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# A Re-evaluation of Hotspot Settlement in Lekking Sage Grouse

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## Abstract

Recent analyses of avian leks have come to conflicting conclusions concerning the role of male settlement on female traffic hotspots. This issue was reexamined in the sage grouse, *Centrocercus urophasianus*, using data on prenesting movements of radio-tagged females and the dispersion of lekking males collected during a 10-year field study. As expected with hotspot settlement, leks were preferentially located in areas through which females traveled between wintering and nesting ranges before mating. In addition, the distribution of males among leks was related proximately to variation in numbers of females visiting each lek during the mating period and ultimately to numbers that nested within a 2-km radius, within which nesting hens were preferentially attracted. The results show both that hotspot settlement can explain certain coarse scale features of male dispersion, and that female behavior during different stages of the prenesting period may influence particular components of male dispersion to differing extents.

During the past decade there have been numerous attempts to explain why males of lek-breeding birds cluster their mating territories at specific nonresource-based sites (Höglund & Alatalo 1995). The question is interesting because the evolution of lekking has been difficult to accommodate within the paradigm that male mating strategies are shaped by the spatial and temporal distribution of receptive females (Davies 1991). Despite considerable research, however, the role of female behavior in the evolution of leks remains a contentious issue (Clutton-Brock et al. 1993).

Females could cause males to form leks in at least three ways. Males might cluster their mating territories because (1) range overlap generates hotspots with locally high female

encounter rates (Bradbury & Gibson 1983; Bradbury et al. 1986), (2) females are preferentially attracted to larger groups of males (Bradbury 1981), or (3) highly skewed mating within leks generates opportunities for less successful males to acquire matings either through close proximity to a successful individual (hotshot or spatial spillover effect: Beehler & Foster 1988; Höglund & Robertson 1990; Gibson et al. 1991) or via inheritance of his territory or social status (temporal spillover: Gibson et al. 1991; McDonald & Potts 1994). Field studies have shown that clustering of lek territories may be driven both by mating skew within leks (Gibson et al. 1991; Gibson 1992; Rintamäki et al. 1995) and by female attraction to larger or more densely packed groups of males (Alatalo et al. 1992; Lank & Smith 1992; Höglund et al. 1993; Hovi et al. 1995). Although these processes explain why males join leks, they do not account for broader-scale features of male dispersion, such as where leks are located or how males are distributed among them. The hotspot hypothesis provides a potential explanation for these features but has not gained wide acceptance, principally because even the most supportive studies showed that female ranging behavior was a relatively weak predictor of male dispersion (Pruett-Jones 1985; Bradbury et al. 1989a; Schroeder & White 1993). It has also received only limited support from studies of lekking ungulates (Apollonio 1989; Balmford et al. 1992).

In contrast, recent studies of the lek-breeding ochre-bellied flycatcher, *Mionectes oleagineus*, suggest that female traffic may influence male settlement much more precisely than was previously suspected. Westcott (1995) found that male display territories in this species are located along well-defined traffic routes used by females when traveling between foraging areas. In addition, leks of *M. oleagineus* and two sympatric manakins were clumped in space and tended to covary in size over time, as would be expected if males of each species settled on conspecific female traffic routes whose locations and usage were similar as a result of interspecific diet overlap (Westcott 1994). Unlike previous studies, which measured only static female locations, Westcott measured the paths of moving females and found that these, and not locations where females spent time, predicted male locations. This difference may explain why he found more compelling support for a hotspot mechanism. One purpose of this study was to reexamine the issue of hotspot settlement in sage grouse, *Centrocercus urophasianus*, in light of this suggestion.

Bradbury et al. (1989a, b) examined male dispersion and its relationship to female prenesting behavior in populations of sage grouse in eastern California. Studies of radiotagged females showed that in early spring, individuals moved from overlapping wintering areas to dispersed nesting ranges and then around 10 days later visited a lek, often close to the nest, to mate. The sequence of temporal changes in male and female dispersion suggested that females selected nest sites independently of the locations of displaying males, and that males moved among leks in response to, and in anticipation of, the changing distribution of females. To investigate the hotspot hypothesis, pooled data on day- and night-time female locations from late winter until the onset of incubation were used to predict where males would display. These predictions were then compared to the actual distribution of lekking males over a range of grid sizes. At spatial scales fine enough to specify lek locations, there was little relationship between predicted and actual male distributions, but at coarser scales (using grid cells sufficiently large to include more than one

lek) the fit was better. Bradbury et al. (1989a) proposed that the nesting dispersion of females determines lek sizes by influencing numbers of hens attracted to each lek. Other factors were invoked to account for lek locations (meadow habitats favored by displaying males) and the tight clustering of lek territories.

In the present study, I used an extended data set to reexamine the role of hotspot settlement in sage grouse in more detail than was previously possible. In addition to incorporating measures of female dispersal trajectories, I considered the possibility that particular times during the female prenesting period may be more relevant than others for determining where a female will mate. I focused on two components of male dispersion, lek location and the distribution of males across leks, rather than treating the spatial distribution of displaying males as a single dependent variable. I also included tests of the notion that females favor larger leks. In contrast to our earlier work, the results provide evidence that lek locations are related to female traffic. They also provide specific support for our previous suggestion that nesting densities influence lek size. Finally, I reconsider the hotspot hypothesis in light of this and other recent studies.

**Methods**

I studied a population of sage grouse resident in Long Valley, Mono County, California from 1984 to 1993. Details of the study area, population, and general methods have been published previously (Bradbury et al. 1989a, b; Gibson et al. 1991). Analyses presented here deal with the following variables.

*Lek Location*
Before the study began, eight leks (1, 2, 3, 4, 5, 8, 9, 10A) were located from records provided by the California Department of Fish and Game. An aerial survey conducted during the peak mating period in 1984 revealed no additional leks. All eight sites remained active throughout the study. In 1985, a new lek (13) was found, which became inactive as birds began using a second site nearby (lek 14) between 1987 and 1989. Some other leks were transiently active in particular years but were not sampled sufficiently often to be included in the long-term data set.

