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First Documented Cases of Polygyny in the Grasshopper Sparrow

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ABSTRACT.—We studied the breeding biology of Grasshopper Sparrows (*Ammodramus savannarum*) on restored grasslands in Maryland from 1999 to present. We report the first documented cases of social polygyny in this species. Polygyny increased reproductive success for males in two of four cases, but its rarity suggests it is only a facultative behavior for this usually socially monogamous species *Received 31 January 2009. Accepted 3 June 2009.*

Social polygyny is a mating system in which males pair bond with, frequently control, or gain access to two or more females simultaneously (Gill 2007). Seventy-one species of passerine birds (26%) within the United States and Canada have been reported to exhibit some form of social polygyny (Ford 1996, Hanley et al. 2007), although within most of these species polygyny seems to be the exception rather than the norm. Ford (1983) lists

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29 species where polygyny is rare often with only one documented case, 14 species with polygyny rates of up to 20%, and 14 species with polygyny rates usually >20%. Social polygyny requires enduring behavioral association of a male with two or more females during a breeding episode.

The Grasshopper Sparrow (*Ammodramus savannarum*) has a wide distribution across much of North America and southern Canada (Vickery 1996), and is common in some midwestern prairies. However, populations in the east including Maryland have been declining (Holmes 1996, Sauer et al. 2008). All previous literature, to our knowledge, asserts the Grasshopper Sparrow is socially monogamous. Vickery (1996) expected occasional polygyny by Grasshopper Sparrows may occur, but none has been reported until now.

METHODS

We conducted demographic studies of grassland birds with an emphasis on Grasshopper Sparrows starting in 1999 on 92.4 ha of restored mid-Atlantic grasslands at the Chester River Field Research Center (CRFRC) in Queen Anne's County, Maryland, USA (39° 23′ N, 76° 00′ W), an area previously described by Gill et al. (2006). These experimental native grasslands were enrolled in the U.S. Department of Agriculture's Conservation Practice 2 program and were established to provide critical habitat for listed species of special concern; they were quickly colonized by several species of grassland specialists including the Grasshopper Sparrow. All adult Grasshopper Sparrows were banded with a U.S. Geological Survey aluminum band and a unique combination of colored plastic bands. Nest searching and territory mapping were conducted daily from April through August. Parentage of each nest was confirmed by flushing the female off the nest into a mist net or by observing both parents bringing food to the nest; in many cases parents were observed bringing food repeatedly to the nest before assignment was given. Locations of nests and adults were recorded on Garmin 12XL global positioning systems (GPS) in the field and mapped on a computer using ArcGIS® (Environmental Systems Research Institute Inc. 2004) software. Territories were defined using only perches from which birds sang. Locations of all other behaviors including chipping, carrying food, foraging, perching, preening, or trilling were recorded with a GPS unit.

OBSERVATIONS

We found an average of 34 (range 9–67) Grasshopper Sparrow nests each year, a total of 337, and monitored an average of 109 territorial males on the restored CRFRC Grasslands each summer from 1999 to 2008. Grasshopper Sparrows in this area engaged in 1–3 sequential breeding episodes from late April to September each year. All but four of 337 males for which we found nests had only one female and attended one nest with her in a breeding episode. Of the 333 social monogamous nests we observed, the territorial male was seen feeding at only one nest; in these cases there were no observations of any socially monogamous male feeding two nests inside or outside his territory. Parents with food were extremely conspicuous when approaching the nest area: if an observer was near a nest the birds perched and chipped repeatedly with food in their bills. Once the observer left the area, the birds would go to the nest with food. We are confident these males were not feeding any additional nests as the feeding behaviors of parents are highly visible.

We report four cases of social polygyny where the males attended at least two nests simultaneously between 2004 and 2008. Three cases (A, B, and C) involved one male and two females; in the fourth case (D) a male may have had three females nesting simultaneously, but the third female could not be positively confirmed (Table 1). The four polygynous males ranged in age from 2 to >6 years. The average distance between the polygynous nests was 60.6 m; in two cases both nests were within 20 m (cases A and B) and two (cases C and D) were >90 m apart. One of two nests was outside the boundary of the males' observed territories in cases A and C, both nests were inside the boundary in case B and both nests were outside the boundary in case D. We confirmed all cases of polygyny with observations of the male feeding nestlings at both concurrent nests or, in one case (D), a male aggressively defending one nest area against other males while also feeding nestlings at the other nest. Each male defended one territory prior to egg laying, during nestling care and after the nestlings fledged, and was not seen singing outside of what we defined as their territory during this period. Male TBTX (abbreviated color-band combination) from case B was subsequently recorded singing outside of his territory and male YRMX from case C

TABLE 1. Characteristics of nests and territories held by Grasshopper Sparrows (GRSP) involved in polygyny on the CRFRC grasslands, Maryland.

