leucophaea* in the Climacteridae (Marchant 1986).

Given the high risk of nest predation in small passerines, long laying intervals seem anomalous. It has been suggested that long laying intervals are related to a female's difficulty in acquiring food during egg formation (Thomas 1974), but this is an unlikely proximate cause in scrubwrens given their fixed laying interval. Two features of the Pardalotidae may reduce the cost of long laying intervals. First, they are hole or dome nesters, which may reduce the risk of predation on the eggs. The very low daily rate of clutch mortality in scrubwrens (0.9%) supports this idea. Second, the long breeding season may mean that delays in initiating incubation have little effect on the success of a brood. This contrasts with birds like the Great Tit (*Parus major*), in which delays of even a day or two may reduce reproductive success because of rapid declines in food availability (Pettifor et al. 1988).

The benefits of two-day laying intervals are unknown. One potential benefit is that it becomes physiologically possible for a female to lay large eggs, which might improve the growth and survival of young (Williams 1994). We suggest a second and related benefit: that for a given egg and clutch size, a female will not have to carry as much additional mass at any

one time because of reduced temporal overlap in the development of eggs. In this manner, the birds would avoid the lower flight performance and subsequent increase in vulnerability to predation that accompany increased body mass (Witter and Cuthill 1993, Witter et al. 1994, Gosler et al. 1995). A clutch of three eggs translates to about 63% of the mass of a female scrubwren (R. Magrath unpubl. data), so the added body mass that would result from a one-day laying interval could substantially compromise her agility during the laying period.

*Incubation and nestling periods.*—Based on the equations of Rahn et al. (1975), the incubation period of scrubwrens ( $\bar{x} = 18.8$  days) is much longer than the 14.9 days predicted for a passerine laying an egg of 2.7 g and still longer than the 13.9 days predicted for a passerine of 12.8 g body mass (mean for breeding females in this population; R. Magrath unpubl. data). In a comparative analysis controlling for egg volume, Ricklefs (1993) showed that the long incubation period is a feature of the Pardalotidae in particular, rather than the Corvida as a whole.

The long period of incubation might reflect the security of hole or dome nests found in the Pardalotidae, or it may be related to the species' longevity (Ricklefs 1993). Hole nests are relatively safe from predators, and dome nests may suffer reduced predation of eggs compared with open-cup nests in similar locations. Dome nests also may offer greater protection from inclement weather (H. Recher pers. comm.). Ricklefs (1993) suggested that long incubation periods assist in the maturation and subsequent efficiency of the immune system, and in comparative studies he found that long incubation periods for a given egg volume were associated with high annual adult survival (Ricklefs 1993) and low prevalence of blood parasites (Ricklefs 1992). The high annual survival of scrubwrens in the study population (ca. 80% for females and 85% for dominant males; Magrath and Yezzerinac 1997) and the maximum longevity of at least 17 years (R. Magrath unpubl. data) are consistent with this hypothesis.

The incubation period of scrubwrens declined from about 21 to 17 days over the breeding season and was associated with a decline for each female. Incubation periods tend to be shorter when ambient temperatures are higher (Skutch 1976, O'Connor 1984). In the Eurasian

Blackbird (*Turdus merula*), for example, the incubation period declines from 13.7 days in March to 12.7 days in June (Snow 1958). Seasonal declines presumably result from the eggs being kept at optimal temperatures for a greater percentage of the time when it is warmer, or because early in the season incubation does not start as soon as the last egg is laid (Nilsson and Svensson 1993). The synchronous hatching of scrubwren nestlings suggests that incubation starts on or after the day the last egg is laid. The large seasonal decline in incubation length probably reflects the long breeding season and marked increase in mean temperature; the season extends from midwinter (mean August temperature = 6.9°C) to almost midsummer (mean January temperature = 20.3°C). Seasonal changes in incubation length might be more marked in species in which only one sex incubates, but we know of no published data that are relevant to this question.

The nestling period of scrubwrens ( $\bar{x} = 15$  days) is not unusual for a small passerine that builds a domed nest (see Lack 1968). We do not know why the nestling period declines through the season; perhaps nestlings grow faster later in the season, or they can afford to leave the nest sooner when ambient temperatures are higher.

*Interval between nesting attempts.*—Scrubwrens appear to have a longer interval between nesting attempts ( $\bar{x} = 10$  to 14 days after failed attempts) than is typical of north temperate species in the Passerida. For example, Song Sparrows (*Melospiza melodia*) have an interval of about 5 days, European Starlings (*Sturnus vulgaris*) 8 days (Welty and Baptista 1988), Eurasian Blackbirds 5 days (Magrath 1992), and American Robins (*Turdus migratorius*) 7 days (Weatherhead 1990). Similarly, 11 species in North America had a mean interval of 8.6 days (Ricklefs 1966). In contrast, the delay until re-nesting in scrubwrens was similar to that of the Splendid Fairy-Wren (*Malurus splendens*; 5 to 14 days; Rowley et al. 1991), an old endemic of Australia, and to those of four Neotropical species ( $\bar{x} = 14$  days; Ricklefs 1966).

The longer and more variable delay until re-nesting after a successful attempt in scrubwrens ( $\bar{x} = 21$  days) may relate to the costs of caring for fledglings and the variability in the duration of care by females (A. Leedman and R. Magrath unpubl. data). Again, the mean de-

lay is more similar to those of Neotropical species ( $\bar{x}$  = 29 days) than to those of Nearctic species ( $\bar{x}$  = 8.5 days; Ricklefs 1966), reinforcing the suggestion that the life histories of south temperate species are more similar to those of tropical species than to those of north temperate species (Martin 1996), or at least that they are intermediate between the two groups (Rowley and Russell 1991).

