

## Breeding ecology and bias in offspring sex ratio in little grassbirds (*Megalurus gramineus*)

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### Abstract

Little grassbirds (*Megalurus gramineus*) are small, sexually monomorphic passerines that live in reed beds, lignum swamps and salt marshes in southern Australia. The breeding biology and patterns of sex allocation of the little grassbird were investigated over a single breeding season. Our observations of this species in the Edithvale Wetland Reserve revealed a highly male-biased population sex ratio, with some breeding territories containing several additional males. Nevertheless, there was little compelling evidence that little grassbirds breed cooperatively. The growth rates of male and female nestlings were similar and, as predicted by theory, there was no overall primary sex ratio bias. However, the primary sex ratio was female-biased early in the breeding season and became increasingly male-biased later in the breeding season.

### Introduction

Patterns of sex allocation in birds have been investigated in either sexually dimorphic species, since they allow easy differentiation between the sexes (e.g. Richter 1983; Weatherhead and Teather 1991; Webster 1992; Anderson *et al.* 1993; Sheldon 1999), or species that have unusual mating or social systems, both factors that may cause biased primary sex ratios (e.g. Hasselquist and Kempenaers 2002; Komdeur and Pen 2002). Nevertheless, Gowaty and Droge (1991) provide compelling reasons to investigate the sex ratios of sexually monomorphic species, since they are likely to provide further comparative insights into why birds of some species manipulate the primary sex ratio of their offspring. However, these studies are difficult, not least because the sex of hatchlings of monomorphic species cannot be identified visually. This problem has been largely resolved by molecular techniques (e.g. Griffiths *et al.* 1996; Lessells and Mateman 1996) that allow monomorphic adults, hatchlings and embryos to be sexed. It is now possible to distinguish between the survival of hatchlings from the variation in the primary sex ratio (Lessells and Mateman 1996; Ellegren and Sheldon 1997; Gowaty 1997).

The little grassbird (*Megalurus gramineus*) is a small passerine (140 mm, including a 60-mm tail) from the Old World warbler family Sylviidae, subfamily Megalurinae. These sexually monomorphic little brown birds live in reed beds, lignum swamps and salt marshes in southern Australia (Frith 1983; Blakers *et al.* 1984; Cayley 1984). The biology of this species is poorly understood, primarily because of its highly cryptic behaviour, and most of our knowledge is derived from anecdotal accounts. Nevertheless, little grassbirds are believed to be resident throughout the year, although seasonal local movement has been recorded between swamps in dry areas (Frith 1983). Records from a few inland sites show

that little grassbirds can move over long distances (Frith 1983). Little grassbirds are assumed to be socially monogamous with no cooperative breeding (MacDonald 1973), but there have been no studies of individually marked and identifiable individuals. This study describes the breeding ecology of little grassbirds, with particular emphasis on their breeding system and patterns of sex allocation.

## Materials and Methods

### *Study site and general methods*

Data were collected from a population of little grassbirds at the Edithvale Wetlands, Melbourne, between July 1997 and February 1998 during the breeding season. Very little is known about the natural history of this species. For this population, the breeding season was defined from the time nests were first located until the time when new nesting sites were no longer located. Field-work ceased when non-banded birds were few, and nests were no longer located. The Edithvale Wetlands consist of 100 ha of rehabilitated wetlands, with common reed (*Phragmites australis*), the narrow-leaved cumbungi (*Typha domingensis*) and ryegrass (*Lolium* sp.) as the dominant vegetation forms surrounding the water (Donnelly *et al.* 1985). Melbourne Water manages the site and public access is restricted.

Little grassbirds were caught using 9-m mist nets (10 mm<sup>2</sup> mesh) that were set throughout the wetland and all the various vegetation types. Nets were also set among vegetation, around the outside perimeter of the wetland, the internal perimeter of the wetland, and at nest sites. In some instances, the birds were flushed from the vegetation into the nets. Captured birds were individually identified using coloured plastic bands and a uniquely numbered aluminium band. The aluminium band was placed around the right tarsus, in accordance with the Australian Bird Banding Scheme, and a unique combination of two coloured bands was placed on the left tarsus to facilitate individual identification. Tarsi and bill lengths (in millimetres, using Vernier callipers), wings (in millimetres, using stop ruler) and mass (in grams, using spring balance), were measured and recorded for each bird at the time of each capture.

