

LEK ORGANIZATION IN SAGE GROUSE: VARIATIONS ON A TERRITORIAL THEME

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ABSTRACT.—During a 5-year study of Sage Grouse (*Centrocercus urophasianus*) in eastern California, displaying males abandoned territoriality throughout one breeding season and did so intermittently in three others. Abandonment followed a severe winter and was correlated with a change from location-dependent to hierarchical dominance relationships between males. Intermittent territorial breakdowns occurred when males left their territories to approach and, in 2 years, to mate with females off the lek. These observations imply that the social mechanisms of sexual selection may vary between leks in this species and suggest a novel function for lek territoriality: territories may act as rendezvous sites with females. Received 4 February 1986, accepted 26 August 1986.

SOCIAL mechanisms that influence sexual selection in avian lek species are the topic of much debate. Among lekking species, the potential for male competition to influence mating directly, and conversely for females to choose mates without male intervention, varies widely and appears to be related to the way males partition space at the lekking area (reviews: Oring 1982, Bradbury and Gibson 1983). At one extreme, several males share a common area and compete for individual dominance status, which regulates mating access (Snow 1963; Foster 1977, 1981). At the other, males divide the lek into exclusive territories and interference in mating activities is limited to local interactions between neighbors (Wiley 1973, Lill 1974). Biased male mating success in the latter situation may primarily reflect female choice, though male interactions also could play a significant role (Wiley 1973, Robel and Ballard 1974, Trail 1985).

Studies of Sage Grouse (*Centrocercus urophasianus*) have been influential in shaping current views of territorial lek systems (Wiley 1973). In this species males visit leks at dawn each day over a 3-month period in the early spring. They spend the remainder of the day foraging away from the lek, often returning to roost there in the evening (Wallestad and Schladweiler 1974, Emmons 1980). Females visit leks less regularly, but typically for several days before mating (Lumsden 1968, Dunn and Braun 1985, pers. obs.). Leks usually occur at the same locations throughout a season and from year to year, and are easily observed because of the birds' open habitat and large size. Previous workers have characterized the organization of Sage Grouse

leks as territorial (Lumsden 1968, Hartzler 1972, Wiley 1973). During studies of this species in eastern California, however, we frequently observed that males abandoned their territories during lek display. The adoption of this behavior by the majority of birds at a lek causes a breakdown of territorial organization.

We describe here the conditions under which territoriality breaks down at Sage Grouse leks, both between and within breeding seasons, and examine correlated changes in male dominance relationships and their relationship to mating success. We discuss our observations in relation to the social mechanisms of sexual selection and to the economics of territoriality that presumably regulate lek organization. Throughout we are concerned with the behavior of adult males (over 1 yr old); younger males attended leks irregularly, rarely established territories, and did not mate during our study (see also Wiley 1973).

STUDY AREA AND METHODS

Most of the data reported here were collected between early February and mid-May 1982–1986 at two areas in Mono Co., California. We studied one lek intensively each day at Wheeler Flat in 1982 and 1983 and a second at Crowley Lake in 1984–1986. Average numbers of males attending these leks per day are shown in Table 1. Supplementary data also were obtained by less frequent visits to 3–5 leks per year at Wheeler Flat (1980–1983), Crowley Lake (1984–1986), and a third location, the Bodie Hills (1980–1983).

Observations were made from first light until the birds left by a team of 2–5 observers from a raised vantage point 200–300 m from the lek. This allowed

TABLE 1. Average numbers of males (adults and yearlings) attending intensively studied Sage Grouse leks in 5 years.

Site	Year	<i>n</i>	Males per day	
			Mean	SD
Wheeler	1982	34	14.6	5.5
Wheeler	1983	30	6.7	1.9
Crowley	1984	53	30.8	10.7
Crowley	1985	59	21.4	8.6
Crowley	1986	63	31.1	33.3

us to survey the entire lek and surrounding area without disturbance. Using 20–45× zoom telescopes, we could identify individual males (see below) by 20–40 min before sunrise. Because birds arrived around 1 h before sunrise and typically left about 2 h later (Jenni and Hartzler 1978, pers. obs.), our observations covered most morning display activity. We did not watch the less regular lek display that occurs at low light levels in the evening and on moonlit nights. Both leks were situated on flat, shrub-free areas that we gridded with numbered surveyors' stakes at 10- or 20-m intervals to allow mapping of male locations.