*Lek Counts*
Peak daily counts of each sex were collected on a regular basis from mid-March to late April in 8 years between 1984 and 1993 (1990 and 1992 were not sampled). These data were used to estimate long-term mean numbers of males and females attending each lek during the mating period, to analyze trends in male numbers over time, and to estimate lek size when analyzing whether individual females choose between leks. When possible, observers classified males as adults (> 1 year old) or yearlings (< 1 year) based on tail length and shape (Patterson 1952).

Long-term mean numbers of males and females at each lek were computed from peak daily counts taken during the first 2 weeks of mating in each sampled year. This period included $84.8 \pm 8.2\%$ of observed matings (range = $76.3 - 100\%$, $N = 9$ lek years) at a subset of leks studied intensively throughout a breeding season. Because of annual variation in

study emphasis, not all leks were sampled each year ($\bar{X} \pm$ sd years per lek = 4.4 ± 2.6, range = 2 – 8). This might lead to bias if leks varied annually in their relative popularity with either sex, or if there were large annual variations in numbers of birds across all leks. To check these possibilities, I analyzed data from a subset of the three largest leks (2, 4, and 8) that were counted in the same 7 years. Numbers of both sexes varied significantly between leks within years (Friedman tests; for both males and females: $\chi^2 = 10.571$, $df = 2$, $P = 0.0051$) but not between years within leks (males: $\chi^2 = 5.714$, $df = 6$; females: $\chi^2 = 8.87$, $df = 6$). As an additional check, I compared mean counts per lek pooled over all sampled years with values computed after scaling annual values as a percentage of the count at lek 2, which was attended by the largest numbers of both sexes in every year. The two measures were highly correlated (males: Kendall's $\tau = 0.889$, $P = 0.0008$, $N = 9$ leks; females: $\tau = 1.0$, $P = 0.0002$, $N = 9$). Together, these analyses suggest that neither potential source of error is appreciable.

In 1993, more precise measures of male and female numbers were collected at seven leks to examine how female numbers scale with lek size. The sample included six long-term leks (1, 2, 3, 4, 5, 8) plus a transient lek (2A) located between leks 2 and 3. Each lek was counted at 10-min intervals from first light until all birds had left (up to 4 h later) on four mornings. As far as possible, males were classified as adults or yearlings as described above. Leks 2, 2A, 3, and 4 were counted simultaneously on April 13, 16, 19, and 21, and leks 1, 5, and 8 were counted on April 14, 15, 17, and 22. The sample period includes the first 10 days of mating in that year. I combined the two sets of leks, because preliminary analyses using Friedman tests indicated no systematic effects of date on counts within each set. The number of hens attracted to a lek each day was estimated by the peak count, which appears to be a reliable measure (peak count = 0.158 + 0.914 × number of individuals; $r = 0.993$, $P < 0.0001$, $N = 7$ days at lek 8 in 1991), because hens arrive relatively synchronously soon after the onset of display. Mean numbers of females per male for a given day were computed as the mean of this ratio across all scans when females were present. Daily lek size was measured as the mean count over all scans when males were present on a given day (see Results).

### Behavior of Individual Females

Between 1984 and 1993, 84 females were captured and fitted with poncho-mounted radio transmitters. Sixty-eight birds were spot-lighted at various times of year and 16 were cannon-netted at leks during spring. Information on ranges before and/or during nesting dispersal was obtained for a subset of individuals radio-tracked at 1- to 3-day intervals during the springs of 1984–1986, 1991, and 1993 (see Bradbury et al. 1989a; Gibson & Bachman 1992). When a hen was tracked in more than 1 year, only the year with most complete data was included in the analysis. Predispersal ranges were measured during a 10-day period before the day each individual dispersed from its winter range if known ($N = 17$ birds) or else prior to 10 days before the first mating of the year, a period when virtually all hens were still in their winter ranges ($N = 9$). Measurement of dispersal dates is described by Bradbury et al. (1989a). Twenty-two birds were tracked in sufficient detail to provide information on the trajectory followed from winter range to nesting area prior to visiting a lek.

For these individuals, the dispersal trajectory was estimated by interpolating between successive daily tracking locations over the period from winter range departure to the first point in the nesting range. Although not based on continuous tracking, this method should be relatively accurate because females move very little during the day and undertake long-range flights primarily at dawn (Gibson & Bachman 1992). Nest locations were also obtained for 24 hens whose nests were found and for a further 10 birds that localized their ranges as if nesting but whose nest was not found because of its inaccessibility, early abandonment, death of the female, or radio failure. For the latter cases, I used the medians of the $X$ and $Y$ coordinates of the presumed nesting range to estimate nest location. Finally, I determined the lek visited for a subset of nesting females that were radio-tracked to a lek ($N = 6$), observed at a lek that was monitored for other reasons ($N = 6$) or cannon-netted at a lek ($N = 9$) during the mating period. All of these cases involved post-dispersal lek visits. I assumed that the lek at which the female was seen or captured was the site at which she mated because all closely tracked hens that nested visited a lek approximately 10 days post-dispersal, and none visited more than one lek at this stage of the breeding cycle. Females occasionally visited additional leks before or during the dispersal period.

Two sets of population dispersion measures were extracted from these data. First, to analyze lek location, I imposed a 1-km grid on the study area; for each cell I counted the numbers of females (a) that were located within it during the 10 days prior to dispersal, (b) that were located within it during the day in the dispersal period, (c) whose dispersal trajectory passed through it, and (d) that nested within it. Each measure was then compared to the spatial distribution of lek sites (see Results). The intent of the analysis was to see how accurately lek sites could be predicted from female traffic measures. The grid size was chosen because it was both fine enough to specify major lek sites in a single cell and coarse enough to provide robust estimates of female traffic.

