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Dispersion of displaying male sage grouse

II. The role of female dispersion

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Summary. The degree to which male sage grouse select lek sites and females select nesting sites to maximize proximity to the other sex was examined by contrasting male dispersions with the dispersions and movements of females in the months preceding incubation. Wintering females exhibit highly overlapping ranges due to shared use of central refugia areas. In late winter and early spring, females move an average 9 km from wintering areas to select nest sites and males begin occupying leks. Pooled evidence suggests that females select nest sites independently of male dispersion whereas males adjust lek occupation so as to maximize proximity to females. Relevant observations include females visiting nest sites before leks, moving further to select a nest site than to select a lek, and increasing their distance to leks as a result of selecting nest sites. In addition, males avoid leks until females have moved to within 5 km of the arenas, abandon early season leks as local female densities drop, and exhibit dispersions in which mean ratios of females/male are similar across leks. Contrasts between predicted and observed dispersions of males showed that hotspot settlement models are adequate to explain male dispersions on very coarse scales (2 km or greater); on finer scales, habitat preferences of males and tendencies for males to cluster tightly must be invoked in addition to hotspots to explain specific lek sitings.

1976; Petersen 1980; Schoenberg 1982). Males must then select lek sites in which to display, and females must select both a site for nesting and a lek for mating. There are a number of ways in which the springtime activities of the two sexes might be related. In the simplest case (independence hypothesis), males would settle leks and females select nest sites using totally independent criteria. Relevant male criteria might include safety from predators during display, proximity to food, proximity to males preferred by females, benign climatic conditions on arenas, and/or optimal signal propagation (see reviews in Bradbury 1981; Beehler and Foster 1988). Earlier studies have shown that nesting sage hens prefer stands of sagebrush which average twice the height of patches used for feeding and four times that of those used for night roosts or leks (Klebenow 1969; Wallestad and Pyrah 1974; Braun et al. 1977; Petersen 1980; Schoenberg 1982). Settlement in which the two sexes relied on such different criteria ought to generate final dispersions in which lek and nest sites were spatially uncorrelated or possibly negatively correlated.

Alternatively, the disposition of the two sexes might be positively linked. An obvious case of linkage arises if both sexes have similar overall habitat requirements, even though they may use subsets of each habitat differently, and the areas of suitable habitat are very patchily distributed (passive linkage hypothesis). As long as patch settlement is independent of sex, the relative densities of the two sexes in each patch after settlement would be about the same. Lek and nesting site dispersions would thus be positively correlated on a coarse scale without either sex exerting any effort to be close to the other.

More active linkage arises if one or the other sex makes an effort to settle close to the other.

Introduction

Each year, male and female sage grouse (*Centrocercus urophasianus*) expand or move out of wintering areas to recolonize breeding habitats (Patterson 1952; Eng and Schladweiler 1972; Braun and Beck

In male first settlement, males select lek sites using criteria which benefit them directly, and females then settle close to existing leks even if this compromises nest site suitability. Conversely, females might select nest sites first and males then favor those lek sites closest to female concentrations (female first hypothesis). A specific case of a female first hypothesis is hotspot settlement (Bradbury et al. 1986). This model argues that males settle at major nodes of female traffic in an ideal free manner. The process is identical to that of animals settling on a patchy resource except that the “resources”, females, are mobile and thus corrections for local competition must include all possible lek sites within the ranges of females contacted by prior settlers. Although male first and female first hypotheses are here presented as qualitative alternatives, they have wide quantitative ranges. For example, independent settlement grades continuously into male first settlement with females making greater and greater compromises in nest site suitability. The extreme, (unlikely to be realized in nature), would have females nesting in the centers of leks. A similar gradient exists between independent and female first settlement with the (again unlikely) extreme of males displaying around nest sites.

In a recent paper, we examined spatial and temporal correlates of lek size in three populations of sage grouse in eastern California (Bradbury et al. 1989). These results suggested that daily variations in male numbers on leks were correlated with female visits even after the effects of common environmental parameters were removed (implying linkage), and that lek size distributions were more compatible with a hotspot settlement hypothesis than with several alternatives. In this paper, we examine contemporaneous sage hen movements and lek occupation phenology to determine which of the above hypotheses (or which quantitative mixture) best explains lek settlement in our populations. As part of the analysis, we also provide two stronger tests of the propriety of a hotspot settlement model for these birds.

Methods

Study site and period

The data in this paper were collected in the Long Valley area surrounding Crowley Lake, Mono County, California, from 1984–86. The sections of the valley utilizable by sage grouse covered 303 km² and annually hosted 9 leks during the three year period of the study. Other details may be found in Bradbury et al. (in press).