Nests							Territories			
									Territory size	
Case	Male[a]	Year	Nest[b]	Nest fate[c]	In or out of territory	Distance apart (m)	# of territory points	# of non-territory points[d]	Area (ha)^2	Perimeter (m)
A	MRTX	2008	NF10GS6	F	Out	17.5	21	20 (c,f,g,z)	0.26	214
			NF10GS7	D	In					
B	TBTX	2004	NF4GS15	F	In	19	42	12 (c,z)	0.388	257
			NF4GS16	D	In					
C	YRMX	2004	NF8GS1	F	In	116	95	27 (c,g,p,t,z)	0.719	344
			NF8GS2	F	Out					
D[e]	OBKX	2007	NF11GS2	F	Out	90	21	10 (c,g,z)	0.282	240
			NF10GS2	F	Out					

[a] Abbreviated color combination of males. X is the federal aluminum band.
[b] N = nest, F# = field #, GS# = GRSP nest #.
[c] D = Depredation, F = Fledged.
[d] C = chipping, F = foraging, G = carrying food, Z = perched, P = preening, T= trill.
[e] The third suspected nest was not included as it could not be positively confirmed.

established a second territory, but in both cases this was well after all nests had fledged.

In case A, male MRTX was seen first singing on 5 May, the clutch completion date was 26 June for nest # 1 and 25 June for nest # 2, and he was last observed singing on 13 August. In case B, male TBTX was first seen singing on 23 April, clutch completion dates were 22 June for both nests #'s 1 and 2, and this male was last observed singing on 18 August. In case C, male YRMX was first seen singing on 19 May, clutch completion dates were 15 June for nest # 1 and 19 June for nest # 2, and he was last observed singing on 20 July. In case D, male OBKX was first seen singing on 1 May, clutch completion dates were 14 June for nest # 1 and 21 June for nest # 2, and he was last seen singing on 30 July (Table 1). Six of the nine nests fledged all nestlings successfully; the other three nests failed due to depredation.

We recorded as many waypoints as possible for all Grasshopper Sparrows on the CRFRC grasslands, but the number of waypoints per territory varied. The frequency and intensity of singing by males varied depending on the stage of the breeding episode. Males sang vigorously upon arrival, during territory establishment, female courtship, nest building, egg laying, and the early incubation period. Singing declined towards the end of incubation and almost no singing occurred during provisioning and fledging of the nestlings. Insufficient territory waypoints were obtained in some cases prior to provisioning and fledging of nestlings. The boundaries of those territories (as we perceived them) were probably smaller than the actual size. Nests, in some cases, were outside of the depicted territory boundaries.

DISCUSSION

Our observations of social polygyny document rare exceptions (0.37%) in this normally socially monogamous species. They are novel for the species and add Grasshopper Sparrows to the growing list of birds for which some social polygyny is now known (Ford 1983). Polyterritoriality, the concurrent holding of two or more disjunct territories (Ford 1996), has not been recorded in the CRFRC population of Grasshopper Sparrows. Males have defended two and sometimes three sequential territories in a breeding season, but have not held more than one concurrently. The observation that polygynous nests were outside the circumscribed boundaries of the males' recorded territories may be due, in part, to an inadequate number of territory waypoints. However, female Grasshopper Sparrows have a strong tendency to place their nests outside or at the edge of territory boundaries (DMS, unpubl. data).

That six of the nests in these four cases of polygyny were successful suggests that Grasshopper Sparrows have the capability of multiple breeding behaviors. We reject the ''deception hypothesis'' (von Haartman 1951, 1956; Alatalo et al. 1981; Hanley et al. 2007), i.e., the mating status of a polygynous male is unknown to the females mating with him. First, the hypothesis specifies the males are polyterritorial, a behavior we have not observed. Second, the proximity of nests in cases A and B (17.5 and 19 m,

respectively) suggest that both females knew they were mated to the same male. It is possible the females were unaware of each other and of the polygynous behavior of the shared male at the nests that were >90 m apart, even though the nests were not separated by other male territories. Most female Grasshopper Sparrows display little aggression towards each other, even when nests were within 5 m of each other.

A second hypothesis of alternative adaptive mating behaviors is the polygyny threshold model (PTM) (Orians 1969), which suggests that females should engage in polygynous mating only if the benefit of mating with an already mated male outweighs the costs associated with such a mating (Verner 1964, Verner and Willson 1966, Hanley et al. 2007). Orians (1969) indicated the best strategy for a female is to mate with a male in the best quality habitat and to rear her young with or without his help, rather than find an unmated male with a territory in poor quality habitat. Our limited observations are insufficient to fully evaluate this hypothesis, but we are disinclined to apply it to our four cases. Conspicuous variation in habitat quality was generated by our experimental management protocols (prescribed burning, herbicide application, brush-hogging, and disking) within and between successive years. Thus, there appeared to be ample areas of high quality habitat for males to establish territories and less reason for females to pair with already mated males. Further, 99.6% of the breeding Grasshopper Sparrows remained socially monogamous. However, if both females at the close nests (17.5 and 19 m) knew they were sharing the same male even though there were unmated males holding territories elsewhere in the CRFRC grasslands, these instances may support the PTM. We have yet to identify the traits used in mate choice in these monomorphic sparrows. These four cases of social polygyny may represent a successful mating alternative to social monogamy, but more likely are only unusual opportunistic behaviors.

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