Second, to examine relationships between numbers of females per lek and local female densities, I extracted the same density measures within circles of a given radius centered on each lek. Because the actual drawing area of any lek was unknown, each measure was computed for increasing radial distances between 1 and 10 km in 1-km increments representing progressively larger hypothesized drawing areas. For each radius, two sets of density measures were extracted, raw counts of numbers of females ("traffic density") and counts in which each female's contribution was divided by the number of leks that claimed her within the same drawing radius ("hotspot density"). The latter measure incorporates the devaluation of a female due to sharing of her mating probability between lek sites, a feature of hotspot settlement models proposed by Bradbury et al. (1986). Each measure was then correlated with numbers of hens attending the lek.

The nest location data from which the preceding dispersion measures were computed include some hens that were trapped at leks by cannon-netting during the mating period. Because females that nest near leks preferentially visit nearby leks (see Results), the inclusion of birds trapped at leks risks inflating nesting density estimates for the leks where they were captured. Only one of 12 cannon-netted females nested within a short distance (2 km) of the lek where she was captured, however, and omission of cannon-netted birds did not alter the patterns reported in the Results. This concern does not apply to other

measures of female traffic, which were only measurable for birds trapped off leks before mating started.

To investigate female choice between leks of different sizes, I analyzed data for a subset of individuals for which I knew both the lek visited for mating and the set of leks available within the prenesting range. The set of leks within each female's range was defined as those within a minimum convex polygon drawn around locations collected from 10 days before she left her winter range until 14 days afterward (14 days is the mean interval between departing the wintering area and the last lek visit: R. Gibson, unpublished data). For each female, I computed sizes of all within-range leks as the mean of peak daily male counts up to the last lek visit, when she was presumed to mate. The size rank of the lek visited for mating was then recorded and summed across all females. For comparison, I computed numbers of visits to leks of each size rank that would have been recorded if each female had picked a lek at random from those within her range. For every female, each within-range lek was assigned a probability of being visited that was computed in different ways according to how her visit was detected. For hens that were radio-tracked to a lek (an unbiased method), each lek was assigned 1 divided by the number of within-range leks. For a hen whose visit was recorded because she attended an observed site, each lek observed on the day of her visit was assigned 1 divided by the number of observed leks, and unwatched leks were assigned 0. For cannon-netted hens, each lek at which females were netted was assigned the number cannon-netted at that lek divided by the number cannon-netted at all within range leks, and other leks were assigned 0. Probabilities of detected visits were then summed for leks of each size rank across females. A similar procedure was used to estimate expected visits to each lek by hens that nested within 2 km of a lek (see Results: Female lek attendance and local densities), except that for each bird I considered all leks within the study area as potentially visited sites.

### Statistical Analysis

Where appropriate, parametric methods were used. Nonparametric tests were substituted where data could not be satisfactorily normalized by transformation. The analysis of lek location uses a randomization procedure described in the Results. Descriptive statistics are given as mean ± sd.

**Results**

### Lek Location

Lek locations showed a clear association with areas through which females traveled between wintering and nesting ranges. Figure 1 plots locations of long-term lek sites relative to topographic features (Fig. 1a) and to the dispersion of females before, during, and after nesting dispersal (Fig. 1b–d, respectively). Females dispersed to nesting ranges from a common wintering area in the south of Long Valley using two primary routes along which the leks are aligned. To test the apparent association between dispersal traffic and lek location, I imposed a 1-km grid on the study area and computed the mean number of females per cell for all cells in which leks were located ($N = 10$). This number was then compared with the distribution of values obtained in 104 trials of a randomization test that picked

the same numbers of cells at random and without replacement from all suitable habitat (cells > 50% occupied by sagebrush-dominated plant communities or meadow, $N$ = 414). This procedure confirmed that leks were located in areas of above-average dispersal traffic ($P$ = 0.0002; Fig. 1c), although not necessarily at points where it was highest: a comparison between lek cells and all cells through which at least one female traveled during dispersal showed no association between the numbers of females and lek location ($P$ = 0.957). Further tests revealed that lek locations showed only weak tendencies to be associated with the daytime distributions of females during the 10 days before nesting dispersal (Fig 1b: $P$ = 0.0687) and during dispersal ($P$ = 0.0885), and that they were not located in areas of above average nest density ($P$ = 1.0; Fig. 1d).

(a)



