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THE SOCIAL ORGANIZATION AND MATING SYSTEM OF THE STRIATED GRASSWREN[1]

JORDAN KARUBIAN[2]
Department of Ecology and Evolution, University of Chicago, 1101 E. 57th St., Chicago, IL 60637

Abstract. This paper summarizes the breeding biology, social organization, and mating system of the Striated Grasswren (*Amytornis striatus*), a member of one of the least-known genera of Australian passerines, the grasswrens. I studied 18 color-banded groups and 14 nests in South Australia for one breeding season in 1996. Mean territory size was 3.0 ha, and territories consisted of sandy dunes dominated by spinifex (*Triodea irritans*). This apparent dependency on mature spinifex, coupled with poor dispersal ability, suggests that the Striated Grasswren is particularly susceptible

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[2] E-mail: jordan@uchicago.edu

to habitat destruction. Most groups consisted of socially monogamous pairs, mean group size was 2.1 adults, and the adult sex ratio was 0.95 (males:females). The average clutch size was 2.2 ± 0.4 eggs and an average of 1.1 ± 1.1 young fledged per nesting effort. A male and a female provided similar amounts of parental care at a single nest. Cloacal protuberance size and amount of sperm collected did not suggest intense sperm competition among males.

Key words: Amytornis striatus, *breeding biology, conservation, social organization, South Australia, Striated Grasswren.*

Organización Social y Sistema de Apareamiento de *Amytornis striatus*

Resumen. Este trabajo resume la biología reproductiva, organización social, y sistema de apareamiento de *Amytornis striatus,* miembro de uno de los géneros menos conocidos de paserinos de Australia. Durante la estación reproductiva de 1996 estudié, en el sur de Australia, 18 grupos identificados con bandas de colores y 14 nidos. El tamaño promedio de los territorios fue 3.0 ha, siendo los territorios dunas arenosos dominadas por *Triodea irritans.* Esta aparente dependencia de sectores maduros de *T. irritans,* en combinación con una limitada capacidad de dispersión, hacen que *A. striatus* sea particularmente sensible a la destrucción del habitat. La mayoría de los grupos sociales fueron parejas monógamas; el tamaño promedio del grupo fue 2.1 adultos, y el cociente de sexos en adultos fue 0.95 (machos:hembras). El tamaño medio de nidada fue 2.2 ± 0.4 huevos, y un promedio de 1.1 ± 1.1 juveniles por intento de nidificación abandonó exitosamente el nido. Un macho y una hembra proporcionaron esfuerzos similares de cuidado parental en un único nido. El tamaño de la protuberancia cloacal y la cantidad de esperma colectados no sugirieron que exista intensa competencia espermática entre machos.

Grasswrens (Maluridae: *Amytornis,* 8 species) are cryptically colored, terrestrial passerines which inhabit some of Australia's most arid and isolated regions. Although a source of keen interest to Australian ornithologists for well over a century (Schodde 1982, Rowley and Russell 1997), they are among the least known Australian birds. The little that is known suggests they have followed a very different evolutionary trajectory than fairy-wrens (*Malurus*), their close relatives. Whereas fairy-wren males are much brighter than females, grasswrens are dull-colored and exhibit mild reverse sexual dimorphism. Also, while fairy-wrens are extremely sexually promiscuous (Brooker et al. 1990, Mulder et al. 1994), the dull plumage and small testes of grasswrens suggest relatively low levels of sexual promiscuity. Finally, fairy-wrens are common in virtually every terrestrial habitat within Australia, whereas grasswrens are restricted to the arid zone, have narrow habitat preferences, and some species may be threatened with extinction (Rowley and Russell 1997).

The most recent species of grasswren was discovered in 1968 (Favaloro and McEvey 1968), and even the Striated Grasswren *Amytornis striatus,* which has the largest range in the genus, remains largely unknown. Published accounts of the Striated Grasswren's biology are either anecdotal (Whitlock 1910, Schodde 1982, Howard and Howard 1984) or based solely upon observation of captive birds (Hutton 1991).

I studied a color-banded population of Striated Grasswrens (*A. s. striatus*) in South Australia for one breeding season in 1996. This study was motivated by two objectives. The first was to provide the first quantitative documentation of the social organization, mating system, and habitat use of this little known species. The second was to make available information which might aid in the conservation of this threatened bird species and of the vanishing mallee habitat in which it lives.