### *Breeding biology*

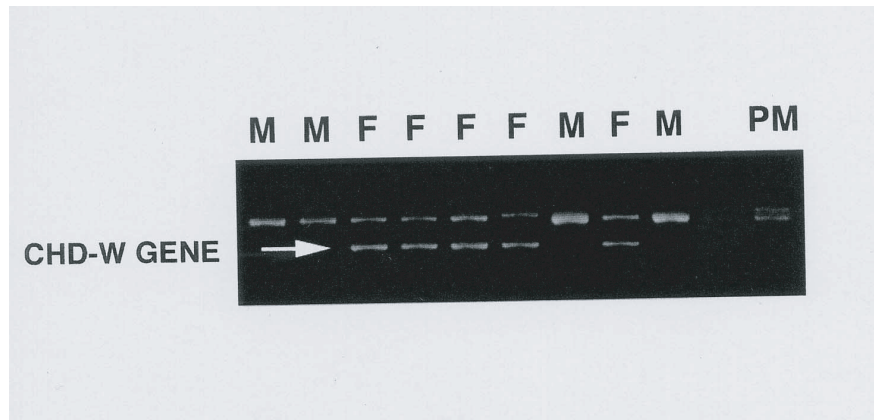
Potential territory locations and the individuals maintained in these areas were determined by capture and recapture data, as were the presence of floaters. Floaters were defined as individuals that were captured at various locations around the field site and that apparently had no fixed territory.

Nests were located by searching through the wetland vegetation. Located nests were censused once a week for eggs until eggs were laid, then approximately every second day until the date of hatching. Nests were approached cautiously in order to minimise the chance of leading possible predators to nests, and false trails were created to minimise the impact of depredation after nests were located. Eggs were labeled with permanent marker and their length and breadth (in millimetres, using vernier callipers) and weight (in grams, using a spring balance) measured, both when they were first located and when the clutch was completed. Egg volumes were calculated using the length ( $L$ ) and breadth ( $B$ ), using the equation  $V = 0.52LB^2$  (Preston 1974; Hoyt 1979). The time between when an egg was laid and when it subsequently hatched was obtained from the eggs of five nests. Initially, nests were checked every day in order to monitor the laying sequence and the subsequent hatching sequence of the eggs. This procedure apparently caused some disturbance to the parents and was not continued in order to reduce the likelihood of the nest being abandoned.

The breeding system of the little grassbird was determined from video recordings of individual feeding adults and the presence/absence of adults additional to the breeding pair. Three separate 60-min video recordings were obtained for each nest between Days 5 and 14 after hatching. The tarsi of nestlings were marked with indelible markers to ensure individual identification. To determine the growth rates of nestlings, biometric parameters (bill, wing, tarsus and mass) were measured every second day after hatching, and every day from Day 10 to 14 until fledging. Fledgling mass was defined as the mass taken within a 24-h period of the nestling leaving the nest. Nestlings were metal banded and colour banded after Day 7.

### *Sex determination*

Blood samples (approximately 50 µL) were obtained through puncture of the brachial vein (wing) of adults and nestlings older than 10 days, and from the leg vein of nestlings that were younger than 10 days. Blood samples were stored in 100% ethanol before genomic DNA was extracted for sexing. The sex ratio of the



**Fig. 1.** Male and female PCR products from genomic DNA of the little grassbird showing four typical male band patterns, the single bands (M), and an individual single-polymorphic male band pattern, the double band (PM). Five female band patterns showing broadly spaced double bands are also present (F), displaying the CHD-W gene on the female-specific W-chromosome.

population was determined from the genomic DNA of captured birds. To determine the primary sex ratio of each clutch, blood was collected from each nestling shortly after hatching. Un-hatched eggs were collected, as were the eggs of clutches that had been abandoned. Many of the eggs collected could not be sexed as they were unfertilised, or the DNA was quite degraded due to the age of the egg. Clutches in which eggs failed to hatch or could not be sexed were not included in the primary sex ratio analysis.

A phenol–chloroform extraction was conducted on digested blood and the extracted DNA precipitated with ethanol. Sexing was conducted with the avian sex-specific primers P8F (10  $\mu$ M) and P2R (10  $\mu$ M) using Polymerase Chain Reaction (PCR) analysis following Griffiths *et al.* (1996). PCR samples (15  $\mu$ L) were loaded onto a 3% agarose gel and were examined under UV light after being stained with ethidium bromide. Gels were then photographed using a Polaroid camera (DS34, Direct Screen Instant) and black and white film (Polaroid 667, positive).

