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Lek Formation in Sage Grouse: The Effect of Female Choice on Male Territory Settlement

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Abstract

Previous studies of female choice in sage grouse, *Centrocercus urophasianus*, have identified two processes that could drive the local clustering of male territories at leks: (1) fidelity of females to previous mating sites (“temporal spillover” hypothesis), and (2) “spatial spillover” of matings from an attractive male to his immediate neighbors (“hotshot” hypothesis). The effects of each process on male territory settlement were investigated using observations of the resettlement of vacant territories and of individual site fidelity during a 7-year field study. The frequency with which vacant territories were resettled both within and between seasons increased with mating success of the site’s previous occupant but not with the success of neighboring males. Territories vacated by the most successful males acted as foci for clusters of territories in the following year. Fidelity of males to their territories within seasons also increased with their previous mating success but was unaffected by the mating success of neighbors. However, between seasons the rate at which males returned to the lek (though not necessarily to the same territory) increased with both their own previous mating success and that of neighbors. Returning neighbors of males that failed to return were at an advantage in competing for the vacant territory. These data support the role of temporal spillover in lek formation and also suggest that territorial males use a “win-stay” rule that should favor the use of established males as cues to settlement by naive individuals. The spatial spillover hypothesis was not supported, perhaps because this process creates conflicts of interest between attractive males and kleptoparasitic neighbors that prevent the formation of stable groups.

In lekking birds and mammals, males cluster their territories at sites visited by females solely for mating. It is evident that local clustering of males may facilitate the extraordinary

unanimity of female choice that is characteristic of leks. However, it has been difficult to explain why males cluster their territories (Bradbury & Gibson 1983; Wiley 1991). Much recent interest has centered on the possibility that lek formation is driven by female choice either within or between leks. In this paper I present data on male territory settlement that show how responses of males to female choice within leks may cause the clustering of lek territories in the sage grouse, *Centrocercus urophasianus*.

Recent field studies have provided evidence that the locations at which males of lekking species display are strongly affected by the spatial distribution of receptive females. Supporting observations include (1) proportional changes in male and female numbers (input matching) across leks of widely varying size (Bradbury et al. 1989a), (2) movements of males between leks or between lek and non-lek display areas in response to changing local distributions of females (Lank & Smith 1987; Bradbury et al. 1989a), and (3) the establishment of lek territories in response to encounters with receptive females and the abandonment of territories that females do not visit (DeVos 1983; Höglund & Robertson 1990a). In contrast, alternative proposed determinants of lekking such as predation and male habitat requirements have received less support (Pruett-Jones 1985; Bradbury et al. 1989b; Balmford 1990).

A simple explanation for these observations is that males settle at "hotspots" of female traffic, generated by the overlap of female home ranges (Bradbury et al. 1986) and enhanced by topographical features that channel female movements (Appolonio et al. 1990). One prediction of the hotspot hypothesis, that male territories become more clumped as female home range size increases, has been confirmed by interspecific comparisons in several families of birds and mammals (Bradbury 1981; Balmford 1990; Thery 1990). A second prediction, that male territory density and female traffic should co-vary within lekking populations, has received less consistent support. It has been confirmed in three of five species of birds (Pruett-Jones 1985; Wegge & Rolstad 1986; Bradbury et al. 1989a; Höglund & Robertson 1990a; Thery 1990), in one of two antelopes (Gosling & Petrie 1989; Balmford 1990), and in some populations of fallow deer (Clutton-Brock et al. 1988; Appolonio 1989). Moreover, even in those cases that provide support, hotspots account only for the coarse scale dispersion of males. For example, in sage grouse, female range overlap predicts the relative numbers of males at different leks, but it fails to predict both lek locations and the high degree of clustering of male territories at leks (Bradbury et al. 1989a). Thus other processes are needed to explain the tight clustering of lek territories at specific sites.