Lek counts

During April of each year, counts of daily peak numbers of males and females were obtained at all 9 leks in the valley. Counts were taken within 15 minutes of sunrise on at least two days (and usually more often) during the peak period of mating which occurred within a two week period following the first copulation. Daily counts of each sex and copulations from February to the end of April were also obtained at one lek in 1984 and at two for the seasons in 1985–1986. These counts also provided data on visits to leks and matings by marked females. All lek sites were known from previous studies and an aerial survey in 1984 revealed no new ones.

Female movements

To measure female movements we captured and fitted poncho-mounted radio transmitters to 37 female sage grouse between 1984 and 1986. A total of 33 birds were captured with the aid of a spotlight, hand net and chainless chainsaw, and the remainder with rocket nets when they attended leks (Giessen et al. 1982). Birds were aged as yearlings (<1 year) or adults (>1 year) by primary feather molt (Eng 1955). During the pre-mating and mating seasons we attempted to locate each bird at least once each day by triangulating radio signals from <500 m range. In practice, birds that moved into remote areas were located less frequently and sometimes at greater range. Birds were also located at longer intervals throughout the rest of the year, particularly in 1985. To minimize nest desertion (Zwicker and Carveth 1978), we located nests of breeding hens during the latter part of incubation.

After excluding 3 birds that died and 4 whose radios failed within 2 weeks of capture, 30 individuals contributed a total of 1925 locations to the sample. Individuals were tracked for periods varying from 3 weeks to 18 months. The distribution of the sample across months and years is given in Table 1. The following measures were taken from these data:

Individual range size. Monthly range areas were computed for each individual using a non-parametric Fourier method (Anderson 1982). We used a Macintosh adaptation by J. Bradbury of the original PASCAL program supplied to us by John Anderson. Minimum area vs probability (MAP) regions enclosing the top 50% of individual occurrence probabilities [MAP (0.50)]

Table 1. Distribution of female radio-telemetry data by month and year (*T*=total tracking fixes; *n*=number of females monitored)

Month	1984		1985		1986		Total	
	T	n	T	n	T	n	T	n
January	—	—	—	—	111	9	111	9
February	21	3	1	1	105	11	127	15
March	71	5	131	6	111	15	313	26
April	40	6	178	13	112	14	330	33
May	19	3	94	11	20	9	133	23
June	23	3	68	9	18	8	109	20
July	17	2	145	9	34	6	196	17
August	12	2	125	10	31	7	168	19
September	9	3	125	9	17	7	151	19
October	—	—	163	9	8	5	171	14
November	—	—	71	8	3	2	74	10
December	—	—	33	5	9	4	42	9

and top 95% of probabilities [MAP (0.95)] were computed for each individual that was located 10 or more times in a given month. Smaller samples yielded unreliable results. Except where noted, MAP (0.50) values were used in analyses since the two measures gave similar outcomes. MAP indices could only be calculated for periods of a month or more. To measure female mobility over shorter periods, we computed “daily displacement”, i.e. the mean distance between locations taken on successive days.

Population dispersion. Population MAP (0.50) values were also calculated for each month using pooled locations of all females tracked over that period. Because of small or variable sample sizes, data were also pooled across years. Population MAP values are sensitive to the number of females monitored, size of each female’s range, and the degree of overlap between female ranges. Since overlap was of interest, we computed a “range overlap index” equal to the summed individual MAP (0.50) values for all females monitored in a given period divided by the population MAP (0.50) for that period. This index should take values >1 if ranges of different females overlap and ≤ 1 if there is no overlap.

Nesting dispersal date. To characterize the time at which individuals localized activity around their nest site, we computed the distance between each location of a bird and its eventual nest from February until the end of April and then plotted the cumulative sum of this value against day. The cumulative sum of a process (eg. distance from a nest) x_1, x_2, \dots, x_s is defined as $\sum (x_i - rk)$ where k is a constant such as the mean value of x . When cumulative sum is plotted against r , (the position in the sequence), discontinuous changes in process rate which might otherwise be obscured by short term variability in the data appear as changes in slope or “turning points” (Woodward and Goldsmith 1964). We defined the date of “nesting dispersal” for each female to be the date of the last turning point after which the slope of cumulative sum decreased.

For 8 birds that localized their ranges in the spring as if nesting (Wallestad and Pyrah 1974; Peterson 1980) but whose nests were not located due to transmitter failure, post-dispersal mortality or presumed early nest abandonment, we identified dispersal dates in the same manner using the bird’s median x and y coordinates in its “presumed nesting area” as a reference point.