**Figure 1.** Positions of leks (open circles) in relation to (a) topographic features (leks are identified by numbers, sagebrush is shown in white, meadows by horizontal shading, water by stippling and forested areas in black), (b) the static distribution of females during the 10 days before nesting dispersal (the intensity of the texture indicates relative numbers of radio-tracked females using each 1-km grid cell, range 1–8), (c) the distribution of female trajectories during nesting dispersal (conventions as in Fig. 1b, range = 1–6 females per cell), and (d) the distribution of nests (inverted triangles).
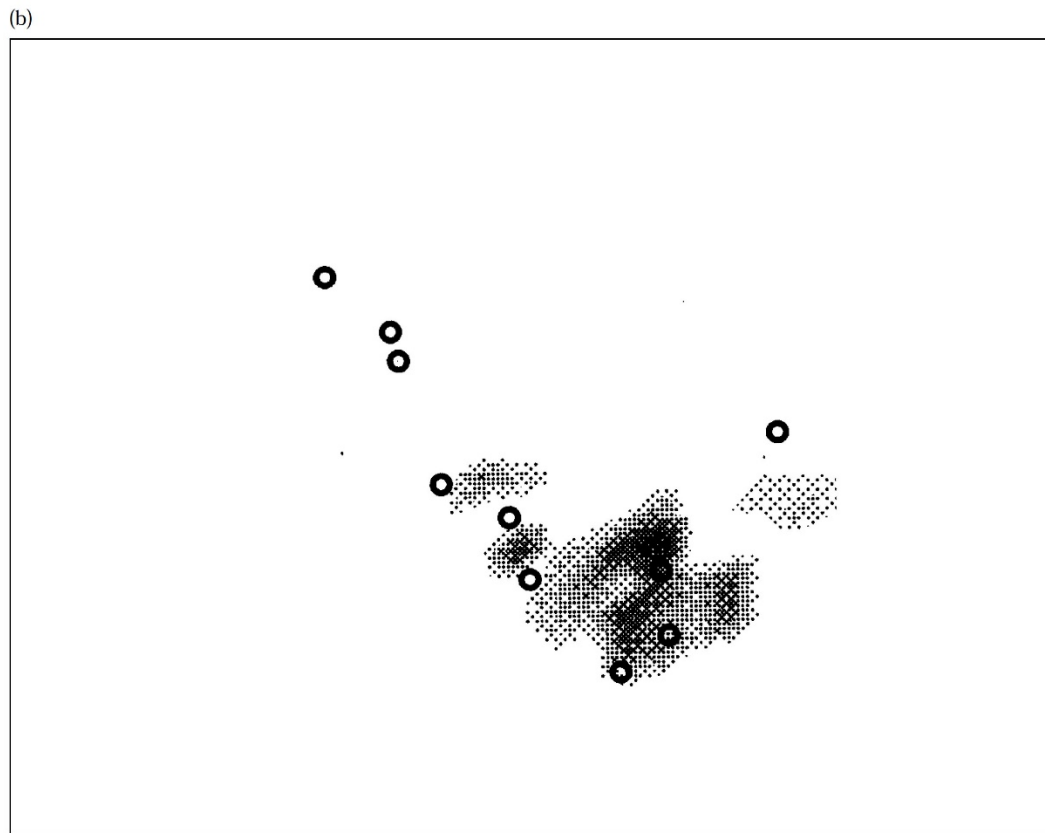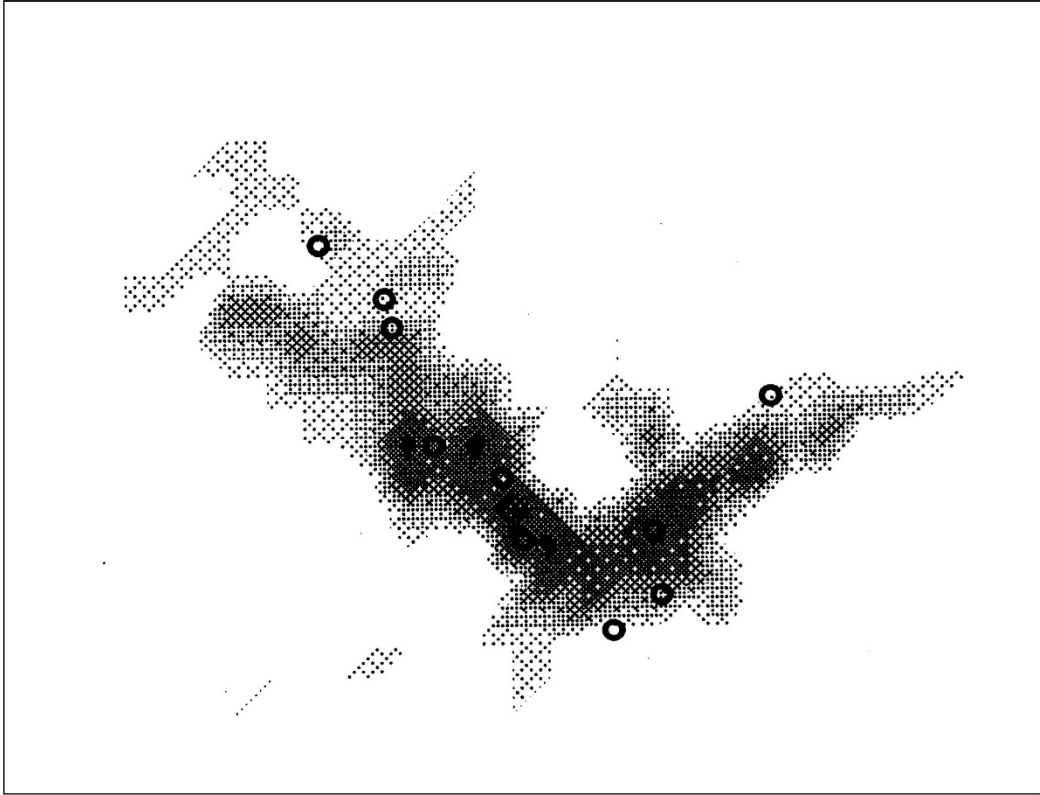
(b)