There are at least three ways in which female choice might promote the local clustering of lek territories. First, females might intensify male clumping by choosing between leks and favoring the largest (Bradbury 1981). Second, if females initially make unanimous choices for particular males (or their territories) and subsequently exhibit site fidelity when mating, "temporal spillover" in matings between successive seasons could cause males to settle preferentially at historically successful sites, leading to lek formation by occupancy of smaller territories, centripetal queueing, or shared use of display courts (Wiley 1973; Warner 1987; McDonald 1989). Finally, clumping might be intensified if some males are initially more attractive than others and less attractive males attempt to steal matings by settling nearby ("spatial spillover," "hotshot," or "attractive male" hypothesis: Arak 1988; Beehler & Foster, 1988; Höglund & Robertson 1990b). Although these alternatives have

been widely discussed, there are few tests of their involvement in lek formation (but see Höglund & Robertson 1990b).

In sage grouse, it is unlikely that choice between leks has an important influence on lek formation. Although pre-nesting ranges of females commonly include several leks (Bradbury et al. 1989a), the majority of hens visit only a single lek in any season and so do not appear to sample and choose between alternative leks (Petersen 1980; Dunn & Braun 1985; unpublished data). By contrast, a recent study found evidence for both temporal and spatial spillover in female choice within leks (Gibson et al. 1991). Females based mating decisions primarily on differences in vocal display performance and secondarily on the choices of other females and fidelity to former mating locations. These combine to generate highly consistent choices for particular territorial males within seasons, which in turn allowed us to predict the locations at which hens would mate in the following year (temporal spillover). In addition, there appeared to be some spatial spillover between successful males and their immediate neighbors because neighboring males experienced similar mating success, even after taking into account similarities in vocal display performance and territory history.

The temporal and spatial spillover hypotheses generate distinct, but not mutually exclusive, predictions about the rules used by males in settling on lek territories. The temporal spillover hypothesis predicts that males should rank sites according to their recent mating history while the spatial spillover hypothesis suggests that sites should be ranked by the recent mating history of males in neighboring territories. I have tested these predictions by examining how both resettlement of vacant territories and the fidelity of individuals to their territories are affected by a territory's past mating history and by that of neighboring males.

Methods

The study was conducted on a resident population of sage grouse in Long Valley, Mono County, California from 1984 to 1990. One lek (lek 4) was studied from 1984 to 1987 and in 1989, and another (lek 2) in 1988. I conducted follow-up censuses in 1990. Mean ($\bar{X} \pm \text{SE}$) daily attendance at lek 4 varied from $23 \cdot 1 \pm 1 \cdot 1$ to $31 \cdot 9 \pm 1 \cdot 2$ males annually, and in each year sampling included almost all territorial males present. Lek 2 was larger ($121 \cdot 6 \pm 1 \cdot 55$ males daily) and observations focused on a group of 8–10 territories (for details see Gibson 1989). At both sites males were recognized using color bands and/or combinations of individually distinctive patterns of tail shape and white spotting on the undertail coverts. Most males at lek 4 were color-banded in each year from 1984 to 1987. Both leks were situated in open meadows on which I marked out a grid using numbered wooden stakes at 20-m intervals to allow mapping of territories and copulation locations. The grid was replaced in the same location in each year.

Observations of territories and matings were made each day during the dawn lek-display period from 15 March to the last week of April. This included the main period of lek display and mating in all years. Teams of two to four observers arrived before dawn and stayed until all males had left the lek. By watching with 15–45× zoom telescopes from a raised vantage point 100–200m away, teams were able to monitor activity throughout the lek and identify individuals without apparent disturbance.

Territories

I defined male territories from mapped locations collected during scan samples at 5- to 10-min intervals on several days distributed throughout each season (details in Gibson & Bradbury 1987). These data were supplemented with focal individual samples in 1984. I considered any male that consistently used the same area and that aggressively excluded others as territorial. Territory sizes were measured, using Anderson's (1981) Fourier transform method, as the area accounting for the top 50% of observations. This measure provides a good estimate of the area within which the resident aggressively dominated intruders (Gibson & Bradbury 1987). I considered pairs of males with adjoining territories to be neighbors.