The molecular sexing technique developed by Griffiths *et al.* (1996) had not previously been used to determine the sex of little grassbirds, and therefore the procedure had to be fully validated. Typically, the males of many bird species have a single-band pattern (Griffiths *et al.* 1996). Approximately 50% of male little grassbirds had this typical male band pattern, while the rest showed two distinct bands. Five breeding pairs were sexed to confirm that the male double band is a male polymorphic Z-product. Three pairs showed the characteristic female band pattern and the typical male band pattern, while two pairs showed the characteristic female band pattern and the male polymorphic Z-product (Fig. 1). This polymorphic Z-product has also been found in 4 species of male auklets (Dawson *et al.* 2001).

#### Statistical analyses

Growth curves of individual male and female nestlings were analysed using mean nestling mass with age of repeatedly measured nestling (ANCOVA). The difference between growth of males and females was analysed by comparing the slopes of the growth curve ( $r$ ) of each male and female over time using a  $t$ -test. Each point in the growth curve is an independent nestling, so there is no pseudoreplication.

Mass differences between male and female fledglings were analysed to control for parental effects, by first calculating a mean male and mean female weight for each clutch. Any difference in male and female fledgling mass was then examined by comparing the mean of all the male means with the mean of all the female means across these clutches using a  $t$ -test.

The effect of time of the season on brood sex ratio was examined using a binomial response model (Mlwin 1.1: Rasbash *et al.* 2000). Brood sex ratio (number of males over brood size) was defined as the binomial response variable (with the number of chicks in each brood as the denominator) with day of the season as the only explanatory variable. Significance was assessed from the  $t$ -value for day of the season. No clutches used for these analyses were produced by the same breeding birds more than once. Unless otherwise stated, values are means  $\pm$  standard error.

## Results

Adult male and female little grassbirds are indistinguishable to the human eye, with no apparent sexual differences. Nevertheless, males were significantly larger for all measured body parameters except the bill (Table 1).

A significantly higher proportion of males than females were caught in the population (42 males, 23 females:  $\chi^2 = 5.55$ ,  $P = 0.018$ ). Capture/recapture data indicated that territories may exist (Table 2), with groups (defined as birds caught at the same location) comprising up to nine individuals. These groups consisted of only one or two females and up to eight males (Table 3).

### *Breeding ecology*

The first active nest was sighted in early October 1997, and breeding continued until late January 1998. Little grassbirds nested in both dense and sparse vegetation. Nests were

**Table 1. Differences in various body measurements between male and female little grassbirds**  
Values are means  $\pm$  s.e.

Body parameter	Male		Female		<i>t</i>	<i>P</i>
	Mean	<i>N</i>	Mean	<i>N</i>		
Bill	14.03 $\pm$ 0.32	43	14.32 $\pm$ 0.19	23	0.798	0.428
Mass	13.90 $\pm$ 0.36	41	12.61 $\pm$ 0.42	24	-3.561	0.001
Tarsi	20.81 $\pm$ 0.12	43	19.63 $\pm$ 0.10	24	-7.521	0.001
Wing	57.46 $\pm$ 0.37	41	54.96 $\pm$ 0.34	23	-4.958	0.001

**Table 2. Recapture frequency of male and female little grassbirds**

Capture frequency	Males	Females	Locality
1	30	17	Single location
2	4	3	Single location
3	0	0	
4	4	1	Varied locations
5	1	0	Varied locations

**Table 3. Frequency distribution of groups of little grassbirds comprising different numbers of males and females**

Group composition		Frequency
Males	Females	
1	0	1
1	1	4
1	2	1
2	0	2
2	1	3
2	2	1
3	0	1
3	1	3
3	2	1
5	1	1
5	2	1
8	1	1

**Table 4. Hatching order and the mass and volume of the eggs of little grassbirds**Values are means  $\pm$  s.e.

	Hatching order				
	1	2	3	4	5
No. of clutches	13	15	15	8	1
Egg mass (g)	1.72 $\pm$ 0.06	1.65 $\pm$ 0.05	1.61 $\pm$ 0.05	1.48 $\pm$ 0.09	1.33
Egg volume (mm <sup>3</sup> )	1.80 $\pm$ 0.03	1.74 $\pm$ 0.04	1.71 $\pm$ 0.04	1.66 $\pm$ 0.03	1.59

found in a variety of plant species, including coast tea-tree (*Leptospermum laevigatum*), blackberry (*Rubus fruticosus*), common reed (*Phragmites australis*), and narrow-leaved cumbungi (*Typha domingensis*). Nests were built up to 1.5 m above the ground or water, in the centre and around the perimeter of vegetation clumps, with no distinct pattern observed.