**Figure 1.** Continued.
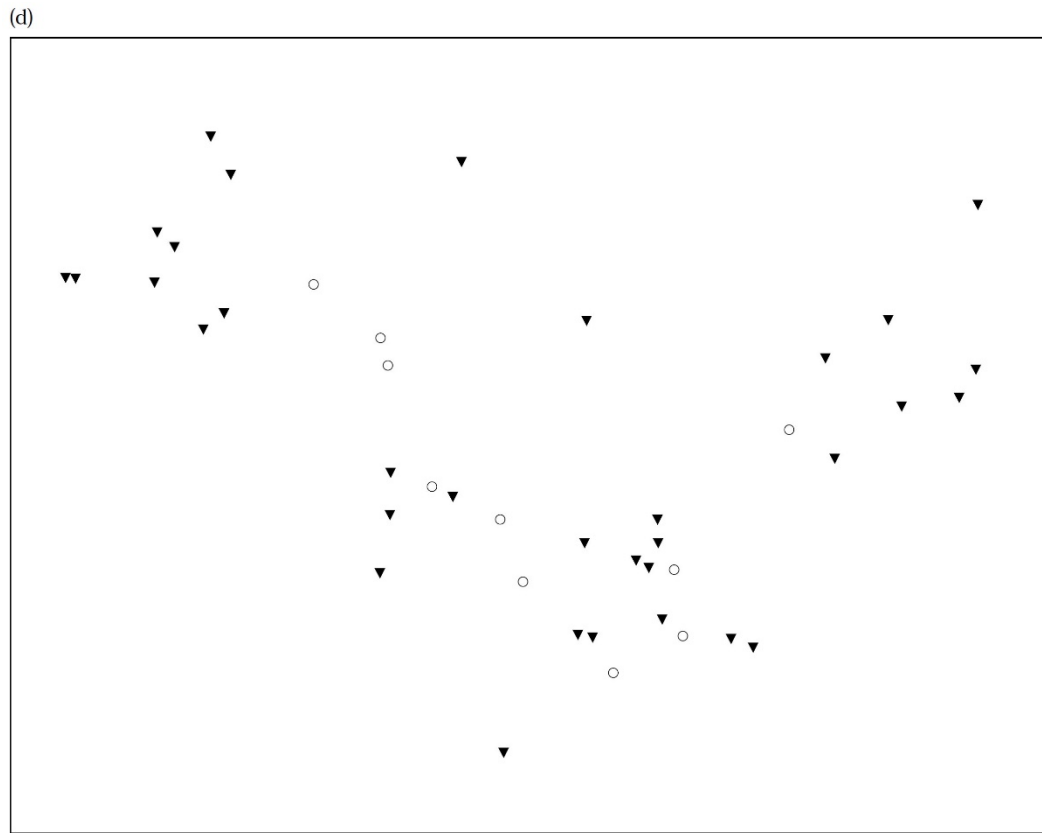
(c)



**Figure 1.** Continued.

(d)



**Figure 1.** Continued.

Lek sites were also associated with meadows. Although meadows occupied only 9.1% of the combined area of sagebrush and meadow habitats, six of the 10 lek sites were in meadows (Fig. 1a: one-tailed binomial probability = 0.00009). Meadows occupied a larger proportion of the area used by dispersing females (16.7% of cells used by at least one female), but after taking this into account there were still more leks in meadows than expected by chance (one-tailed binomial probability = 0.0025). Meadows did not appear to be the primary factor determining lek location, however. Not only were several leks located in sagebrush far from meadows, but lek location also remained significantly associated with female dispersal traffic after controlling for the presence of meadows by limiting the analysis to sagebrush-dominated habitats (randomization test: *P* = 0.0003).

**Lek Size**

*Female attendance and male numbers*
As we found previously (Bradbury et al. 1989a), numbers of males per lek covaried positively with numbers of females that visited during the mating peak ($r = 0.896$, $P < 0.001$, $N = 9$,

log-transformed values; Fig. 2). This association could have arisen because males settle according to numbers of females that visit a lek because females prefer sites with more males, or for both reasons. The following analyses explore these possibilities.
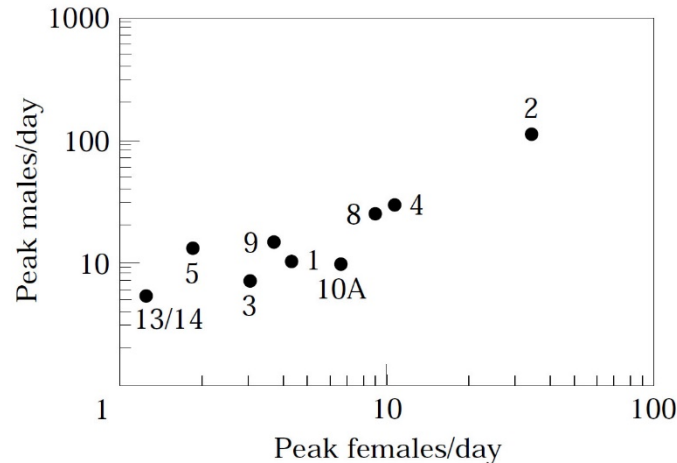


**Figure 2.** The relationship between mean peak male and female counts between leks during the first 14 days of mating. Values are long-term means over all sampled years. Lek identity is indicated next to each point.

**Male responses to female numbers.** There was evidence that males responded numerically to female availability on at least two time scales: over periods of a few minutes within morning display sessions and seasonally. As an illustration of short-term changes in male numbers within mornings, Figure 3 plots changes in male numbers across successive 10-min scans in relation to changes in female numbers in 1993. As the 95% confidence intervals show, male numbers increased significantly when females arrived, remained stable when females were present and their numbers remained constant, and declined both when females left the lek and when none were present. Although this pattern could have arisen if females arrived and departed in mixed-sex groups, this was rare: rather, male numbers changed after female arrivals or departures due to local movements between the lek and surrounding sagebrush habitat. The same trends were found within adult and yearling males when analyzed separately. For adults, however, the only significant effects were declines when females left the lek or were absent. Sample sizes for yearlings, which comprised only 16.1 ± 3.7% of males on leks during the 1993 breeding peak, were too small for statistical tests.
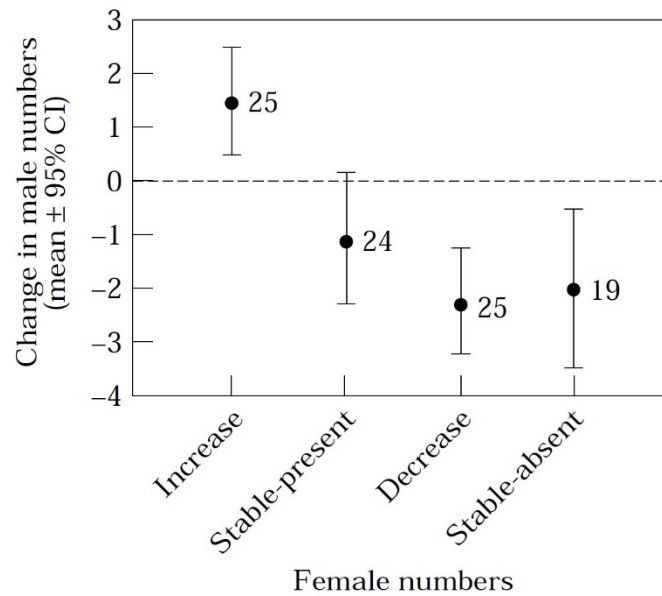
**Figure 3.** Changes in male numbers between successive 10-min scans in relation to changes in female numbers and female presence over the same period. Separate mean values were computed for each day at each of seven leks studied in 1993 and then pooled to yield the plotted mean. Sample sizes (lek-days) are indicated beside each point.