Nesting dispersal distance and direction. Distances and directions moved by birds from wintering to nesting areas were computed between the median x and y coordinates in the 3 months prior to dispersal and either the nest site or the median x and y location in the presumed nesting area (see above). Dispersal distances were computed for several females that were not tracked regularly enough to yield reliable estimates of dispersal date as well as for those that were.

Simulations

To compare observed male dispersion to that predicted by a hotspot settlement model, ranging data from March and April for each of the 30 females observed during 1984–86 were mapped onto a 32×32 cell grid and the probability of each female being found at each cell point computed using Anderson’s (1982) Fourier method. The average displaying male population of Crowley Lake (250 individuals) was then settled on the gridded ranges of these females using a program similar to that of Bradbury et al. (1986). Note that unlike the latter paper, female ranges were here variable in shape and size, and

not utilized uniformly. Males were settled sequentially and allowed to examine 50 random points in the basin before selecting one as a display site. The selected site was that from among the 50 examined which gave the highest number of expected matings at settlement. This high number of examined sites was used not because it mimics actual behavior of the birds, but because it provides nearly perfect information about site suitability. In nature, similar levels of information could be achieved by quite different proximate mechanisms (Bradbury et al. 1986). The simulation also assumed that mating probabilities for each female were continuously partitionable among males and ideal free, and that settling males could correct for the devaluation of sites due to already settled males. That is, males had perfect knowledge about how many males were already sharing each female’s range at settlement. The locations of each settled male were recorded and the results compared to observed dispersions as described in the results. Perhaps because of the large number of males settled, repeated simulations gave nearly identical outcomes.

Statistical analysis

Where possible, parametric statistical methods were used to analyse the data. Some variables, however, resisted attempts to transform them to meet the assumptions of parametric tests. In such cases equivalent non-parametric alternatives were used.

Results

Female dispersion

Overall seasonal patterns. Both the movements of individual females and their dispersion relative to each other followed a clearly defined annual pattern illustrated in Fig. 1. Individual monthly ranges (MAP (0.50)) were at their lowest during nesting (May mean = 14 ha) and late summer (August mean = 11 ha) and at their highest during the two months preceeding mating (February mean = 487 ha, March mean = 347 ha). Mean monthly values for daily displacements ranged from a low of 406 meters/day during late summer to a peak of 1.0–1.9 km during the pre-breeding and mating period (February–April). These variations in individual range size and day to day displacement were highly significant across months (Kruskal-Wallis ANOVAs; MAP (0.50): $H = 36.63$, $df = 9$, $P < 0.001$; Daily displacement: $H = 37.37$, $df = 11$, $P < 0.001$; two months with a sample size of 1 were dropped from the analysis of MAP (0.50) values).

Throughout the winter (December to February), radio-tagged hens utilized a restricted area in the south of the study area where they moved in large extensively overlapping ranges. The total area used by the population expanded rapidly during March and April with the dispersal of many, but not all, females from the wintering area. Range overlap, though decreasing, remained high at this

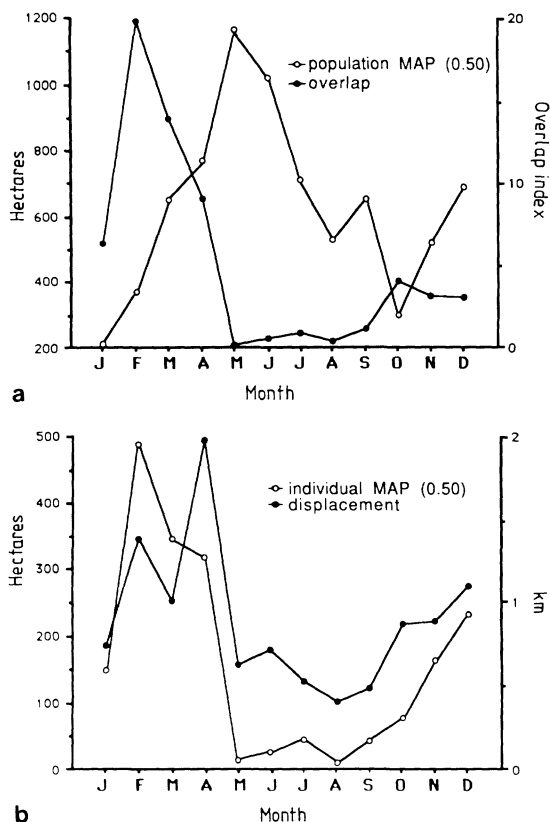


Fig. 1a, b. The annual cycles of pooled female range use and overlap in the Crowley basin (a) and monthly means for individual female range size and daily displacements (b). See text for definition of measures

time and daily relocation distances were maximal. The area occupied by the population peaked during incubation in May (at a value 6 times the January minimum), while mean range size and overlap were minimal during this month. Range sizes remained low throughout the summer, although the area utilized by the population decreased with the progressive concentration of birds around wet meadows. Range size and overlap began to increase again in October. The winter pattern was re-established between October and early December with movements back to the central wintering area following the first major snowstorm of the winter. The same pattern was observed in each year, with only minor variations in the timing of spring dispersal and fall return to the wintering area. Two individuals that were followed for more than 12 months returned to the same locations at equivalent times of year; one whose nest was found in successive years returned to within 50 m of her former nest site.