In each year except 1982 (when only 5 males at the study lek were banded), we could recognize individually 50–100% of the males each day by color bands or using a combination of tail shape and the pattern of white spots on the under tail coverts (Wiley 1973). Unbanded males were aged as yearlings (under 1 yr old) or adults (over 1 yr) based on tail length and shape (Wiley 1973). Ages of banded birds were checked at capture by inspection of primary molt (Eng 1955). Birds were captured by spotlighting and, for a few individuals in 1984–1986, with rocket nets (Giesen et al. 1982). Rocket nets were not used when females attended leks. For all captured birds we recorded body mass and lengths of culmen, tarsus, wing, and tail. A principal components analysis (BMDP) was used to collapse the last 4 measures to a single index of linear size, the first principal component.

At leks we recorded the numbers of males and females present, matings, individual use of space, and agonistic interactions between males (described by Wiley 1973). Matings were scored as unsuccessful if the female did not perform a postcopulatory "display" (Lumsden 1968, Hartzler 1972). Skew in male mating success in each season was measured by the ratio of the variance in mating success to its mean. This ratio is the "opportunity for selection" (*I*) of Arnold and Wade (1984).

Use of space by individual males was measured by scanning the lek at intervals and plotting the locations of each male on a map of the lek grid or by focal samples in which each individual's location was plotted every 1–2 min for 10-min periods. When birds

moved off the grid, as occurred frequently in 1983, locations were plotted relative to identifiable topographic features whose exact locations were determined later. Mapped locations were converted to x-y coordinates for analysis.

Display areas were measured for males with at least 10 points covering 5 or more days during a season using Anderson's (1982) nonparametric method. Areas and boundaries of 50% minimum area vs. probability areas (MAPs) were computed to contrast individuals and years. For each individual we also calculated the mean percentage of his 50% MAP area that overlapped with the 50% MAP area of each other male. Range or territory centers for each male were computed as the median x and y coordinate values for each individual. For two males that each used two disjunct areas on the same lek in the same season, the center of the more heavily used area was computed.

To quantify off-territory excursions by males in 1984–1986 one of us (RG) familiar with territories of males at the Crowley lek subjectively scored 67 movements involving 15 individuals as on- vs. off-territory in the field. Comparisons with maximum straight-line distances moved by the males during lek display, based on maps collected concurrently by a second observer, indicated that movements greater than 60 m were consistently scored as off-territory while those less than this distance were not. We refer to shifts of >60 m during a display period as "relocations." This criterion allowed us to score movements even when the identity, and hence territorial affiliation, of the male concerned was unknown. Numbers and identities of relocating males were recorded whenever possible. For 1983 a more conservative criterion of 200 m was used, reflecting the greater average mobility of males in that year.

For agonistic interactions between males we recorded the individuals involved, location, and outcome on an ad-lib basis. Outcomes were scored as inconclusive unless the interaction terminated with one individual chasing the other away.

To detect the presence of hierarchical dominance, we used a method based on Kendall (1962). Frequencies of transitive ($a > b, b > c, a > c$) vs. circular (e.g. $a > b, b > c, c > a$) triadic dominance relationships were counted for the m subgroups of 3 males within a lek of size n . Then, null probabilities of obtaining as few circular triads as those observed were estimated by 1,000 computer simulations. In each simulation we allocated dyadic dominance relationships at random within a group of size n and then randomly sampled m triadic subgroups without replacement. The rationale is that circular triads should occur less frequently if dominance relationships are hierarchical than if the dominance relationship within each dyad is independent of other dyads.

When dominance was hierarchical, an index of dominance status was computed for each male. We

TABLE 2. Mean 50% MAP areas and 50% MAP overlaps between males at Sage Grouse leks in eastern California in 5 years. Values (except No. of males) are means, with standard deviations in parentheses.