I measured preferences for territories in two ways: (1) by resettlement of recently vacated sites and (2) by fidelity of males to their territories.

Resettlement of vacancies

When a marked male disappeared from the lek either within or between seasons, or moved permanently to a non-overlapping site elsewhere on the lek, his territory was considered to be vacant. I divided vacancies into those occurring within seasons (between the onset of mating and the end of April) and those between seasons (between the end of April in one season and the onset of mating in the next). Sites were classified as "resettled" if other individuals included part or all of the vacated area within their own territories in the period immediately following either the remainder of the season or the following breeding season for within and between season vacancies respectively. Within-season resettlements occurred within a day of vacancy and all between-season cases occurred by early or mid-March, before the onset of regular hen attendance and mating.

Fidelity to territories

I examined site fidelity of territorial males both between the first and second halves of the mating period (broken at the date of the median mating) in each year and between the end of April in one year and the start of the next season. Within seasons, males that returned to the same site were classified as showing site fidelity in that year, while those that moved elsewhere were not; I excluded males that died or disappeared in mid-season. Between seasons, I classified males that returned to their former territories as demonstrating site fidelity. Some of those that failed to return might have died rather than abandoned their former territories. In many instances (12 of 22) it was not possible to determine whether the individual had dispersed or died. However, it was clear that a substantial number of those that failed to return to the same territory had survived: of 10 individuals whose fates were known, 8 were known to be alive during the next season (based on their occupancy of a different territory on the same lek, brief visits to the same lek, or sightings at other leks) while only 2 were known to have died. The inclusion of males that died in the analysis should not bias the conclusions unless mortality rates decrease with previous mating success or with the mating success of neighbors (see Results). Neither seems likely.

Mating Success

I characterized the mating history of a territory by the mating success of its occupant measured either over the prior season (for year-to-year comparisons) or over the first half of the current season (for within-season comparisons). Although some off-territory mating occurred (Gibson & Bradbury 1987), over 97% of 175 matings recorded at lek 4 were performed by males located within their territories. I defined mating success as the number of females with which a male mated during each morning lek, summed over all days of the season or, for early season success, to the day of the median copulation. Because observation teams monitored the entire lek area continuously, it is unlikely that matings were missed, except during the first 10–15 min of the morning when visibility was poor. I did not make systematic observations of the less predictable leks that occurred at dusk and on moonlit nights, although pilot observations suggested that few hens visited at these times.

To analyze the effect of neighbor mating success, I used the success of the most successful neighbor. Although some individuals had several neighbors that mated, the pooled mating success of all neighbors and that of the most successful individual were highly correlated ($r = 0.944, 0.972, N = 43, 51$ for seasonal and early-season mating success, respectively, $P < 0.001$ for both) and analyses based on the pooled measure gave almost identical results.

Mating success was standardized for most analyses by expressing matings as a percentage of the total copulations at the lek in the entire season (for between-year comparisons) or in the first half of the season (within-year). One exception was the analysis of within-season vacancies, which is based on actual (rather than fractional) numbers of copulations. In this analysis I combined data from both leks and used numbers because total copulations were not recorded at lek 2. The results are unlikely to be affected because in a large sample, pooled over two leks and four seasons, actual and fractional matings were closely related ($r = 0.890, N = 115$ males, $P = 0.0001$).