Movement to nesting areas. During March and April, most females moved from their wintering ranges to nesting areas where their activity became

localized around the eventual nest site. Over the three years of the study, dispersal dates of radio-tagged individuals to nesting ($n=9$) or presumed nesting areas ($n=8$) fell between March 13 and April 8 (dates identified by cumulative sum analysis; see Methods). The timing of these movements was strongly age-related with adults dispersing an average of 10.4 days before yearlings ($t=3.77$, $df=15$, $P<0.002$). There was also slight variation across years, although samples were too small for tests.

Distances moved between wintering and nesting areas were highly variable (mean = 9.9 km, $SD=13.54$, $n=20$) and showed no significant relationship to dispersal date or year. Yearlings tended to disperse further than adults (8.0 ± 5.8 vs 11.9 ± 5.2 km; $n=10$ in each case), but this difference was not significant. Dispersal direction was significantly non-random (Rayleigh test: $r=0.936$, $n=20$, $P<0.001$), with the major dispersal traffic moving northwest out of the wintering area. This is the same approximate axis around which many of the basin's leks are distributed.

Lek attendance and mating. Whereas nesting dispersal dates occurred between March 13 and April 8 annually, matings did not begin until March 23–28 depending upon the year. Once initiated, matings then occurred rapidly with 50% of the annual total accruing in 5–10 days after the first copulation. In 1986 we obtained sufficient data to contrast the nesting dispersal dates of 9 radio-tagged females with daily records of female attendance and matings at two leks: Lek 4, situated within the wintering area and Lek 8, 6.8 km to the NW. Nesting dispersal occurred significantly earlier than matings at both leks (Mann-Whitney tests; Lek 4: $W=51.0$, $n_1=9$, $n_2=51$; Lek 8: $W=45.0$, $n_1=9$, $n_2=70$, both $P<0.0005$). Although female attendance and nest dispersal overlapped extensively at Lek 4, attendance at Lek 8 was significantly later than dispersal (Lek 8: $n_1=9$, $n_2=268$, $P<0.0005$). Between 1984 and 1986, 8 individuals for which dispersal dates were determined were seen at leks from 1–3 days each (mean = 2.0, $SD=0.8$ d). Most (81%) of these lek visits occurred after nesting dispersal (mean 11.8 d post dispersal, $SD=13.54$ d, $n=16$) and 3 birds that were seen mating did so 9, 11 and 15 days post-dispersal. Each individual had been radio-tracked to its nesting or, in one case, presumed nesting area between dispersal and mating. In short, females typically disperse to nest sites 1–2 weeks prior to visiting leks and mating.

During the display season, female ranges average 300–350 hectares/month. This is clearly large

enough to include several active leks if properly positioned. Examination of individual monthly ranges showed that tracked females had an average 2.2 active leks ($SD=1.54$, $n=20$) within their 95% home range areas in March, 1.87 ($SD=1.85$, $n=15$) in April, and 3.05 ($SD=1.88$, $n=21$) over the two months combined. Data from the few radio-tagged females that we observed at leks suggested that a majority visited the lek closest to their nest site, though there were notable exceptions. Of the 7 tagged females that made their lek visits after nesting dispersal, 4 visited and one mated at the lek closest to their nests (mean distance 2.5, $SD=1.7$ km). The remainder attended more distant leks (mean = 7.6, $SD=0.5$ km). Two of the latter birds mated on leks within their prior winter ranges, in one case bypassing several closer leks *en route*. One, a yearling, had visited the same lek before dispersing.

Changes in range size vs movements to nests and leks. Increases in female mobility during the display season (Fig. 1) could have arisen as hens began to search for nesting sites, to visit leks, or both. To explore this issue we used daily displacement as a measure of female mobility and examined its relationship to females' proximity to nest sites, proximity to leks, and lek visits from a month before to a month after nesting dispersal. To control for variation in timing of breeding activity among birds of different age and in different years, we expressed date as days before or after the date of nesting dispersal for each individual. The period was divided into 21 three-day periods and individual mean values were calculated for each period. The results are plotted in Fig. 2.

