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OBSERVATION OF POLYANDRY IN ENDANGERED GREATER SAGE-GROUSE (*CENTROCERCUS UROPHASIANUS*) IN ALBERTA, CANADA

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Key words: Alberta, behavior, Canada, *Centrocercus urophasianus*, Greater Sage-Grouse, lek, lekking, mating, paternity

Greater Sage-Grouse (*Centrocercus urophasianus*; hereafter Sage-Grouse) are a polygynous galliform that inhabits the sagebrush steppe of western North America. Sage-Grouse are a lekking species in which males congregate on communal display grounds (leks) in the spring and females make multiple, lengthy visits to assess males before they mate once and raise young on their own (Johnsgard 1973; Wiley 1973; Gibson 1992, 1996). Depending on the location within the species range, males can begin displaying as early as the end of February and finish displaying in late May or early June (Eng 1963; Schroeder and others 1999; Aldridge 2000; Hausleitner 2003). In Alberta, males return to leks at the end of winter and start displaying in March before females arrive in early April (Aldridge 1998). While males spend months on leks, females spend a much shorter period of time visiting leks. Females are thought to visit a single lek over the period of 2 to 3 d and mate only once, presumably with a dominant male (Wiley 1973). Once most of the females have visited the leks and mated, yearling males arrive in late April and some obtain territories at the periphery of the lek (Aldridge 1998). Based on behavioral studies, only a few males are thought to obtain the majority of matings on a lek in a given breeding season (Scott 1942; Wiley 1973, 1978; Gibson and others 1991). Despite the short time period that leks are used by both sexes, they are a focal point for breeding and comprise a unique mating behavior.

In 2006, I observed and video-recorded the mating behavior of 3 Sage-Grouse leks in Alberta, Canada. These observations revealed

females mating with multiple males, and the 1st recorded instance of polyandry (a female mating with multiple males in a species without pair bonds) in Sage-Grouse in Alberta.

This study was conducted on Sage-Grouse from 3 leks in southeastern Alberta, Canada (Fig. 1; 4000 km²; Aldridge and Brigham 2001) as part of a larger study examining Sage-Grouse ecology, behavior, and genetics in Alberta. Birds of both sexes were captured using methods outlined in Bush and others (2011), and were fitted with a numbered metal leg band and a year-specific colored plastic leg band to allow for identification of individual birds.

In 2006, 8 leks were active and lek counts (maximum number of males counted in a morning) averaged 11 males (lek 2/24 = 1, lek 10/11 = 12, lek 16 = 25, lek 22 = 7, lek 30 = 18, lek 31C = 9, lek 34 = 11, lek 35 = 6). Leks were named in the order that they were discovered in Alberta and leks with 2 names, such as 2/24, represent the merger of 2 leks. Three focal leks (10/11, 16, and 34) were selected for behavioral observations on 12 mornings between 31 March and 26 April 2006. Observations were conducted from wooden blinds approximately 100 m from the center of the lek. The blind was entered before 1st light and exited after the last bird had left, so as not to disturb the lek. Video footage was taken using a Canon GL2 digital video camcorder once light levels were adequate for filming (after 06:30) until the birds left for the morning. Mating and behavior observations were made both manually (writing down observations as they occurred) and from observing the video footage. Males were identified based on their metal and plastic leg bands, location on the lek, and unique physical characteristics (such as missing feathers, injuries, etc.). Polyandrous behavior was only detected on lek 10/11 on 16 April 2006.