To investigate how males responded seasonally to the availability of females at particular leks, I examined seasonal trends in peak daily counts during the mating period in relation to the mean number of females per male per day at sites that were counted daily throughout the breeding season. The rationale is that males attempting to maximize opportunities to court females should seek sites with higher female availability.

Table 1 summarizes the data and illustrates two points. First, seasonal trends in male numbers varied both between different leks in the same year (for example, in 1985 male numbers declined at lek 4 but tended to increase at lek 8) and between different years at the same lek (e.g., males declined at lek 4 in both 1984 and 1985 but increased in 1991). This result suggests that local factors associated with a particular lek and year affect the balance between recruitment and loss. Second, this variability is related to female availability, as indicated by a positive relationship ($\tau = 0.491$, $P = 0.05$, $N = 11$ lek-years) between mean females per male per day and the Pearson correlation between male number and date over the same period. In short, male numbers declined at leks where female availability was low and increased where it was high (Fig. 4).

**Table 1.** Seasonal trends in male numbers and female availability in 11 lek-years

| Lek | Year | Seasonal trend $r$ ($N$) | Mean females/male/day |
|---|---|---|---|
| 2 | 1988 | 0.143 (42) | 0.129 |
| 4 | 1984 | −0.612 (28)*** | 0.028 |
|   | 1985 | −0.633 (24)*** | 0.104 |
|   | 1986 | 0.203 (32) | 0.259 |
|   | 1987 | 0.347 (24) | 0.263 |
|   | 1989 | 0.156 (24) | 0.184 |
|   | 1991 | 0.536 (17)* | 0.438 |
| 8 | 1985 | 0.288 (28) | 0.164 |
|   | 1986 | 0.540 (23)** | 0.235 |
|   | 1987 | −0.179 (24) | 0.288 |
|   | 1991 | 0.411 (14) | 0.766 |

$N$ = number of days. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Seasonal trends vary between samples (ANCOVA: lek-year versus date interaction: $P < 0.0005$).
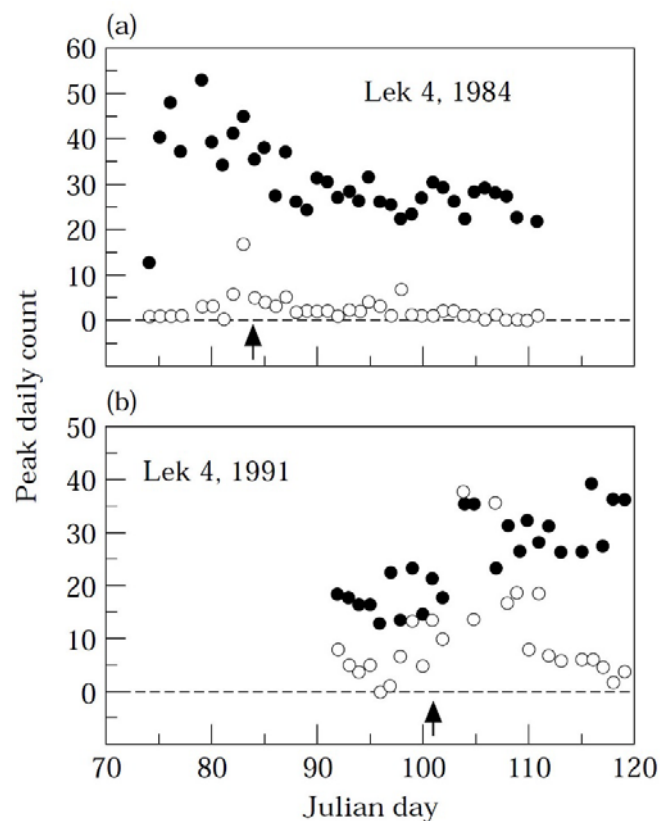


**Figure 4.** Examples of (a) a seasonal decline in male numbers at a lek with few females per male and (b) an increase when there were relatively more females. Males are shown by filled symbols and females by open symbols. Arrowheads mark the onset of mating.

This adjustment appeared to result from settlement by yearling males. In a subset of 7 lek-years for which there were sufficient data to analyze adults and yearlings separately, seasonal trends in yearling numbers tended to covary positively with mean numbers of female per male ($\tau = 0.619$, $P = 0.07$), whereas those of adults did not ($\tau = -0.048$).