Statistical Analysis

For each analysis I pooled all available cases across leks and years. In most instances this resulted in independent samples. However, for analyses of site fidelity, 28–29% of cases represented repeated observations of individuals that attended the lek for more than one year. To ensure independence, in these cases I analyzed a subsample in which each multiply-sampled individual was represented by a single randomly chosen observation. I used logistic regression to examine the effects of a site's mating success and that of neighboring males based on the probability that a site was resettled if its owner disappeared, and on site fidelity of its occupant. Models were fitted by a maximum likelihood method, and the reduction in log likelihood ratio due to the model was tested by chi-squared with $df = 1$ (Dixon et al. 1988). I used Spearman rank correlations to examine the effect of a site's mating history on the numbers of males settling there because both had highly right-skewed distributions.

Results

Resettlement of Vacant Territories

Mating history

Males showed a clear preference for territories in which matings had occurred in the same or the previous year, as predicted by the temporal spillover hypothesis. Nine vacancies occurred after mating had started within seasons: three were created by the death, eviction, or disappearance of a breeding male, while the remaining six resulted from relocations of unsuccessful individuals (see below). All three territories in which matings had occurred were immediately resettled by neighbors or by a combination of neighbors and new settlers, whereas all six territories abandoned by unsuccessful birds were left unoccupied. A logistic regression showed a significant increase in the probability of resettlement with the previous occupant's mating success ($\chi^2 = 11.46$, $P = 0.0007$).

I found a similar pattern for territories that fell vacant between the end of one season and the onset of mating in the next. Nineteen vacancies arose through the disappearance ($N = 16$) or relocation ($N = 3$) of permanently marked males. Twelve vacancies were resettled by a total of 23 males before the onset of breeding in the following year. The probability that a territory was reoccupied, in whole or part, was positively correlated with the mating history of the territory in the previous season (logistic regression: $\chi^2 = 9.49$, $P = 0.0021$).

The numbers of males that settled on vacant territories between years also increased with the previous occupant's mating success (Fig. 1: $r_s = 0.735$, $N = 19$, $P = 0.0018$). This relationship was not caused either by variation in territory size or by annual variation in mean settlers per available territory because a similar correlation was found when these factors were removed by dividing settler number first by territory area and then by settler density summed over all vacancies in the same year ($r_s = 0.804$, $N = 16$, $P = 0.0018$; areas were unavailable for three territories). Most males established their territories well before the onset of female attendance and thus presumably responded to the distribution of matings in the previous rather than the current year. As a result, territories vacated by the most successful males became foci for clusters of territories in the following year.

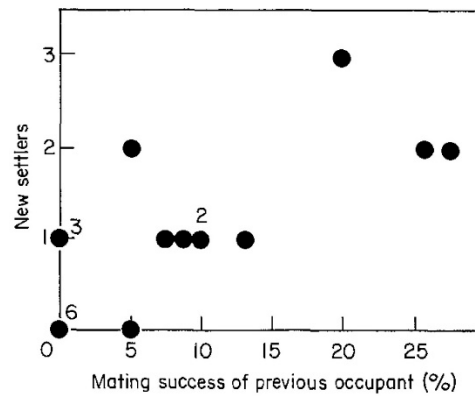


Figure 1. The numbers of males settling on vacant territories between seasons at lek 4 plotted against the mating success of the site's occupant in the previous year (scaled as a percentage of all matings at the lek). Numbers above points indicate $N > 1$.

The breeding histories of neighbors

The spatial spillover hypothesis predicts preferences for vacancies adjacent to successful males, but reoccupancy rates were not significantly related to the success of the most successful neighbor either within or between seasons (within seasons $\chi^2 = 1.27$, $N = 9$, $P = 0.2605$, between seasons $\chi^2 = 0.67$, $N = 7$, $P = 0.4135$). Although samples are small, this result was not explained by reduced statistical power because trends were not in the predicted direction. For example, among the nine vacancies observed within seasons, two of six adjacent to a male that mated during the first half of the breeding season were resettled versus one of three adjacent to males that did not mate. Between seasons, there were seven cases in which a vacant territory occurred adjacent to a returning territorial male who did not take it over. Within this sample, only one of three vacancies adjacent to a returning breeder was resettled, versus three of four vacancies in which the returning neighbor was previously unsuccessful.