Site	Year	50% MAP		Sample size	
		Area	% overlap	No. of males	Samples per male
Wheeler	1982	0.010 (0.004)	6.1 (7.5)	4	46 (25)
Wheeler	1983	2.830 (3.372)	56.0 (30.6)	8	16 (6)
Crowley	1984	0.026 (0.022)	0.6 (0.8)	14	58 (38)
Crowley	1985	0.284 (0.423)	8.6 (4.1)	13	39 (24)
Crowley	1986	0.108 (0.128)	9.8 (7.9)	15	34 (11)

used an iterative procedure that first ranked each male by the proportion of opponents that it beat and then incorporated weightings based on the ranks of each opponent (see Gibson and Guinness 1980). This was more realistic than just ranking males by the proportion of other individuals that they beat because each male interacted with a different set of opponents.

The preceding analyses were performed only when we found consistent dominance relationships within dyads. When this was not the case, the outcome of each interaction was analyzed in relation to disparities between the contestants involved. Including all interactions could have biased the results because a few dyads contributed disproportionately to the sample. We therefore analyzed a subsample to which each dyad contributed only one randomly chosen interaction.

Data were analyzed using nonparametric statistical tests because most measures could not be transformed to meet the assumptions of parametric methods.

RESULTS

ANNUAL VARIATION

Use of space.—Areas used by displaying males varied between years from small exclusive territories to large overlapping ranges (Table 2). There was significant annual variation in the average size of individual display areas (Kruskal-Wallis $H = 38.98$, $df = 4$, $P < 0.0001$) and in the degree to which they overlapped with those of other males ($H = 33.59$, $df = 4$, $P < 0.0001$).

Territorial use of space was observed in 4 years (1982 and 1984–1986). In each year 50% MAP areas were small and relatively exclusive, individuals returned to the same locations each morning, and, with the exception of temporary breakdowns described below, the leks remained at the same locations throughout the season. Nine banded males that returned to the Crowley lek in successive years, including 5

that had bred in previous years and 4 that had not, also reoccupied their former locations, contributing to lek stability across years. The lek did alter over this period, however: individual 50% MAP areas and overlaps increased from 1984 to 1985 (Table 2; both significant at $P < 0.0001$, Mann-Whitney tests) coincident with a reduction in average attendance (Table 1) and an extension of the total area occupied by display territories.

At Wheeler in 1983 males used areas that were 10–100 times larger (Mann-Whitney tests, $P < 0.01$ – 0.0005) and overlapped more extensively than in all other years ($P < 0.05$ – 0.0005). Samples on which individual 50% MAP values are based were smallest in 1983, but this did not explain the increase: 1983 areas were also significantly larger in a reanalysis in which 50% MAP areas for all other years were recalculated from random subsamples of 16 locations per male (the mean for 1983). Large, overlapping ranges in 1983 were generated by shifts of the entire lek by 200–400 m from day to day and movements of similar extent during morning display periods (see below). Individual males did not maintain the same locations relative to each other during these movements. The lek moved over an area that included two sites 600 m apart used as leks in previous years (one was the primary study lek of 1982). Except at the start of the season, however, the birds showed little attachment to these locations.

Male dominance relationships.—Determinants of male dominance differed between 1983 and other years. Data from Crowley in 1984–1986 were analyzed to characterize the territorial situation; samples from Wheeler in 1982 were too small for comparable analyses.

At Crowley there were, with minor exceptions noted below, no consistent dominance relationships between individuals. Fifty-three to

TABLE 3. Conclusive agonistic interactions between adult male Sage Grouse at Wheeler lek, 1983.

Winner	Loser								Dominance index ^a
	BT	Q	WBW	R	N	D	YYY	OG	
BT	—	4	1	2	1	1	3	0	0.713
Q	4	—	3	3	3	5	8	1	0.703
WBW	0	0	—	0	1	1	1	0	0.550
R	0	0	0	—	3	0	1	0	0.517
N	0	0	0	0	—	1	1	0	0.428
D	0	0	0	0	0	—	0	1	0.366
YYY	0	0	0	0	0	0	—	0	0.291
OG	0	0	0	0	0	0	0	—	0.267

^a Calculated by the method of Gibson and Guinness (1980).