STUDY AREA AND METHODS

This study took place at Calperum Biosphere Reserve (34°10′S, 140°45′E), within the UNESCO Bookmark Biosphere Reserve in South Australia. Calperum Reserve, a former pastoral property, is a large (242 800 ha) tract of relatively undisturbed mallee habitat (Lindsay 1995). The 3-km^2 study area is characterized by sand dunes roughly 20 m in height interspersed with clay-rich swales. Vegetation on the dunes is dominated by spinifex (*Triodea irritans*) and multi-stemmed mallee eucalypts, most commonly red mallee (*Eucalyptus socialis*) and ridge-fruit mallee (*E. incrassata*). In the swales, chenopod shrubs, grey mallee (*E. dumosa*), and red mallee are the most common plants. Similar habitat, known to contain Striated Grasswrens, surrounds the study area. Calperum Reserve averages 259 mm of precipitation annually, varying from less than 88 mm to more than 500 mm per year (Australian Government Bureau of Meteorology, unpubl. data).

Field research was conducted from 16 September–20 December 1996. Birds were captured in mist nets aided by amplified playbacks of tape-recorded male song. I weighed each captured individual and measured tarsus length (from the tibiotarsal notch to the first split scale at the base of the toes), folded-wing length (from the bend of the wrist to the tip of the longest primary), and tail length (the length of the longest rectrices). I also recorded the presence or absence of body molt for all captured birds. As in most malurids, male Striated Grasswrens have a cloacal protuberance (Mulder and Cockburn 1993). I used three measures of the cloacal protuberance: length (L), or the distance from the anterior portion of the cloacal opening to the posterior edge; maximum depth (D); and maximum width (W) to calculate volume as $\pi \times D/2 \times W/2 \times L$ (Mulder and Cockburn 1993, Tuttle et al. 1996). Sperm samples were collected, stored, and counted by E. M. Tuttle following the methods in Tuttle et al. (1996). Finally, I banded each bird with an Australian Bird and Bat Banding Scheme metal identification ring and a unique combination of three colorbands.

Group composition and social behavior were established by repeated monitoring of banded individuals. Habitat selection was determined by observation of banded individuals in the field. Territorial boundaries were mapped by attaching flagging tape to vegetation where males engaged in territorial singing with neighboring males. An enlarged aerial photograph of the

TABLE 1. Morpholgoical measures of adult male and female Striated Grasswrens at Calperum Biosphere Reserve, South Australia.

	Males (n = 30)		Females (n = 18)		
	Mean ± SD	Range	Mean ± SD	Range	P
Mass (g)	20.2 ± 1.0	18.0–22.5	19.1 ± 1.2	17.0–22.0	<0.01
Wing (mm)	59.0 ± 1.2	56.6–61.3	56.5 ± 1.7	53.5–60.4	<0.001
Tarsus (mm)	24.9 ± 1.0	22.8–27.1	24.4 ± 0.8	22.6–25.7	0.10
Tail (mm)	85.8 ± 5.1	71.1–93.2	83.6 ± 4.1[a]	76.7–89.8	0.15

[a] n = 17 females.

study site on which individual shrubs were recognizable was used to map the locations of sightings, and straight lines were then drawn between known points. Territory areas were calculated by superimposing a grid of 25-m^2 squares onto the map and counting the number of squares within each territory. Singing within 15 m of a known nest was considered to be singing around the nest; otherwise it was considered to be territorial song.

Nest width and height were measured using a tape measure. Nest height was measured from the ground to the bottom of the nest's opening. Clutch sizes were determined by counting number of eggs or young present in each active nest. Nests were checked every other day to determine duration of the breeding season and dates of laying, hatching, fledging, and predation. When calculating clutch sizes, I assumed there had been no partial predation of nests. Parental care at a single nest was observed from a hide placed 15 m from the nest. A total of ten 90-min nest watches were conducted between 07:30 and 18:00 over eight days.

All statistical tests were two-tailed, and values reported below are means ± SD. P-values < 0.05 are considered significant.