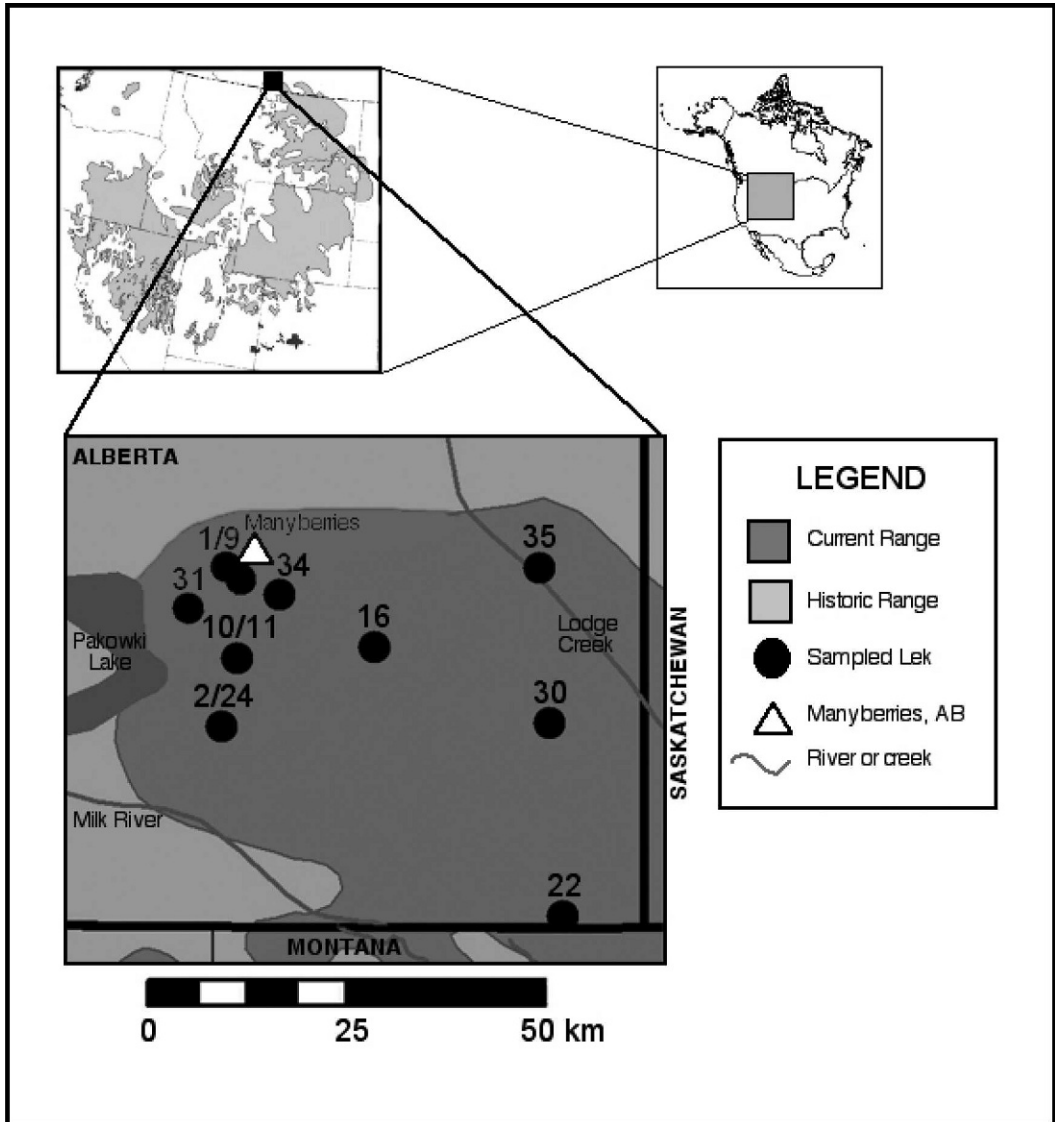


FIGURE 1. Map of the study area in Alberta, Canada with sampled Sage-Grouse leks highlighted.

On the morning of 16 April 2006, between 05:55 and 09:00 MST, 2 female Sage-Grouse were observed mating multiple times on lek 10/11 (Fig. 2). Male attendance for lek 10/11 varied between 9 males at 05:45 to a peak of 12 males at 07:50. Two males appeared to be dominant, occupying the center of the lek and defending it rigorously. Two females attended the lek that morning. Neither female was radiocollared or banded, but they were easily identifiable from one another. Female #1 was

a small slim female, possibly a yearling; female #2 was much larger.