**Female responses to male numbers.** I first examined whether females were preferentially attracted to larger leks by examining how peak hen numbers and mean females per male scaled with mean numbers of males across seven leks sampled intensively in 1993 (Fig. 5). Peak female counts covaried closely with mean male numbers (both log-transformed: $r = 0.958$, $P = 0.0007$, $N = 7$). The slope of the regression, however, barely exceeds one female per male added (untransformed data: $Y = -0.110 + 1.089X$; 95% confidence interval for slope = 1.041 – 1.137) and the relationship shows no hint of the upward curvature expected if larger leks attract relatively more females. Consistent with this interpretation, numbers of females per male did not significantly increase with male numbers (males log-transformed: $r = 0.417$, $P = 0.352$, $N = 7$).
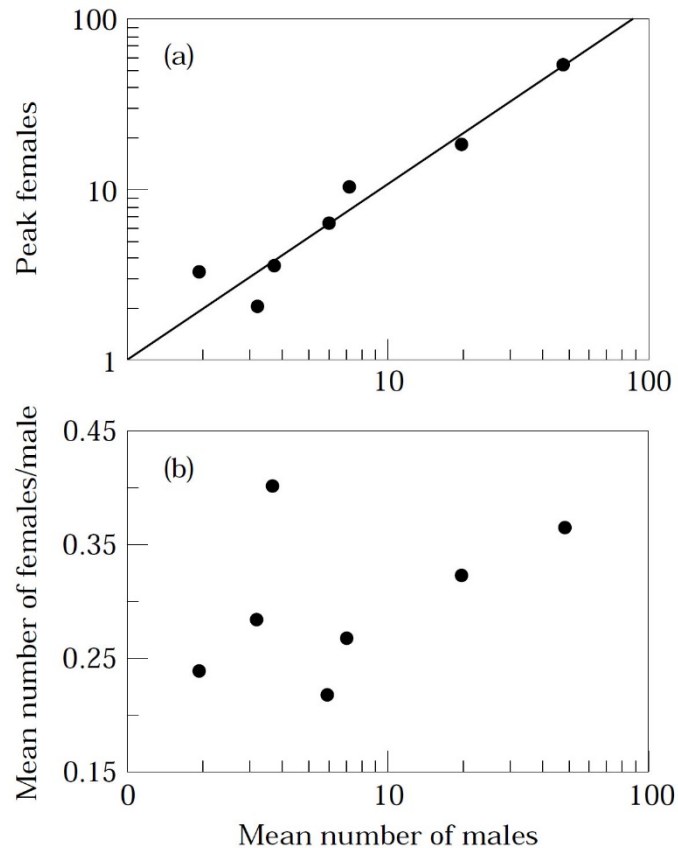


**Figure 5.** (a) Peak females per day and (b) mean females per male per day plotted against mean male counts for seven leks in 1993. Values are means across four days during peak mating.

One weakness of the preceding approach is the assumption that lek sizes remain static relative to the time over which hens choose a lek. This is problematic, because male numbers can change rapidly in response to numbers of visiting females (Fig. 3). Such behavior could inflate estimated lek size above the value assessed by a female prior to her arrival, making detection of a preference for larger leks difficult. Although the previous analysis used mean rather than peak numbers of males to minimize this problem, it is still possible that the sizes of larger leks measured in this way were disproportionately inflated. I therefore undertook a second analysis that is less vulnerable to this criticism.

Numbers of marked hens that visited leks of different size rank within their ranges were compared with a null expectation that all within-range leks were equally likely to be visited. Data were available for nine birds whose ranges were mapped in detail and all leks counted. Four individuals visited the largest lek in their ranges, three visited the second largest, and one each visited the third- and fourth-ranked leks. None visited a fifth-ranked lek. Although this bias might appear to support choice for larger leks, it is produced by an observational emphasis on these sites. Given the distribution of observation time between the leks, and assuming that hens choose a lek at random within their ranges (see Methods), 4.03 visits are predicted to the largest lek and 4.97 to the remainder, which is statistically indistinguishable from the observations (goodness-of-fit $\chi^2 \approx 0$, $df = 1$, $P \approx 1$). Thus, this analysis also fails to show that females prefer larger leks.

In short, males distributed themselves between leks in proportion to female availability. There was no compelling evidence that females favored leks based on the numbers of males present, although sample sizes testing this hypothesis were small. The next section considers alternative explanations for variation in numbers of females per lek.

*Female lek attendance and local densities*
I found evidence that numbers of females visiting a lek were related to numbers that nested nearby, but not to levels of female traffic earlier in the prenesting period.

Figure 6 plots Kendall rank correlations between hens per lek and numbers nesting nearby as a function of drawing area radius, within which nest density was computed. Correlations peak at 2 km for both traffic and hotspot density estimates and decline as the drawing area is progressively enlarged (for both density estimates: $\tau = -0.600$, $P = 0.016$, $N = 10$). If tests at each drawing area size are treated as independent hypotheses, the correlation at 2 km between visiting females and nests is significant for the traffic density estimate ($P < 0.05$) and marginally nonsignificant for hotspot density ($P = 0.055$), which tended to have lower correlations with visiting females at all drawing area sizes. Forty-one percent of all nests were located within 2 km of a lek. There were no significant relationships between females per lek and measures of female density during or prior to nesting dispersal.
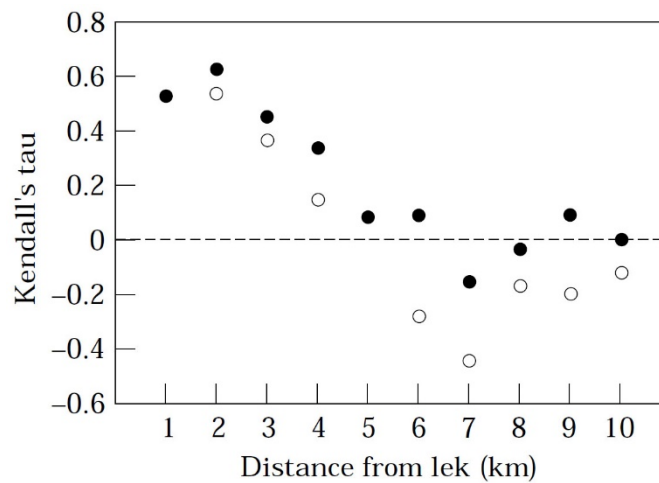
**Figure 6.** The correlation (Kendall's τ) between females per lek and numbers of nearby nests as a function of the distance from the lek within which nests were counted. Filled symbols show values for actual numbers of nests ("traffic density") and open symbols values for numbers of nests devalued by sharing among leks ("hotspot density").

These data suggest that leks selectively recruit hens that nest within a 2-km radius, which was confirmed by an analysis of individual behavior patterns. Of nine hens that nested within 2 km of a lek and whose lek visits were observed, six visited a lek within 2 km of their nest and only three went further. The proportion traveling less than 2 km is significantly higher than expected with random choice between all leks in the study area (goodness-of-fit $\chi^2 = 3.874$, $df = 1$, $P < 0.05$; expected values per lek were corrected for observation and capture bias as described in the Methods). There were insufficient data to determine whether this was because hens nesting near leks preferred close leks, because they visited closer leks due to their availability, or for both reasons. The success of nesting but not prenesting traffic measures in predicting numbers of hens per lek, however, implies a preference for closer leks.