The data suggest that both the establishment of nesting areas and visits to leks contribute to high female mobility, but at different times and on different scales. Mean daily displacement begins to increase about 7–9 days prior to the identified "dispersal date" and generally remains high (0.7–5.1 km/day) from days 6–18 post-dispersal. During this period, females reduce the distance to their nest sites from an initial mean of 9.9 km to a final one of 2 km, and increase their distances to nearby leks from 1 to 3 km. The initially low value of lek distances arises from the presence of several active leks within the wintering range. Finally, mobility drops to less than 1 km/day around day 20, presumably with the onset of incubation. The visit on day 30 of a tagged female may represent remating after nest loss (Dalke et al. 1963; Petersen 1980).

In brief, an average female travels 7–10 km from her wintering range to her nesting site. Al-

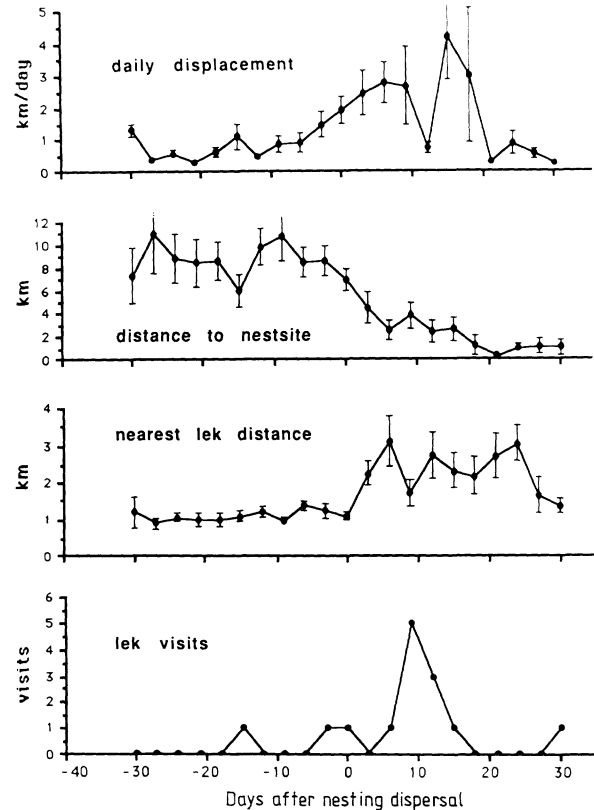


Fig. 2. Seasonality of daily locations for 20 breeding females relative to three types of reference sites (position on prior day, eventual nest site, and nearest active lek), and to dates of lek visitation. Time scales for different females are aligned by setting day of nesting dispersal equal to zero. Distance measures are means (\pm standard errors of means) for successive 3-day intervals. Sample sizes per interval average 5 values for daily displacement measures, and 9 for each of distances to nest sites and distances to the nearest lek. Sixteen lek visits by tagged females were recorded

though this is a major relocation, females are rarely more than 2–3 km from at least one of the 2 active leks within their ranges throughout this entire period. Once nest sites are located, females move to a nearby lek, mate, and then move back to their nests. Exceptions to this pattern include those females who nest within the wintering area and show no large movements either to nest or lek, and a few females who select nest sites at a distance from the wintering range, but then return to leks within that range for mating.

The relationship between female and male dispersion

Phenology of lek occupation. Although only 20–30% of the leks in the Crowley basin are occupied by males at the onset of display (Bradbury et al. 1989), and despite a 6-fold increase in the area used by the population during later winter and early spring, we have seen that females incor-

porate 1–3 active leks within their current ranges throughout March and April. This implies that female use of an area and male occupation of nearby lek sites are phenologically linked. Contrasts between visits by each sex to Lek 4 (in wintering zone) and Lek 8 (peripheral lek) during 1986 show this linkage clearly (Fig. 3).

At Lek 4, male attendance began in February, peaked in early March, and then fell to a steady level which persisted throughout April when the majority of female visits and all copulations occurred. Throughout the former period, most of the 11–15 tagged hens were located within 3 km of the lek and groups of up to 50 females occasionally attended the arena. The transition to a steady lower number of males coincided precisely with the dispersal of many females out of the wintering area and into the surrounding basin.