RESULTS

MORPHOLOGY AND MOLT

I captured a total of 69 individuals: 30 adult males, 18 adult females, 4 juveniles, and 17 nestlings or fledglings. Males tended to be larger than females in all measures, significantly so for wing length and mass (Table 1). Body molt in adults was observed throughout the study but was more prevalent in the second half of the study (16 November–16 December) than the first half of the study (16 October–15 November; χ^2_1, $P < 0.05$). There was no difference between the sexes in the timing or intensity of molt. At the time of capture, all but one adult female had a brood patch and all adult males had enlarged cloacal protuberances (see below).

HABITAT SELECTION AND TERRITORIALITY

All territories contained spinifex-covered sand dunes, where most foraging and nesting occurred. Average territory size for 17 contiguous territories was 3.0 ± 1.1 ha (range 0.6–5.2 ha). The density of adults on the study area was 0.5 birds ha^{-1}. The birds were highly territorial and boundaries of territories appeared to change little during the course of the study. Males sang at their territory boundaries for at least one hour each morning from 1–2-m perches in shrubs, trees, or fences. As many as five males were observed counter-singing within a 1-ha area where several territories adjoined. Males were sometimes joined by females in territorial singing but usually sang alone while the female foraged, preened, or perched nearby. The male member of a pair was engaged in territorial singing in 97% of 60 cases in which the identity of the singer was known. Around the nest, however, females were more vocal (12 of 19 song bouts around the nest were by females). The song of both males and females was long, complex, and much more varied than those of *Malurus* fairy-wrens (for sonograms see Rowley and Russell 1997). The common features of most song types were short, staccato bursts followed by high-pitched notes and whistles.

SOCIAL ORGANIZATION AND BEHAVIOR

I monitored and recorded group composition for 18 groups in which all, or all but one, of the individuals were color banded. Mean group size, excluding juveniles, was 2.1 (range 2–3), and adult sex ratio was 0.95 (males:females). Fifteen groups were simple pairs, but three groups had additional members whose age and sex were not clear from field observations. Three of these additional birds were sexually immature, but a fourth had bright red plumage under the wing, indicating that it was an adult female. This individual was in a group containing a breeding male with an enlarged cloacal protuberance and a breeding female with a brood patch. It is likely that this additional female was an adult helper, though I never found the nest of this group and therefore never saw it feed at the nest.

Family groups spent most of their time foraging together. Dust-bathing and allopreening were other frequent group activities. I also observed the rodent run display (Rowley and Russell 1997) and a threat display similar to that described by Hutton (1991), in which an adult male erected feathers on his crown, nape, and throat to form a ring around his face. This display had a striking effect, as all the streaking around the head formed radiating lines and focused one's vision directly at the face.

BREEDING BIOLOGY

In 1996, the breeding season at Calperum Reserve probably lasted at least five months, from August to January. When I arrived in mid-September, some groups were already feeding young in the nest (implying that nesting had been initiated in late August), and

when I left in December there were still four active nests (three with eggs, one with nestlings). Females whose nests failed in early December were found rebuilding in mid-December, suggesting that the breeding season potentially extended into mid-January. Further, there was no decrease in cloacal protuberance volume in males during the study (see below).

Six of 14 nests (43%) successfully fledged at least one young, three (22%) were depredated, two (14%) were abandoned during incubation, and three (22%) had unknown fates because the female was still incubating when I left. All three predations occurred during the nestling stage. Considering only those nests in which at least one egg was laid and the fate was known, the average clutch size was 2.2 ± 0.4 eggs (range 1–3, $n = 6$ nests), and an average of 1.1 ± 1.1 young fledged per nesting effort (range 0–3, $n = 11$ nests).

Incubation did not begin until the last egg was laid, and eggs hatched on the same morning 14 to 19 days after the last egg was laid ($n = 2$ nests). Females usually incubated eggs; no males had brood patches, but on one occasion I flushed a male off a nest with eggs on it. Males often fed females on and off the nest with insects and seeds. Incubation bouts usually lasted 45–90 min, interspersed with 30–60-min foraging bouts.

I quantified provisioning rates for 937 min over the course of six days (26 November–2 December) at a single nest with two nestlings in it. The nest was tended by one adult male and one adult female. There was no difference between the feeding rate of the male and female (2.0 ± 0.1 feeds hr^{-1} vs. 2.3 ± 1.5 feeds hr^{-1}, $P > 0.3$) nor the brooding rate of the male and female (3.9 ± 0.7 min hr^{-1} vs. 5.4 min hr^{-1}, $P > 0.3$). Insects were the most commonly identified food item. At this one nest, the duration of the nestling stage was 14 days, and the two young fledged within 20 min of each other at midday.