Female #1 flew onto the lek at 05:55 and proceeded to walk around the lek. At 06:07, she mated with dominant male #1, which was disrupted by another male after approximately 5 s. Female #1 then walked to the center of the lek where she groomed, foraged, and observed the displaying males for about an hour and a half. During this time female #1 would run away from males if they approached and would



FIGURE 2. Photograph of Female #1 (right) and Female #2 (left) with 2 displaying males on Lek 10/11 in Alberta, Canada.

perform an action similar to a post-copulatory shake (female ruffled her feathers, shook her entire body, and then groomed herself). After 07:30 female #1 walked to the east periphery of the lek and mated with the most peripheral male at 07:40. This mating was disrupted by another peripheral male after approximately 3 s. For the next 15 min, female #1 walked around the lek and groomed herself. At 07:55, 07:57, and 08:00, female #1 mated with dominant male #1. None of the 3 copulations were disrupted. However, the first 2 instances involved dominant male #1 falling off of female #1 after 3 s and 4 s, respectively. At 08:29, dominant male #1 attempted to breed with female #1 for a 5th time, but dominant male #2 knocked dominant male #1 off of female #1 as soon as he attempted copulation. At 08:31, female #1 mated with dominant male #2 for 7 s with no interruptions and then slowly walked off of the lek while grooming and foraging.

Female #2 flew onto the lek at 07:50 and walked around the lek in the solicitation stance

(tail in the air, wings away from the body and pointed down, with the occasional wing flare). Her 1st mating occurred at 08:05 with dominant male #2. This was disrupted by dominant male #1 after about 3 s. At 08:09, dominant male #2 attempted to copulate with female #2, but male #1 disrupted the mating attempt as soon as it was initiated. Female #2 mated with dominant male #2 at 08:10 with no interruption for 5 s. For the next 20 min she groomed and foraged. At 08:31, female #2 mated with dominant male #2 for 4 s then slowly walked off of the lek.

The 2 females had no interaction with each other on the lek. Female #1 spent most of her time observing the males displaying, grooming, and foraging, while female #2 spent most her time on the lek either actively soliciting males by walking around their territories or by standing at the center of the lek in the solicitation pose. Copulations ranged in duration from 3 to 7 s ($n = 9$ s).

The length of non-disrupted copulations videotaped at lek 10/11 ranged from 3 to 7 s

($n = 9$) versus 4 to 6 s ($n = 6$) at other leks in Alberta. The length of copulations is consistent with Scott (1942), but less than Simon (1940), which ranged from 6 to 12 s. However, it is unlikely that observations in the 1940s were accurately timed. The extremely short duration of undisrupted copulations suggests that most, if not all, of the disrupted copulations at lek 10/11 would have resulted in insemination, as all were ≥ 3 s in length. If we consider all copulations over 3 s as successful, female #1 mated 6 times with 3 different males and female #2 mated 3 times with a single dominant male. Wiley (1973) assumed that all disrupted copulations were unsuccessful, but considering that all disrupted copulations in this study were within the time length range of undisrupted copulations, Wiley's assumption is likely incorrect. This leads to more observations of multiple mating and polyandry in Sage-Grouse, as interrupted copulations accounted for 18.3, 13.0, and 12.1% of all copulations observed during Wiley's (1973) 3-y study. Scott (1942), Patterson (1952), and Wiley (1973) also reported observations of individual females mating multiple times with either the same or different males due to "aberrant behavior".