An inverse pattern was observed at Lek 8. During February the lek was rarely attended by males, and no tagged females were located within 5 km. In early March, a few males displayed for several days coincident with a drop in the daytime distance between females and the lek. When most females withdrew further from the lek, the displaying was temporarily abandoned. In late March, when female daytime locations again dropped to within 5 km from the lek, male attendance quickly increased to asymptotic values. The onset of female visits to the lek was contemporaneous with this sudden rise in male numbers. Female proximities changed little through the remainder of April, but female visits quickly declined as the month drew to a close. These respective phenologies were consistent for all years in which censusing and tracking were undertaken (1984–6 for Lek 4, 1985–6 for Lek 8) and the basic patterns were the same at both leks: neither sex visits a lek site unless females have daytime locations within 5–6 km of the lek, and male attendance at a lek is positively linked to local densities of females.

Models of male settlement on female ranges. One way in which this tight linkage between male and female recolonization of breeding habitats could be maintained is settlement of males on areas of high female traffic. We examined two rules by which this might occur. In both cases, we imposed a grid on the study area, calculated the average number of males seen in each cell during the three years of the study, computed the number of males expected in each cell given a specific model, and then examined the degree of correlation between observed and expected distributions. In the simplest model, we tabulated the number of locations

for radio-tagged females in each cell during the months of March and April. If males settled according to female traffic levels without correcting for local competition with established settlers, the number of female fixes ought to be a good predictor of male numbers in any site (“female traffic model”). Our second model used the same data but allowed males to correct for local competition during settlement as predicted by “hotspot” settlement rules (see Methods for details). For each model, both parametric and nonparametric (Spearman rank) correlations at grid cell sizes of 0.5, 1, 2, 4, and 8 km were undertaken. Since the two types of correlations gave identical rankings and significance conclusions, the parametric outcomes are summarized in Fig. 4.

Correlations were significant for both models at all grid cell sizes of 2 km or greater ($P < 0.05$ or less), and both explained a substantial amount of the observed variation in male settlement. It is clear from Fig. 4 that the variance in observed male dispersion explained by either model rises rapidly above grid cell sizes of 1 km and has reached asymptotic values by a grid size of 4 km. Although the two models do not differ at the lowest grid sizes, the hotspot model gives a better fit to observed lek distributions at all higher grid values.

In addition to predicting the observed siting of male aggregations, ideal free hotspot settlement ought to exhibit a positive linear relationship between the number of matings and the number of males on a lek. This prediction is not an obvious outcome of models in which males select sites independently of female ranging behavior and is unlikely to result if males do not control for local competition during settlement (e.g. female traffic model). Since we have more extensive data on numbers of females visiting study leks during the peak mating period (the 14 days starting with the first mating observed in each year) than on copulations, and since copulations and the average daily number of females seen on a lek during this period are highly correlated in the subsample of leks for which both copulations and female attendance were recorded ($r = 0.971$, $n = 7$, $P < 0.01$), we compared average male and average female daily attendance at all censused leks during the three year study period. Figure 5 plots the untransformed numbers of each sex on the same lek and the line resulting from a simple linear regression of numbers of females on numbers of males. Although the latter regression is highly significant ($r^2 = 88.3\%$, $P < 0.0001$), the points show a slight hint of a downward curvature at higher lek sizes.