**Discussion**

The data provide two lines of evidence consistent with hotspot settlement. First, males place leks in open areas within habitats through which females travel between wintering and nesting areas in the premating period. Second, males distribute between leks in proportion to numbers of hens that visit, which apparently vary as a consequence of spatial variation in nesting densities and a propensity for females to favor a lek near the nest.

The finding that leks are placed within female dispersal corridors confirms Westcott's suggestion that males may be more responsive to patterns of female movement than to their static distributions. It also makes sense in light of the coincidental timing of long-range movements by females and male display activity, the visual conspicuousness of displaying males at long range even in low light (personal observation), and because females often return to mate at a lek along the path between their winter and nesting ranges. The

correspondence of lek locations with female traffic routes is similar to that found in the ochre-bellied flycatcher (Westcott 1995). In Westcott's study, however, female travel routes were narrow and followed topographic features. By contrast, the major dispersal corridors used by female sage grouse in Long Valley were broad, not closely constrained by topography and represented direct routes between the major wintering area and nesting habitat in outlying areas.

The conclusion that a patchy dispersion of nesting females accounts for the stable partitioning of males among leks confirms a previous suggestion of Bradbury et al. (1989a). Bergerud & Gratson (1988) also proposed that nesting densities affect lek size in grouse on the basis of correlations between lek size and the amount of adjacent nesting habitat (sharp-tailed grouse, *Tympanuchus phasianellus*: Pepper 1972) and declines in lek size following destruction of adjacent nesting habitats (sage grouse: Wallestad 1975). The analyses presented here, however, appear to provide the most detailed evidence to date on the way in which this linkage arises.

One incompletely resolved issue is the nature of the settlement process that matches male to female numbers across leks. Short-term adjustments within mornings redistribute males between a lek and its immediate surroundings, but are unlikely to explain variation between leks. Late season settlement by yearling males provides a more likely explanation. Not only are yearlings known to visit multiple leks (Emmons & Braun 1984), but those that attend a lek late in the season typically return to the same site the following year (R. Gibson, unpublished data). In addition, some adult males that have failed to mate move to another lek in the following season (Gibson 1992). Relocation of adults could contribute to the match between male and female numbers, although it must be less important than settlement by yearlings, because only 8–12% of adults move each year (R. Gibson, unpublished data).

Another unresolved issue is how males assess potential lek sites. There are at least three potential cues. First, the siting of several leks adjacent to areas in which females roost, feed or loaf during the dispersal period suggests that female presence in such areas could provide initial cues, both when leks are first established and to naive males choosing between established leks for the first time. Because densities of hens at this time are not well correlated with numbers that later visit to mate, reliance on such cues should produce initial distributions of males that are poorly matched to later mating opportunities. This hypothesis may explain both why male numbers sometimes adjust substantially to female availability later in the season (Fig. 4), and why early season leks are occasionally abandoned once mating begins at other sites (Bradbury et al. 1989b). A second class of cue is provided by relative numbers of hens that visit during the mating period, as demonstrated here. Finally, because successful males and their immediate neighbors show high levels of fidelity to leks across years (Gibson 1992), locations of established males provide cues to sites that females are likely to return to later (Gibson et al. 1991). The extent to which males use each source of information remains to be determined.

Although this paper has emphasized the effects of female dispersion on the spatial distribution of lekking males, other factors also affect lek location and size. The presence of open areas favored by displaying males influences lek location, as indicated by the preference for meadows. Another factor is harassment by predators, which can cause leks to shift

substantial distances (Ellis 1987) and depress male attendance (Bradbury et al. 1989b). In addition, it is not yet clear why leks are characteristically spaced so evenly through available habitat. The absence of persistent interstitial leks implies that birds in such sites relocate to larger leks nearby. Theoretical discussions of this pattern have invoked attraction of females to larger leks (Bradbury 1981). I found no support for this effect at the level of existing lek spacing, but the power of these analyses is low, and this effect might still play a role at a more local scale. In addition, both attraction of females to larger female groups (as occurs within leks: Gibson et al. 1991) or of males to other males (as suggested by the conspecific cueing hypothesis: Shields et al. 1987; Stamps 1988) could be involved. This issue could be resolved by comparing the dynamics of adjacent leks that are unusually close together with others that are more widely spaced.

Together with Westcott's recent studies, this paper provides new support for the proposition that female dispersion and movements may influence male dispersion in lekking birds. Do these new results suggest, however, that hotspot processes play a more central role in avian lek evolution than has been suggested recently (Gibson 1992; Clutton-Brock et al. 1993)?

Hotspot settlement models predict that males will cluster with increases in female range size and decreases in female density, and that males will settle on local peaks of female traffic (Bradbury et al. 1986). The former two points are borne out by comparative data on grouse (Bradbury et al. 1986) and the latter by Théry's (1992) study of six sympatric manakin species. This evidence on its own is not compelling, however, because high mobility and low population density present special problems for the sexes in finding mating partners, which could lead to clumping via other mechanisms. The last prediction is supported with respect to lek position by data from lesser prairie chickens, *T. pallidicinctus* (Schroeder & White 1992), ochre-bellied flycatchers (Westcott 1995) and sage grouse (this study). Lek size is also affected, albeit indirectly, by local nest densities in sage grouse. Only Westcott's study, however, has shown that female traffic can specify locations at which males display with any precision, and our studies of sage grouse provide evidence that other processes drive the clumping of male territories into classical leks (Gibson et al. 1991; Gibson 1992). In short, although current evidence suggests a modulating role of female traffic in locating avian leks and allocating males between them in some species, both the interspecific distribution of lekking and the clumping of male territories that is a defining feature of classical leks are likely to have other explanations.

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