The nest was a woven cup with a dome of darkly coloured feathers, typically of the purple swamphen (*Porphyrio porphyrio*), over the top. This feather cover may provide insulation to the nestlings, and camouflage against predators. The eggs were pale pink with a darkly speckled base, and were often sparsely speckled all over. Female little grassbirds laid 2–5 eggs, but 14 clutches ( $n = 19$  clutches) consisted of three or four eggs (mean = 4.75, s.d. = 2.75). The mean incubation period for an individual egg was  $8.56 \pm 0.31$  days (s.d. = 1.278,  $n = 17$  eggs from five nests).

Individuals involved in provisioning food to nestlings could be identified by their coloured leg bands for only five of the nine groups that had been subject to video recordings. There was no indication of cooperative breeding. In one group, comprising a male and a female, only the female fed the nestlings. Both the male and female fed the nestlings in two groups that comprised the breeding pair only, and in two groups that comprised the breeding pair and additional individuals.

For the entire breeding season, 63 eggs and 28 young were sampled from 23 nests. Of these eggs, 28 hatched and 20 reached fledging. Of a total of 23 nests, 4 were abandoned, 10 were depredated, and 8 successfully fledged. Two predation events were observed (one involving a red fox, *Vulpes vulpes*, and the other involving ravens, *Corvus* sp.), and rats (*Rattus* sp.) were common at the study site and are also likely potential predators.

Consecutively laid eggs typically decreased in size (Table 4). The volume of eggs declined significantly with the laying order of the first three eggs (repeated-measures ANOVA: Eggs 1–3,  $F_{2,16} = 6.52$ ,  $P = 0.009$ ), but the mass of eggs did not (repeated-measures ANOVA: Eggs 1–3,  $F_{2,16} = 1.88$ ,  $P = 0.091$ ). Data for the fourth and fifth eggs were excluded from these analyses because of their small sample sizes. There was no significant difference between the volume of male and female eggs (male mean =  $1.83 \pm 0.15$ ,  $n = 11$ ; female mean =  $1.70 \pm 0.08$ ,  $n = 6$ ;  $t_{15} = -1.69$ ,  $P = 0.142$ ), or the mass of male and female eggs (male mean =  $1.73 \pm 0.20$ ,  $n = 11$ ; female mean =  $1.54 \pm 0.15$ ,  $n = 6$ ;  $t_{15} = -1.58$ ,  $P = 0.172$ ).

The nestling period occurred over 10–14 days. Growth curves were similar for male and female nestlings (male:  $r^2 = 0.922$ ,  $P = 0.664$ ,  $n = 11$ ; female:  $r^2 = 0.979$ ,  $P = 0.815$ ,  $n = 9$ ) (Fig. 2). Comparison of the mean nestling mass with age of repeatedly measured nestlings revealed no differences in the individual growth curves between males and females (repeated-measures ANCOVA:  $F_{9,5} = 0.53$ ,  $P = 0.481$ ). There was no difference in the slope of the growth curves between male and female nestlings ( $t = 1.10$ ,  $P = 0.295$ ).

There was a general trend for the third hatched nestling ( $n = 2$ ) to fledge at a younger age and at a lower weight than the first hatched nestling ( $n = 6$ ) and the second hatched