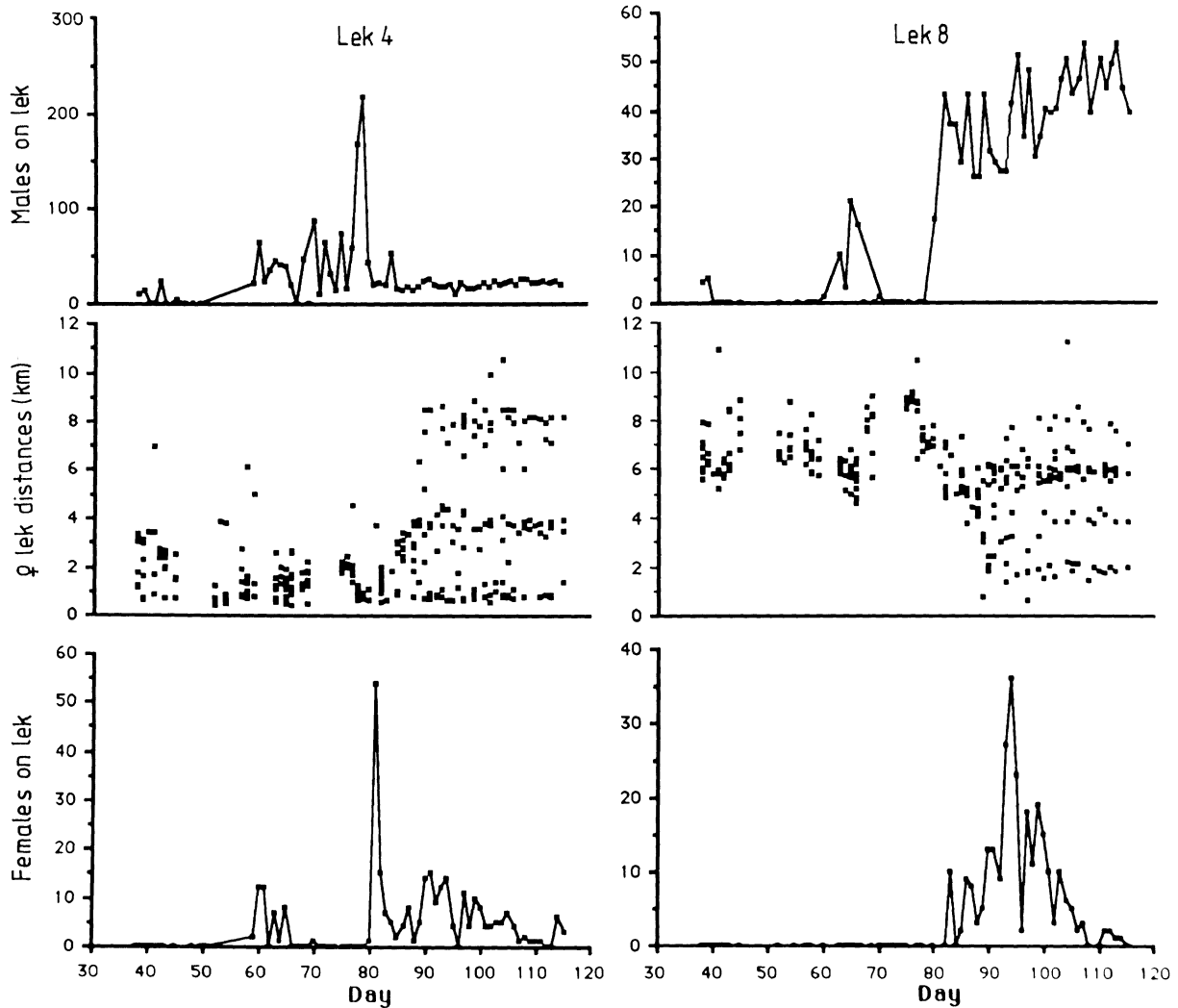


Fig. 3. Seasonal patterns in displaying male attendance, proximity of females during non-display hours, and female attendance at one lek within (Lek 4) and one lek outside (Lek 8) the population wintering area in 1986. Copulations began on day 89 at Lek 4 and day 92 at Lek 8, and both leks had accrued 50% of their annual mating totals by day 97. Days are measured from January 1 (day 1)

The typical scarcity of leks at intermediate sizes (Bradbury et al. 1989) results in non-uniform residuals and makes it more difficult to assess any curvature in the relationship. Accordingly, we reanalyzed the data using a) a linear regression of the log-transformed variables and b) a second order polynomial regression of the untransformed data. Although both regressions were significant ($r^2 = 67\%$, $P = 0.001$; $r^2 = 89\%$, $P = 0.0001$ respectively) both indicated that any curvature in the relationship was minor: the slope of the log-transformed line was 1.008 (95% confidence limits of 0.634 and 1.382), and the coefficients of the x and x^2 terms in the polynomial regression were 0.398 and -0.001 respectively. As a final check, we computed the ratio of females/male at each lek and

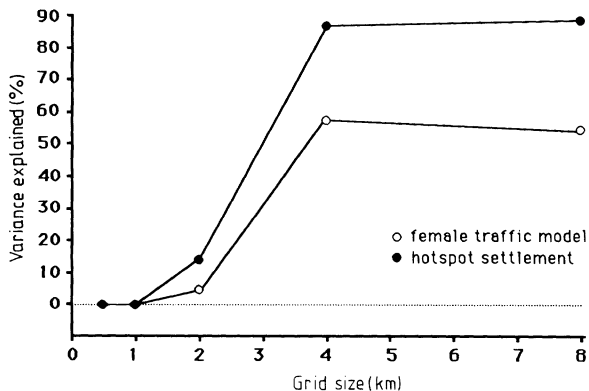


Fig. 4. The fraction of the variance in numbers of displaying males per grid square explained by each of two male settlement models, plotted in relation to grid square width