78% of interactions per year ($n = 94-201$) ended with the mutual withdrawal of both participants, and the best predictor of the outcome was the distance of each individual from his territory center. Winners of conclusive interactions were closer to their territory centers than were losers in 81% of 41 cases (binomial test, $P < 0.0001$), and the probability that an interaction had a conclusive outcome increased with the disparity between contestants in this distance (logistic regression, $\chi^2 = 7.18$, $n = 72$, $df = 1$, $P < 0.01$). Data were combined across years after preliminary analysis showed similar patterns within each year. Equivalent analyses showed that disparities in linear size (see Methods) and body mass, which might also be expected to affect fighting ability, did not significantly affect fight outcomes.

Although the preceding results imply that each male could dominate all others when near his territory center, there were some exceptions. These included one adult male present in 1985 and 1986 that displayed at two disjunct areas in each year but did not successfully defend either location, and 12 transient adults that attended irregularly and did not establish territories.

At Wheeler in 1983 dominance clearly depended on individual identity rather than location. Eighty-eight percent of 75 interactions had a clear winner, and 7 of 9 dyads for which more than one interaction was recorded showed consistent dominance relationships (Table 3). The exceptions were males BT vs. Q, who split interactions evenly, and BT vs. R, who had 4 inconclusive interactions (not shown in Table 3) and 2 conclusive ones, both won by BT. Dominance relationships were linear except for the similar status of Q and BT, the two most dominant males (Table 3), suggesting that some

males were more successful fighters than others. This was confirmed by a test of independence of dominance between dyads that gave a P -value of 0.01 (see Methods).

Correlates of lek organization.—The breakdown of territoriality at Wheeler in 1983 followed an exceptionally severe winter. Lek sites used in the 2 previous years remained covered by deep snow into early May. In 1983 males did not begin attending leks until early April, 12 days before the first mating, whereas in 1982 and 1984–1986 45–57 days elapsed between the onset of lek display in February and the start of mating. The numbers of males attending leks were reduced by 71–74% between 1982 and 1983 at Wheeler and in the Bodie area, where similar unstable leks were observed. However, the abandonment of traditional lek sites was not due simply to the absence of experienced birds: of 12 individuals that attended the Wheeler lek in 1983, 4 were banded as adults in 1981–1982, including 1 that held a territory at the study lek in 1982.

DAILY VARIATION

Even in years when leks were stable, males frequently left their territories. Relocations (movements over 60 m; see Methods) by one or more displaying males occurred at Crowley on about half of all days in 1984 and 1985, and on 12 of 14 days for which comparable data were obtained in April 1986. In 1984 and 1985 movements on 88% of such days were into areas 100–300 m peripheral to the lek, and an appreciable number of males usually took part. In 1984 an average of 8.5 males ($SD = 8.0$), representing 31.2% ($SD = 26.9\%$) of those present, was involved in each of 15 episodes for which accurate counts were made. Equivalent figures for 1985

TABLE 4. The effect of female presence on the daily incidence of male relocation during morning display sessions at the Crowley Lake lek in 2 years.

Year	Females	Male relocation	
		No	Yes
1984	Absent	9	3
	Present	13	16
1985	Absent	10	3
	Present	10	18

were 7.0 (SD = 5.7) and 23.4% (SD = 12.6%, $n = 10$). In 1986 males moved off the lek on only 4 of 12 days on which relocations occurred; the remaining cases involved intrusions into the territories of other males.

Most relocations involved territorial individuals, although transient nonterritorial males also took part. From 1984 to 1986, 71% of 41 territorial males were known to have relocated at least once. Among territorial males, breeders (individuals that mated) were as likely as nonbreeders to relocate at least once during a season (G -test on data for all 3 yr, $G = 0.010$, $df = 1$, not significant). In 1986, when measures of relocation frequency were obtained, the proportion of days on which a male relocated did not differ significantly between breeders and nonbreeders (Mann-Whitney test, $W = 39.5$, $n_1 = 7$, $n_2 = 5$, $P = 0.372$) and was also unrelated to numbers of copulations ($r_s = -0.287$, $n = 12$, not significant).

Males left their territories most often on days when females visited the lek. At Crowley in 1984 and 1985 relocations were observed on a significantly higher proportion of days when females were present than when they were absent (Table 4; 3-way G -test, $G = 9.501$, $df = 2$, $P < 0.01$; year had no significant effect). In 1986 all but one relocation occurred when females were present, though the sample was too small for formal testing. Relocations in mornings by males at the Wheeler lek in 1983 were also closely associated with female presence ($G = 15.64$, $df = 1$, $P < 0.0001$).