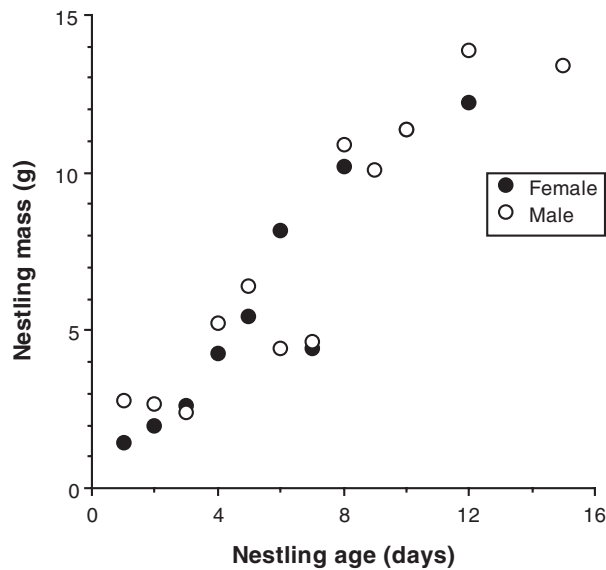


Fig. 2. The growth curves of male and female little grassbird nestlings, from hatching (Day 1) to fledgling (Days 10–15).

Table 5. Hatching order, group size and mean sex ratio of little grassbird nestlings

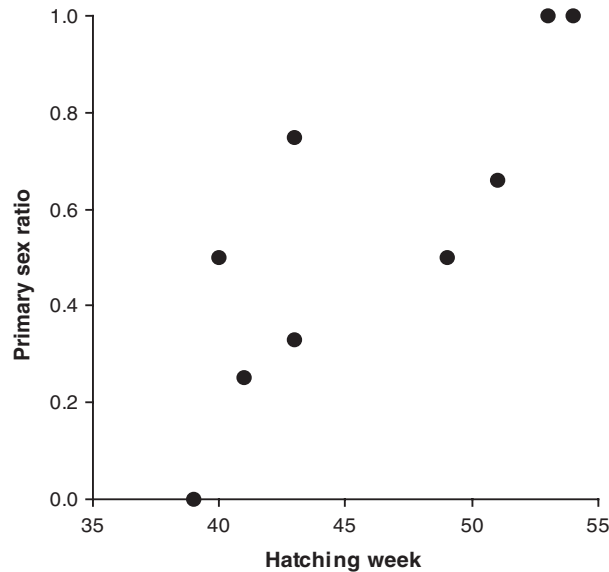
	Hatching order		Number of adults in the group	
	Chick 1 & 2	Chick 3 (& 4)	2	>2
Mean $\pm$ s.e.	0.38 $\pm$ 0.35	0.43 $\pm$ 0.45	0.25 $\pm$ 0.29	0.75 $\pm$ 0.35
No. of clutches	8	7	6	2

nestling ( $n = 4$ ). All nestlings within a clutch fledged within a day or two of each other. There was no difference in mean fledgling weight (grams) of all male and female fledglings when controlled for within-clutch effects (male:  $11.15 \pm 0.52$ ,  $n = 4$  clutches; female:  $11.23 \pm 0.50$ ,  $n = 7$  clutches;  $t = -0.102$ ,  $P = 0.921$ ). There were no within-clutch effects on mean fledging mass of males and females within the same nest (male mean =  $11.15 \pm 1.04$  g, female mean =  $10.87 \pm 1.29$  g) (matched-pairs  $t$ -test:  $P = 0.632$ ,  $n = 4$ ). There was no significant seasonal (hatching week) effect of mean fledgling weight of the sexes combined ( $r^2 = 0.049$ ,  $n = 11$ ,  $P = 0.78$ ).

#### Offspring sex ratios

The sex ratio was not influenced by any 'within-clutch' effects (Table 5). The sex ratio of the first two hatched nestlings and the sex ratio of the last two hatched nestlings were not influenced by hatching order ( $r^2 = 0.03$ ,  $n = 8$ ,  $P = 0.90$ ), hatching week ( $r^2 = 0.36$ ,  $n = 8$ ,  $P = 0.10$ ), or adult group size ( $r^2 = 0.37$ ,  $n = 8$ ,  $P = 0.10$ ). These tests may, however, lack statistical power.

The primary sex ratio from nine independent nests was 0.65 (17 males, 13 females) and did not differ from 0.5 (exact binomial probability = 0.111). However, there was considerable variation in the sex ratio between individual clutches, and this variation was explained by the time of the breeding season (binominal response model:  $t_8 = 2.31$ ,



**Fig. 3.** Changes in primary sex ratio with time of year in the little grassbird. Hatching week commences on 1 January 1997, and sex ratio is the proportion of males in the clutch.