Young were completely dependent when they fledged, and remained hidden less than 25 m from the nest in spinifex or some other shrub for the first week after fledging. Although extremely cryptic, recently fledged young were highly vocal, and their high-pitched calls were audible to the human ear from more than 40 m. After one week, although still dependent and largely hidden, the young began to range more widely. By 25 days, the young were seen feeding themselves and were mostly independent, though the female continued to provide some food for another two weeks.

Seventeen nests were located in spinifex, usually in older and larger clumps with an average volume of 0.3 ± 0.02 m^3. Most nests were located on sandy dunes and were cryptic. The mean nest height was 26.2 ± 12.0 cm. The orientation of the nests was random with respect to the cardinal directions.

CLOACAL PROTUBERANCES AND SPERM PRODUCTION

Cloacal protuberances averaged 120.3 ± 48.1 mm^3 ($n = 28$ males, range 40–197 mm^3). An average of 8.3 ± 9.7 × 10^6 sperm was collected from each male sampled ($n = 9$ males, range 0.2–30.6 × 10^6), and the average concentration of sperm was 4.5 ± 6.0 × 10^6 per μl ($n = 9$ males, range 1.0–14.9 × 10^6).

There was no relationship between cloacal protuberance volume and time of day ($r^2 = 0.004$, $P > 0.7$) or the date the measure was taken ($r^2 = 0.001$, $P = 0.6$). Nor was there a relationship between male body mass and volume of the cloacal protuberance, or between body mass and concentration or volume of sperm collected. There also was no relationship between volume of cloacal protuberance and concentration or total volume of sperm gathered. Finally, there was no relationship between the total volume of sperm and concentration of sperm for each male (all $P > 0.2$).

DISCUSSION

SOCIAL ORGANIZATION AND BREEDING BIOLOGY

This study provides the first account of the mating system and social organization of the Striated Grasswren. In the population I studied, grasswrens formed simple breeding pairs and adult helpers were rare. Only one of 18 groups had more than two confirmed adults and I never witnessed more than two adults feeding nestlings or fledglings. Likewise, previous reports of the Striated Grasswren mention only pairs of adults, with no evidence of adult helpers (Izzard et al. 1973, Miller 1973). In most species in the family Maluridae, however, three or more adults have been seen provisioning a single nest (Rowley and Russell 1997), including the two other species of grasswren which have been studied in any detail, the White-throated Grasswren (*A. woodwardi*) and the Thick-billed Grasswren (*A. textilis*). The White-throated Grasswren was observed mainly in pairs during the breeding season, but a small number of larger groups were recorded and three adults were seen feeding at one nest (Noske 1992). Similarly, most groups of a color-banded population of Thick-billed Grasswrens were simple pairs, but in one group three adults were observed feeding at a single nest (Brooker 1988). In general, helping behavior appears to be present in low levels in grasswren species studied to date.

The 1996 breeding season probably extended into January despite previous reports that breeding in South Australia is usually completed in November (Schodde 1982, Rowley and Russell 1997). Annual rainfall in 1996 (251 mm), however, was slightly below the yearly average (259 mm). Further, rainfall totals in the months of October (23 mm), November (13 mm) and December (3 mm) were well below average (28, 21, and 18 mm, respectively) (Australian Government Bureau of Meteorology, unpubl. data). Because grasswrens are thought to breed in relation to rainfall (Rowley and Russell 1997), the probable extension of nesting into January despite relatively low rainfall levels indicates that the breeding season may normally extend later than has previously been thought.

The feeding rate I recorded at a single nest with two nestlings (male and female combined averaged 4.3 feeds per hr) is low compared to other malurids with similar-aged nestlings (8–14 days; Pruett-Jones, unpubl. data; Karubian, unpubl. data). However, observation of a single Striated Grasswren nest in New South Wales with two 10-day-old nestlings revealed a similar rate of 3–4 feeds per hr (Howard and Howard 1984).

Song is highly elaborated in Striated Grasswrens.