I also considered the possibility that positive effects of neighbor success on territory preferences might have been obscured by the effect of the territory's mating history. However, even with the previous occupant's mating success partialled out, the mating success of the most successful neighbor still had no significant effect on the probability of resettlement (within years: $\chi^2 = 1.72$, $P = 0.1893$; between years: $\chi^2 = 0$, $P = 0.989$). The same analyses did show significant partial effects of the territory's mating history (within seasons: $\chi^2 = 10.19$, $P = 0.0014$; between seasons: $\chi^2 = 6.12$, $P = 0.0134$).

Fidelity to Territories

Fidelity of males to their territories was also more closely related to their own mating history at that site than to the mating histories of neighboring males. Within seasons, most males retained the same territory. However a minority (6 of 51) abandoned territories in mid-season and either moved to another location within the lek ($N = 3$) or wandered throughout the lek following hens for the remainder of the season ($N = 3$). All six males

had failed to mate during the first half of the mating period and the probability of abandonment decreased significantly as early season mating success increased ($\chi^2 = 5.95$, $P = 0.0147$). A higher proportion of successful versus unsuccessful males tended to return to their territories in the following year (19 of 35 versus 2 of 10), although in a logistic regression the effect of mating success in the first year was not significant ($\chi^2 = 3.55$, $P = 0.0595$).

In contrast, fidelity to a territory was not related to the mating success of the most successful neighbor either within the same season ($\chi^2 = 0.80$, $P = 0.3723$) or between successive seasons ($\chi^2 = 1.44$, $P = 0.2297$). To ensure that effects of neighbors were not obscured by a male's own breeding success, I repeated these analyses with the effect of a male's own mating success partialled out but obtained similar results (within seasons, $\chi^2 = 0.74$, $P = 0.3894$; between seasons, $\chi^2 = 1.46$, $P = 0.2262$).

Although the mating success of neighbors had no effect on a male's fidelity to a former territory within the lek, it appeared to influence his chance of returning to the same lek in the following year. When I reclassified males according to whether they occupied any territory on the lek in successive years, I found effects of both a male's own success in the previous year and that of his most successful neighbor. In bivariate comparisons the effect of a male's own success was significant ($\chi^2 = 4.04$, $P = 0.0444$), whereas that of his most successful neighbor was not ($\chi^2 = 3.6$, $P = 0.0576$), but both exerted significant partial effects in a multiple logistic regression (own success: $\chi^2 = 4.69$, $P = 0.0304$; success of best neighbor: $\chi^2 = 4.25$, $P = 0.0393$).

I identified one process which might explain why neighbors of successful males returned at a higher rate: former neighbors were at an advantage in competition to resettle the breeder's territory if the breeder failed to return. For nine territories that fell vacant between years and were subsequently reoccupied, I knew the histories of all new settlers. Six of the 14 settlers were former neighbors while the remainder had occupied territories elsewhere in the lek in the previous year or were in their first season at the lek. The number of former neighbors resettling was more than four times that expected from a random draw of all territorial males present on the lek (randomization test based on 10,000 simulations, holding numbers of settlers per vacancy at observed values: $P = 0.0015$).

Discussion

The data confirm that temporal spillover can influence the locations and clustering of male territories within leks. Successful males were more likely to return to their territories within seasons, and territories vacated by successful males were reoccupied more often both within and between seasons. Territories vacated by the most successful males became foci for clusters of territories in the following year.