Some males obtained matings by approaching off-territory females or following those that were moving away. In 1985, 2 matings were performed by a male that had followed 3 females 200 m from his territory into adjoining brush; this male had obtained 3 copulations on his territory in 1984. Another male performed

2 off-territory matings in a similar situation in 1986 and also completed 13 copulations on his territory in the same year.

In 1986 we also recorded 16 cases in which females approached a male on his territory after he had displayed to them at another location earlier that morning. In 4 instances the female(s) mated on the male's territory. We did not determine whether off-territory display caused the females to approach the male.

AGONISTIC INTERACTIONS AND MATING SUCCESS

Two kinds of direct competition that could have affected matings were observed: attacks on males displaying near females and copulation disruption in which one male knocked another from the back of a hen during copulation.

Although attacks on displaying males occurred in all years, they were most likely to have influenced mating success in 1983, when overlapping ranges and hierarchical dominance relationships (see above) potentially allowed dominant males to interfere with the display of subordinates. Consistent with this idea, skew in mating success, measured by Arnold and Wade's (1984) opportunity for selection (I), was greater in 1983 ($I = 10.09$) than in any of the years 1984-1986, when dominance was not hierarchical ($I = 1.532-7.280$; numbers of copulations ranged from 21 to 49 per year). As a more direct test, we correlated mating success in 1983 with an index of male dominance (Table 3; see Methods). Of 19 matings by identified males in 1983, 14 were by one of the two highest-ranked males (Q), but the other dominant individual (BT) did not mate and the remaining copulations were performed by two mid-ranked individuals, R (1) and N (4). Although one dominant male performed most copulations, the correlation between the dominance index and matings ($r_s = 0.327$, $n = 8$) was not significant. This suggests either that dominance did not affect mating success or, more likely, that in this small sample the effect of dominance was obscured by other factors. In either case, dominance evidently was not sufficient to guarantee mating success.

We observed disruption of copulations infrequently and only when males mated on their territories. From 1984 to 1986, 13.6% of 118 copulation attempts at the Crowley lek were dis-

rupted. Of 21 copulations at Wheeler in 1983 (including 2 by unidentified males) and 4 off-territory copulations at Crowley (see above), none was disrupted. Disruptions were relatively ineffective. In only 4 cases (3.1% of all attempted copulations) was a disrupted copulation unsuccessful (see Methods), and 2 of the females involved immediately remated with the same male. One of the remaining females remated with another male (not the disruptor), while the fourth left the lek without remating. None of the females whose disrupted copulations were scored as successful remated before leaving the lek.

DISCUSSION

Across the 5 years of our study, leks varied from stable aggregations of male territories to unstable groups of males that moved in large overlapping ranges. In 3 seasons territorial leks showed intermittent instability. These observations contrast with previous accounts of Sage Grouse behavior and raise several issues.

First, to what extent are our data typical of this species? While the breakdown of territoriality throughout a season is probably rare, intermittent breakdowns may be more common than suggested previously. Previous studies (Scott 1942, Lumsden 1968, Hartzler 1972, Wiley 1973) noted occasional shifts by territorial males that were attributed to various factors, including female presence and disturbance by raptors. These workers observed from blinds located on leks, however, and could have underestimated the frequency of off-lek activity (pers. obs.). We might have overestimated lek instability if small leks, such as those at Wheeler, were inherently less stable than the large leks observed by Scott (1942) and Wiley (1973). However, our data did not show any clear relationship between lek size and stability, and one of the most unstable leks we observed at Crowley (but did not study intensively) was regularly attended by over 100 males.

Although previous studies have discussed the mating system of Sage Grouse in the context of territorial lek structure, we found that matings occurred in two distinct contexts: on male territories and within shifting groups when territoriality broke down. Our observations in the former situation, like those of Wiley (1973) and Hartzler (1972), suggest that male interactions

had a relatively minor effect on matings. When on their territories, individuals had relatively equal dominance status; although males disrupted the copulation attempts of neighbors, this was infrequent and relatively ineffective. Female choice presumably had a major effect on male mating success in this context. Data from the Crowley lek (Gibson and Bradbury 1985) suggest that females choose males on the basis of the repetition rate and acoustic quality of the strut display, rather than by territory location (Wiley 1973). The fact that unsuccessful males that returned to the lek in successive years reoccupied their former territories, rather than moving to locations at which matings had occurred in previous years, also argues that location *per se* is not a critical determinant of mating success. Hartzler (1972) reached similar conclusions after studying a single lek for three consecutive years.