$P = 0.025$ ) (Fig. 3). Females produced clutches with a higher proportion of daughters early in the breeding season, and then produced clutches with a higher proportion of sons later in the season. These data contain no pseudoreplications; no two clutches in the sample of nine were produced by the same breeding pair. There was no correlation between sex of the offspring and the hatching order within each clutch ( $r^2 = 0.05$ ,  $n = 8$ ,  $P = 0.882$ ), or the number of birds in a group ( $r^2 = 0.12$ ,  $n = 8$ ,  $P = 0.761$ ).

There was no bias in the secondary sex ratio of fledglings, which consisted of nine males and ten females (fledgling sex ratio = 0.53,  $\chi^2 = 0.05$ ,  $P = 0.251$ ). There was also no evidence of sex-related differences in nestling mortality (female median = 0.83, male median = 0.75,  $n = 6$  nests; Wilcoxon  $Z = 0.447$ ,  $P = 0.655$ ).

### Discussion

Little grassbirds breed in male–female pairs, and no additional helpers at the nest were observed in this population. The demographic information obtained from the Edithvale Wetland shows that there was almost double the number of males in the population than females. Field observations of aggressive interactions between birds, and capture/recapture data, supported the identification of breeding territories in this population. Some breeding territories contained several extra males, while others contained only the breeding pair. Cooperative breeding occurs where individuals (helpers) forego breeding to assist in the care of another pair's brood (Greenwood and Harvey 1982; Brown 1987; Koenig *et al.* 1992). In addition to brood care, helping behaviour of the philopatric (non-dispersing) sex may involve territory defense (Emlen 1982; Curry 1988; Veltman 1989; Poiani 1994). The 'extra' little grassbird males did not help at the nests of the territories they shared, although it is not known whether they assist with territory defense. Thus, there is little evidence that little grassbirds breed cooperatively. Perhaps the additional males obtain fitness benefits by remaining in the group through extra-pair fertilisations.

Breeding pairs nested in variable vegetation types, with repeated breeding attempts if clutches were depredated or unsuccessful. The variety in vegetation chosen as nesting sites, including the introduced blackberry, displays a high degree of flexibility. Foxes and ravens may be responsible for the high level of depredation (43%) in this study.

The primary sex ratio of the offspring of the little grassbird did not differ from parity, as predicted for a species with equal parental investment in both male and female offspring (Fisher 1930; Hamilton 1967; Charnov 1982; Clutton-Brock *et al.* 1985). Surprisingly, the primary sex ratio did vary between clutches and this could be explained by the date in breeding season. Little grassbirds produced more female nestlings early in the breeding season, and more male nestlings later in the breeding season. There was no differential mortality of male or female nestlings, and the comparable growth curves and fledging weights suggests no differential costs of production.

Such seasonal variations in the offspring sex ratio have been observed in sexually dimorphic birds, but not in a sexually monomorphic passerine. For example, male-biased offspring sex ratios earlier in the season have been reported in Harris' hawk (*Parabuteo unicinctus*) (Bednartz and Hayden 1991) and American kestrels (*Falco sparverius paulus*) (Smallwood and Smallwood 1998), while in marsh harriers (*Circus aerinosus*) the offspring sex ratio is male-biased later in the season (Zijlstra *et al.* 1992). The change in sex ratio in Harris' hawks involves sequential clutches, where the sex ratio of the first clutch is biased toward males and the offspring in this first clutch are larger than those in subsequent clutches. In contrast with little grassbirds, both marsh harriers and American kestrels are sexually dimorphic, which may influence the facultative adjustment of sex ratios.

The seasonal bias in the sex ratio in the little grassbird may be a response to differential dispersal strategies of males and females. If males and females have different dispersal strategies, a female should adjust the sex ratio of her offspring to limit local resource competition for reproductive resources (Trivers and Willard 1973; Bulmer and Taylor 1980; Taylor 1994). This seasonal bias in the sex ratio may also be due to differential maturation times between the sexes. For example, females may benefit by dispersing early in the season if their reproductive success is increased, perhaps by having more time to locate breeding territories or more time to reach sexual maturation. In contrast, males may benefit by remaining in their natal territory when mating opportunities are limited or when there is limited habitat available into which they can disperse (Pruett-Jones and Lewis 1990). However, this study is based on a single breeding season and we require data from more breeding seasons and other aspects of the breeding biology to confirm and explain this pattern. Nevertheless, these data indicate that this monomorphic, socially monogamous, little brown bird is more interesting than previously thought.

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