The yearly variation in the interval between nesting attempts generally had a similar influence on the delay after a failed or successful attempt. The mean delay was longest in 1994, the year with the fewest breeding attempts and the shortest breeding season (see below). These data suggest that female scrubwrens face energetic constraints in the timing of relaying, particularly if their previous nests are successful, or that they assess conditions for breeding before they attempt another clutch.

*Postfledging care.*—The period of postfledging care of young scrubwrens (ca. 6 to 7 weeks) is longer than that of north temperate species but similar to or shorter than that of tropical species (Skutch 1976). Small passerines in north temperate latitudes typically become nutritionally independent of their parents two to four weeks after leaving the nest (Skutch 1976, O'Connor 1984). The long period of postfledging care in scrubwrens supports Rowley and Russell's (1991) suggestion that parental care is prolonged in Australian passerines. Fogden (1972) suggested that the long period of care of passerines in Sarawak resulted from the difficulty of finding suitable prey. That is, if insects are sparsely distributed and have many forms of antipredatory defense, it may take a long time for young birds to learn how to forage efficiently. We suggest an explanation that is related to seasonality of food supplies. If the seasonal increment available for breeding is small, then the young may not fledge during a period of food abundance, which is in contrast to many north temperate species. Thus, the young may take longer to acquire the necessary skills for survival, not because Australian arthropods require particular skill to find and eat, but because a greater level of skill is required for survival when food is not abundant. This second hypothesis seems more plausible, because it does not require the assumption that more skill or learning is required to capture arthropods in different geographic regions.

The few data on old endemic Corvida of Australia suggest that a long period of postfledging care is common. Pardalotids typically have periods of postfledging care of 6 to 7 weeks (Brown Thornbill [*Acanthiza pusilla*], D. J. Green pers. comm.; Yellow-rumped [*A. chrysorrhoa*] and Buff-rumped [*A. reguloides*] thornbills, D. Ebert pers. comm.; Speckled Warbler [*Chthonicola sagittatus*], J. Gardner pers. comm.). Similarly, Helmeted Honeyeaters (*Lichenostomus melanops*) do not reach 80% self sufficiency until about 6 to 8 weeks after leaving the nest and are occasionally fed up to 14 weeks (Franklin et al. 1996), and Rufous Whistlers (*Pachycephala rufiventris*) are fed for at least 8 weeks (Bridges 1994). Species of *Malurus* appear to be an exception in that Splendid Fairy-Wrens (Rowley et al. 1991) and Superb Fairy-Wrens (*M. cyaneus*; A. Cockburn pers. comm.) reach independence in about 4 weeks. Among the large Corvida, extremely long periods of parental care occur in White-winged Choughs (*Corcorax melanorhamphos*; ca. 29 weeks; Heinsohn 1991) and Superb Lyrebirds (*Menura novaehollandiae*; ca. 37 weeks; Lill 1986).

*Length of breeding season and multibrooding.*—The 5.4-month breeding season of scrubwrens is typical of those of tropical birds (3.9 to 7.8 months) but longer than those of north temperate species (2.7 to 3.1 months; Ricklefs 1966). The breeding season appears to be at the long end of range among the Pardalotidae (Woinarski 1985). It is similar to that estimated for the Spotted Pardalote (*Pardalotus punctatus*) but about two months longer than that for the Buff-rumped Thornbill and the Chestnut-rumped Thornbill (*Acanthiza uropygialis*). Even controlling for the effect of latitude (one month per 11°; Wyndham 1986), the Pardalotidae examined by Woinarski (1985) have long breeding seasons (3 to 5 months) relative to ecologically comparable Northern Hemisphere species, which typically have breeding seasons of 2 to 3 months.

Our data from White-browed Scrubwrens support Rowley and Russell's (1991) conclusion that variation in reproductive effort in Australian passerines comes not through differences in clutch size, but through variation in the number of breeding attempts per season. In contrast to the duration of individual breeding attempts, the length of the breeding season and the number of breeding attempts per year var-



ied significantly among years. However, it is unclear whether multibrooding per se is an important difference between passerines in Australia versus those in north temperate regions (e.g. Woinarski 1985, Rowley and Russell 1991). Martin (1996) argued such differences have been overstated, because many north temperate species have multiple broods (see Crick et al. 1993).

*Does a general life-history "syndrome" exist for Australian old endemics?*—Our data show that the breeding cycle of White-browed Scrubwrens is slow compared with those of Northern Hemisphere passerines, particularly in having a two-day laying interval, a long incubation period, and a long period of postfledging parental care. However, these differences appear to be characteristic of the Pardalotidae, and possibly some other families, but not of the old endemic Corvida in general. Overall, the suggestion that a general syndrome of leisurely reproduction exists among Australian passerines originates from a sample of leaf-gleaning insectivores, with all of the Australian representatives coming from the Pardalotidae (Woinarski 1985, Ford 1989). Clearly, a more representative sample of taxa is required. White-browed Scrubwrens appear to be typical of old endemic Australian passerines in having a small clutch size (Yom-Tov 1987) and a long interval between nesting attempts, and they resemble Australian passerines in general in having high adult survival (Yom-Tov et al. 1992). They also have a long breeding season, which appears to be typical of Australian birds (Wyndham 1986).

We agree with Rowley and Russell (1991) and Martin (1996) that fundamental gaps exist in our knowledge of the basic breeding biology of Corvida in the Southern Hemisphere. Further study of these birds will increase our understanding of the evolution of reproductive traits and help disentangle the effects of environment and phylogeny on the life histories of passerines. In particular, we need detailed studies of a phylogenetically diverse range of taxa and more emphasis on verifying periods of postfledging care, renesting intervals, and the extent of multiple brooding.

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