When territoriality broke down, dominance relationships were hierarchical and opportunities existed for dominant males to suppress the mating success of subordinates, as suggested by the near-monopolization of mating by one of two dominant males in 1983. Dominant males could not force females to mate with them, however, as indicated by the lack of matings by the other dominant male. Thus, while male interactions could play a more important role at unstable leks, they apparently do not preempt female choice in this situation. This raises the intriguing possibility that the relative importance of male competition and female choice may vary between leks in this species. Whether this results in different male traits being favored at stable vs. unstable leks is, however, moot. Case histories of the two males that obtained off-lek copulations at Crowley suggest that similar factors affect mating success both on and off territories. A more critical test comparing factors that affect mating success at stable vs. unstable leks was precluded by the lack of data on correlates of mating success at unstable leks.

Our data indicate that territoriality can break down over two distinct time scales, between years and within days, perhaps for different reasons. The season-long breakdown of territoriality in 1983 was associated with several factors. The unusually late start to the season and, perhaps, deep snow cover that obliterated surface features of territories established in previous years could have impeded territory

establishment at the start of the season. Reduced lek size, either by itself or if correlated with the absence of experienced territorial males, also might have been relevant, though as discussed previously neither possibility is likely. A much larger sample of years would be necessary to pinpoint factors causing annual changes in lek stability.

Temporary breakdowns of territoriality at stable leks occurred when males left their territories to approach, and in some cases mate with, females away from the lek. Most territorial males adopted this tactic. At least two hypotheses might explain why males switched between these two tactics.

One hypothesis is that most females prefer to mate at particular geographic locations that then become the focus for male territorial behavior (Wiley 1973). Off-territory display would be an alternative tactic adopted by males that failed to obtain primary mating territories (Oring 1982). However, although the lek itself is apparently an area favored by females, our results and those of Hartzler (1972) argue against the idea that particular territories are favored by females. Moreover, mating success, which according to the hypothesis should indicate territory quality, was uncorrelated with involvement in off-territory display.

An alternative hypothesis assumes that territories act primarily as rendezvous sites. As in some other lekking bird species (Lill 1974), female Sage Grouse visit leks several times before mating and appear to investigate males carefully during their visits (Lumsden 1968, Gibson and Bradbury unpubl. data). If during early visits females choose a male on the basis of display or other nonspatial cues and then use his location as an additional or substitute cue when returning later to mate, a male might increase his mating success by waiting at, and excluding other males from, a site at which he has previously encountered females (DeVos 1983). Males should defend or abandon a territory depending on the relative mating success to be gained by waiting for returning females vs. leaving to approach those already at the lek. Several variables, including the probability of further female arrivals, a male's recent success in attracting females to his territory, and his off-territory dominance status, would be relevant to this decision. The hypothesis also suggests an explanation for lek instability throughout the 1983 season: if dis-

play to females occurs before territory establishment is complete, as apparently happened in that year, the rendezvous-site convention could break down.

Although data on how females choose their mates are currently inadequate to critically evaluate the rendezvous-site hypothesis, it is worth noting that it may reconcile conflicting views on the roles of spatial vs. phenotypic cues in female choice (Hartzler 1972, Wiley 1973, Lill 1974, Bradbury and Gibson 1983) and also explain several features of lek behavior that are difficult to understand without invoking spatial preferences by females. These include year-to-year site fidelity by males (see above) and the role of experience with females in territory establishment (DeVos 1983). It may also be relevant to other lekking grouse in which lek instability and off-lek copulation have been observed (Sexton 1979, Oring 1981).

Our finding that territorial behavior of male Sage Grouse is labile indicates that the social mechanisms of sexual selection may vary between leks in this species and also suggests a novel function for lek territoriality: territories may function as rendezvous sites. This hypothesis could be tested by more detailed studies of the conditions under which individual males abandon their territories and of the tactics of female mate choice.

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