There are several reasons why Sage-Grouse females may exhibit polyandry. Sage-Grouse are endangered in Canada (Alberta Sage-Grouse Recovery Action Group 2005; Lungle and Pruss 2008), so females may mate more than once to overcome male infertility. However, this is unlikely because fertility in Alberta was high across all years studied (1998–2006; 99.2%; Bush 2009) and genetic diversity was high across leks (Bush and others 2010; Bush and others 2011). A more likely explanation is that sperm competition (Birkhead and Møller 1992; Birkhead 1998) or sperm choice (Birkhead and others 2004; Thuman and Griffith 2005) is occurring, as Sage-Grouse exhibit varying levels of multiple paternity (Semple and others 2001; Bush 2009; Bird and others 2013). However, multiple mating does not necessarily translate to multiple paternity. In Black Grouse (*Tetrao tetrix*), 25% of females were observed to mate with more than 1 male, but only 9% of females had clutches with multiple paternity (Lebigre and others 2007). This suggests that multiple mating occurs more frequently than multiple paternity and

both may be a common occurrence in lekking grouse species.

It is likely that multiple mating is not a rare event in Sage-Grouse, but is only rarely detected and reported. Most behavioral studies on Sage-Grouse occur on large leks, which make the identification of unmarked individual males and females almost impossible. Without the ability to identify individuals, interactions and matings cannot be properly quantified and assessed. However, Scott (1942), Patterson (1952), and Wiley (1973) all reported females with "atypical" behavior that copulated repeatedly. Wiley (1973) also reported females that mated with multiple males due to disrupted copulations, which makes this a more common phenomenon than previously believed. As disrupted copulations most likely result in successful inseminations (provided that they are >3 s in duration), they are likely the main cause of multiple mating. Off-lek breeding may also account for some multiple mating since this behavior is difficult to observe, but is known to occur (Dunn and Braun 1986; Gibson and Bradbury 1987). Recent genetic work has shown that both multiple mating and off-lek mating occur (Semple and others 2001; Bush 2009; Bird and others 2013). In a study of 10 Sage-Grouse broods in California, 40% of broods were found to be fathered by the male that the female was observed mating with, 20% of broods were found to have more than 1 father, and 40% were found to have fathers that were not residents of the studied lek (likely males from another lek or off-lek males; Semple and others 2001). Similar results were found by Bird and others (2013) where 7.9% of broods exhibited multiple paternity, and in years where the majority of lekking males were genetically sampled, unsampled males were still fathering young. These results provide further evidence for off-lek mating and the presence of unknown lek locations.

The observation that 2 female Sage-Grouse mated multiple times in a single morning suggests that the mating behavior of lekking species is more complicated than previously reported. While the 2 observed females appeared to have a preference for dominant males, female #1 mated with a peripheral male. This, combined with the paternity results for Alberta, which showed that on average 45.9% of genetically identified males in the Alberta

fathered young (Bird and others 2013), highlights several new insights into lek mating behavior. It appears that there are 2 likely options for explaining polygamous behavior and multiple mating. First, dominant males may not obtain the majority of total matings. Off-lek mating (Gemmell and others 2001), mating on unknown leks (Wilmer and others 1999), or mating on leks that move throughout the season (Gibson and Bradbury 1987) may contribute to the decreased success of dominant males fathering offspring. Second, dominant males may actually be obtaining the majority of total matings, but factors such as sperm competition or selection may result in a more even distribution of paternity. Dominant males may be losing out to the sperm of subordinate males because dominant males may be more prone to disease due to increased mating (Thrall and others 2000), making them ultimately less desirable as a mate. Other possibilities include: decreased fertility due to increased mating (Scott 1942); decreased fertility due to age (older males tend to be the dominant males, but also experience decreased fertility; Sæther and others 2001); non-conformity of female choice (not all female Sage-Grouse desire the same traits in the father of their offspring; Bird and others 2013); or a post-copulatory mechanism that gauges genetic similarity-dissimilarity to the female (Birkhead and others 2004). Regardless of the mechanism(s), it is apparent that Sage-Grouse mating behavior and female mate choice is not as simple as it appears, and considerable future research will need to be conducted to better understand the mating behavior of this species.

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