There was little evidence that males settled preferentially to obtain benefits of close proximity to more successful individuals. This seems surprising in view of evidence that such benefits arise both through spatial spillover in matings (see Introduction) and through an increased probability of acquiring a successful neighbor's territory should he disappear (see Results). It is possible that weak effects were overlooked as a result of small sample sizes, but two observations argue against this. First, whereas preferences for territories adjacent to the most successful males should produce leks in which successful males

are centrally located, mating success and relative location within the lek were not correlated in this population (Gibson et al. 1991). Second, if unattractive males attempt to kleptoparasitize more attractive individuals by settling nearby, phenotypically attractive males should frequently have less attractive males as close neighbors. However, comparisons of vocal display demonstrated the opposite pattern in which neighbors were more (not less) similar than expected by chance (Gibson et al. 1991). Thus neither the dynamics of territory settlement nor the resulting spatial patterns are predicted by the idea that males attempt to increase proximity to successful neighbors.

One reason why spatial spillover may not produce clustering is that, although this benefits less attractive satellite males, it also imposes costs on attractive individuals, which consequently attempt to prevent satellite settlement. Applications of spatial spillover to leks have assumed that satellites win this conflict (Arak 1988; Höglund & Robertson 1990b), although there is no a priori reason why this should be so (Pulliam & Caraco 1984; Parker & Sutherland 1986). Sage grouse may provide an example in which satellites lose. Comparisons between attempted versus actual settlement would provide a critical test.

This interpretation could also explain why males did not queue to inherit a successful neighbor's territory. However it is also possible that the benefits of such a strategy would be low, both because successful males were more likely than others to retain their territories within and between seasons (although the latter effect was not significant) and because effects of mating history are relatively short lived, lasting only from one season to the next (Gibson et al. 1991).

These results imply that male settlement is affected by long-term memory of the previous season's distribution of mating activity. Such information may not be available to newly settling males, raising the issue of whether alternative cues are available. Two recent discussions of territory settlement in resource defense systems have pointed to the role of conspecifics in providing cues to resource quality additional to those obtainable by direct assessment (Shields et al. 1988; Stamps 1988). The locations of established individuals will be informative when these employ a "win-stay" settlement rule, while the value of the information will increase when the resource is difficult or costly to assess. Because successful males exhibit fidelity to the lek and tend to return to the same territory between seasons, locations of older territorial males might also be important cues for male settlement in sage grouse. This would provide an additional process causing males to cluster at leks. It is unlikely that initial territory settlement in this species would be based only on conspecific locations. Juvenile male sage grouse visit leks during the mating period of their first spring but rarely establish lek territories before the end of the season (Wiley 1973; Emmons & Braun 1984; Dunn & Braun 1985; personal observations). Thus they have opportunities to observe mating activity on particular territories as well as the locations of established males before settling. However, established males might provide the primary cues in other species such as sharp-tailed grouse, *Tympanuchus phasianellus*, in which juvenile males establish lek territories in their first autumn, several months before female attendance and mating (Kermott 1982).

The mechanism generating the patterns of settlement described here combines two features: site fidelity by hens from one season to the next, and unanimous female choice within seasons (Gibson et al. 1991). While the former might be sufficient to maintain any

dispersion of males from widely dispersed to clustered (e.g., Warner 1987), the latter is clearly necessary to induce clustering. In sage grouse, mating skew increases with the numbers of hens that visit the lek at the same time, apparently because under these circumstances hens often copy the choices of others (see also Wade & Pruett-Jones 1990; Gibson et al. 1991). This suggests that the extent to which females visit leks simultaneously may be an important influence on clustering of males. Lek formation driven by such a mechanism has the potential to be self-reinforcing because any initial unanimity in choice should enhance male clustering at that site, which in turn will reduce the number of sites at which females might encounter males, and hence further increase the number of females that visit any given cluster.

In conclusion, this study illustrates how female choice may drive the local clustering of male territories within leks. This process is complementary to hotspot settlement, which provides an explanation for the coarse scale distribution of males between different leks (Bradbury et al. 1989a). This confirms recent suggestions that different processes affect lek dispersion on different spatial scales. It also suggests that to understand why leks form we need to explain both why females mate at leks and why they choose among males.

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