Both males and females have surprisingly variable vocal repertoires, and males spend considerable amounts of time singing from territory boundaries each day. Both Schodde (1982) and Rowley and Russell (1997) have discussed the range of grasswren vocalizations, and I also was struck by their vocal lability. Fairy-wrens, conversely, have relatively stereotyped song with little variation within or among individuals. It may be that song has evolved as the most important display for Striated Grasswrens, perhaps in response to the open environment in which grasswrens live, in which conspicuous plumage could incur a predation risk (Rowley and Russell 1997).

TERRITORIALITY, HABITAT USE, AND CONSERVATION

Striated Grasswrens were highly territorial, and song was the main territorial display. The density I recorded (0.5 birds ha^{-1}) lies between those recorded for other grasswren species. In the Northern Territory, Noske (1992) recorded a density of 0.08 White-throated Grasswrens per hectare, with an average territory size of 10 ha and a smallest territory of 7 ha. In Western Australia, Brooker (1988) reported 2.2–2.8 Thick-billed Grasswrens per hectare.

Birds showed a marked preference for sandy soil with high densities of spinifex. Individuals used spinifex as a food source (both seeds and insects), for shelter, and as a nesting substrate, and every territory contained some area with sandy soil and spinifex where the birds spent most of their time. Other reports of the Striated Grasswren invariably mention the presence of mature spinifex (e.g., Izzard 1973, Schodde 1982, Rowley and Russell 1997), and it appears that spinifex is a habitat requirement for the Striated Grasswren. The White-throated Grasswren (Noske 1992) shows a similar dependence on spinifex, although the Thick-billed Grasswren (Brooker 1988) does not. Spinifex-dominated habitat is still widespread across Australia but is threatened by clearing, burning, and livestock.

The preference Striated Grasswrens display for spinifex is coupled with a highly terrestrial lifestyle. I rarely saw an individual fly more than a few meters at a time, and all the birds I caught in mist nets were caught within a few centimeters of the ground. Even when ascending to a perch a few meters off the ground, birds usually hopped from branch to branch rather than flying up. This apparent unwillingness to fly makes it difficult to imagine an individual dispersing over areas of unsuitable habitat larger than a few km.

The combination of relatively specific habitat preferences and probably poor dispersal ability indicate that habitat fragmentation is a serious threat to the conservation of the Striated Grasswren. Although it has the largest range of any grasswren species, it is fragmented into isolated populations, and two of its subspecies are potentially threatened (Rowley and Russell 1997). Habitat loss and fragmentation is a threat of varying severity to most *Amytornis* species (Noske 1992, Rowley and Russell 1997).

SPERM COMPETITION

Sperm competition occurs whenever females mate with more than one male during the span of a single breeding attempt. Because sperm production is tightly correlated with levels of sexual promiscuity in birds (Birkhead et al. 1993, Møller and Briskie 1995), it can be used as a general indicator of the level of promiscuity exhibited by a particular species. The Striated Grasswren produces very little sperm compared to other Maluridae for which data are available. Three species of fairy-wren (*Malurus splendens, M. lamberti,* and *M. leucopterus*), each of which weighs roughly one-half as much as the Striated Grasswren, produced on average three to four orders of magnitude more sperm per ejaculate sample than did Striated Grasswrens sampled by the same investigator using identical methods (Tuttle et al. 1996).

Cloacal protuberance size is also positively correlated with intensity of sperm competition (Birkhead 1993). Although the presence of a cloacal protuberance does imply some low level of sperm competition, the Striated Grasswren has a relatively small cloacal protuberance. In two surveys of 80 species (Birkhead et al. 1993, Briskie 1993), only 17 species (21%) had cloacal protuberances smaller than that of the Striated Grasswren. All 17 of these species weighed less than the Striated Grasswren. The small cloacal protuberances and low volumes and concentrations of sperm produced by the Striated Grasswren suggest relatively little sexual promiscuity.

Based on this study, the Striated Grasswren appears to be a socially monogamous species with low levels of cooperative breeding. The social monogamy seems to be complemented by low levels of sexual promiscuity, as inferred from common indices which indicate very low sperm competition between males. The breeding season extended longer than was previously believed. Density of adults was intermediate for that reported for other grasswren species and territories were restricted to areas containing spinifex. This dependency on a particular habitat type, in conjunction with seemingly poor dispersal ability, makes the Striated Grasswren especially vulnerable to habitat loss.

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