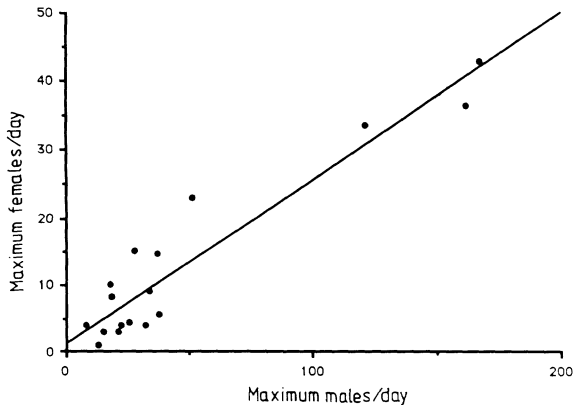


Fig. 5. The relationship between mean numbers of males attending leks per day during the mating peak and the mean number of females per day. Data were pooled across years. The simple linear regression through the points without transformations is shown (number of females/day = 1.42 ± 0.24 [number of males/day]; $r^2 = 88.3\%$; $P < 0.0001$). Linear regressions on the transformed data and a second order polynomial regression for the untransformed data are discussed in the text

regressed this on lek size (males/lek). The resulting regression was not significant ($r^2 = 1.3\%$, $P = 0.66$) and had a trivial slope ($m = -0.0004$). In short, partitioning of females among leks appears to be largely ideal free with a possible slight bias favoring smaller lek sizes.

The relationship shown in Fig. 5 provides an explanation for the relatively low number of tagged females that we observed at leks (see above). Assuming that each female usually visits a single lek (Petersen 1980; Dunn and Braun 1985), that the fraction of marked females visiting any given lek is approximately proportional to its size, and using the observed distribution of lek sizes in the population, we calculated that we should have seen 7 of the 30 radio-tagged females visit our intensively-observed leks. This is what we indeed saw.

Discussion

The phenological contrasts between leks 4 and 8 (Fig. 3) demonstrate a marked linkage between the dispersions of the two sexes in our population of sage grouse. Linkage is also inferred from the observations that the vector of female dispersal is identical to the major NW axis along which many Lake Crowley leks are aligned, that the order of lek occupation along this axis is that predicted by the direction of female recolonization, that 57–68% of sage hens mate on or are captured visiting leks within 2–3 km of their nest sites (this study; Patterson 1952; Poley 1969; May 1970;

Wallestad and Pyrah 1974; Braun and Beck 1976; Petersen 1980; Schoenberg 1982), that the ratio of visiting females/displaying male is constant across leks, that some leks settled early in the season by males are later abandoned as females move out of wintering areas (Bradbury et al. 1989), and that daily variations in male attendance on leks are often correlated with female attendances beyond that expected due to common climatic factors (Bradbury et al. 1989).

While the linkage between male and female dispersions in sage grouse seems clear, the mechanism generating this linkage is not so obvious. Passive linkage could certainly generate the coordinated lek occupation by males and females and the constancy of visiting females/displaying males across leks. There are several reasons, however, to doubt that this is the major factor generating the observed intersexual linkage. First, although females nest throughout the Lake Crowley basin, leks tend to be centralized along the valley axes (see Fig. 1, Bradbury et al. 1989). While this is a predicted outcome of hotspot settlement when female ranges are large relative to a finite “world” (Bradbury et al. 1986), it is not an obvious prediction of sexually shared habitat preferences. Secondly, since the two sexes clearly differ in local habitat usage, one needs to identify some other shared requirement which could generate local convergence. The only likely possibility is the patchy dispersion of snow free areas for feeding during the lek season. Throughout the winter and early spring, sagebrush has not yet begun new leaf flush and snow levels can determine which of last year’s leaves are currently available as grouse forage. Unfortunately for this hypothesis, snow melt was complete before nesting dispersal in 2 of the 3 years of this study. Finally, if males and females were settling according to common habitat cues, we would have expected the “female traffic” simulation to provide as good or better fit to observed male dispersions than would the hotspot simulation. In fact, hotspot simulation was as good or better at all grid sizes.

There are a number of observations which suggest that female first settlement models better fit sage grouse than male first models. The fact that male and female dispersions are linked is not relevant here as this is predicted by both models. Female first settlement is supported by the facts that females use the entire valley for nesting although leks are concentrated in central areas, that numbers of males on Lek 4 rose and fell in synchrony with fluctuations in local female densities, that both the female traffic and hotspot settlement simulations accounted for a large fraction of the

dispersions of females each spring. This stability in female dispersions would be further enhanced by the tendency of surviving females to return to the same nesting locations in successive years (Patterson 1952; Berry and Eng 1985). Since meadows are also stable in our study area, the two primary factors which we are invoking to explain male spacing, female dispersion and meadow dispersion, are likely to be similar in successive years. This would not only produce similar lek site occupation each year, but since hotspot settlement depends only on the relative female traffic distribution, and not on the absolute one, it could also produce the observed stability in lek size ranks across large annual variations in population density (Bradbury et al. 1989).

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