

Summer 1991

Mate Choice in Lekking Sage Grouse Revisited: The Roles of Vocal Display, Female Site Fidelity, and Copying

Robert M. Gibson

University of California, Los Angeles, rgibson@unl.edu

Jack W. Bradbury

University of California at San Diego, jwb25@cornell.edu

Sandra L. Vehrencamp

University of California at San Diego, slv8@cornell.edu

Follow this and additional works at: <https://digitalcommons.unl.edu/bioscifacpub>



Part of the [Biology Commons](#), and the [Ornithology Commons](#)

Gibson, Robert M.; Bradbury, Jack W.; and Vehrencamp, Sandra L., "Mate Choice in Lekking Sage Grouse Revisited: The Roles of Vocal Display, Female Site Fidelity, and Copying" (1991). *Faculty Publications in the Biological Sciences*. 574.

<https://digitalcommons.unl.edu/bioscifacpub/574>

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications in the Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Published in *Behavioral Ecology* 2:2 (Summer 1991), pp. 165–180; doi: 10.1093/beheco/2.2.165
Copyright © 1991 International Society for Behavioral Ecology; published by Oxford University Press. Used by permission.
Submitted January 7, 1991; revised April 3, 1991; accepted April 5, 1991; published July 1, 1991.

Mate Choice in Lekking Sage Grouse Revisited: The Roles of Vocal Display, Female Site Fidelity, and Copying

Robert M. Gibson,¹ Jack W. Bradbury,² and Sandra L. Vehrencamp²

1. Department of Biology, University of California, Los Angeles, CA, USA
2. Department of Biology, University of California at San Diego, La Jolla, CA, USA

Abstract

In lekking sage grouse (*Centrocercus urophasianus*), females exhibit relatively unanimous mate choice for particular males, but a satisfactory explanation for this unanimity has been elusive. We present analyses of mating distributions from two leks over 4 years that provide evidence for female choice based on differences in vocal display performance of males, the locations at which hens mated in the previous year, and the choices of other females (copying). The unanimity of female choice varied markedly among leks and years in correlation with changes in the mean numbers of hens that mated at the same time and hence the opportunity to copy. The results confirm that hens assess phenotypic traits of males directly but also indicate that the secondary tactics of site fidelity and copying are often important components of female choice. The occurrence of these secondary tactics has three implications: the variance in mating success among lek males will be a poor predictor of the intensity of sexual selection on specific traits; female preferences may generate more clustered dispersions of displaying males than predicted by hotspot settlement models; and direct assessment of males by females may be difficult or costly, a conclusion that supports adaptive models of sexual selection over a nonadaptive Fisherian process.

In lekking birds and mammals, almost all matings are performed by a small minority of the males at the lek. Although in some species, the skew in male mating success may be largely due to aggressive dominance by a few males (Beehler and Foster, 1988), most observers concur that in the majority of lek species, the skew is a result of relatively unanimous female mate choice (for review, see Bradbury and Gibson, 1983; Wiley, 1991).

Unfortunately, a satisfactory explanation of the processes that generate this degree of female unanimity has been elusive. The question is interesting because the answer promises to shed light both on the problem of lek evolution (Beehler and Foster, 1988; Höglund and Robertson, 1990; Warner, 1988) and on the central issue of why females should choose mates in nonresource-based mating systems (Heisler et al., 1988). In this paper we present data that show how unanimity of choice is generated in the sage grouse (*Centrocercus urophasianus*), a bird that exhibits classic lekking behavior.

At least three mechanisms for the evolution of unanimous female choice on leks have been proposed. First, females may base choices on phenotypic or social traits exhibited by male courtship. Such preferences might have evolved by a Fisher process with no adaptive benefit to the females expressing them (Kirkpatrick, 1982; Lande, 1981), by good-genes sexual selection in populations with persistent heritability of overall fitness (Pomiankowski, 1988), or by direct selection on females to reduce intrasexual interference (Trail, 1985; Trail and Adams, 1989), reduce disease transmission (Borgia and Collis, 1990), or increase fertility (Avery, 1984).

Female choice for behavioral or morphological traits of males appears to be common in lekking species, despite the uncertainty about its adaptive basis. Although several early studies failed to find phenotypic correlates of male mating success (for review, see Bradbury and Gibson, 1983), more recent work has identified clear correlations in 8 of 10 species of birds and mammals (Andersson, 1989; Balmford, 1990; Clutton-Brock et al., 1988; Gibson and Bradbury, 1985; Gratson, 1989; Höglund and Lundberg, 1987; Landel, 1989; McDonald, 1989; Petrie et al., 1991; Pruett-Jones and Pruett-Jones, 1990; Trail, 1984). Data from correlational studies are open to a variety of alternative interpretations. The most common is that some unmeasured factor, such as attractiveness of a male's territory or male dominance, is the true determinant of female choice and that phenotypic traits are correlated with mate choice only because they are also linked to the critical trait (Wiley, in press). One way to resolve causation is direct manipulation of the possible factors. In several instances, this has been done, and the results have confirmed that individual identity or specific components of display or morphology affect mate choice independently of other factors such as territory location and aggressive interactions among males (Clutton-Brock et al., 1989; Gibson, 1989; Höglund et al., 1990).

A second mechanism that could generate unanimity is a female preference for males in particular territories within the lek. Female site specificity might arise in short-lived insects in which a preference for some conspicuous topographic landmark would allow the sexes to meet with minimal search costs (Alcock, 1987). For longer-lived species (e.g., most vertebrates), fidelity of females to sites in which they had previously mated might be favored because mate choice was risky or costly in time (Warner, 1987, 1988). Once females favor males in certain sites, adaptive sexual selection (assuming male competition for sites reliably links male quality with location) might further favor the preference.

The usual evidence cited for female site specificity is a correlation between proximity of a male to a lek "center" and mating success (Bradbury and Gibson, 1983; Gosling and Petrie, 1990; Kermott, 1982; Landel, 1989; Trail, 1984). Unfortunately, such a correlation can also be generated by the centripetal clustering of less successful males around successful ones (Gibson and Bradbury, 1986; Höglund and Robertson, 1990; Landel, 1989). A better

approach is to monitor the success of specific lek territories through successive owners. Balmford (1990) has used this approach to demonstrate that previous history of a territory does affect subsequent mating success in Uganda kob.

The third mechanism for unanimity is female copying of the choices of others. As suggested by theoretical analyses of resource assessment, copying may be advantageous where assessment of males is difficult and/or where sampling is costly (Boyd and Richerson, 1985; Clark and Mangel, 1984; Kiester and Slatkin, 1974; Losey et al., 1986; Shields et al., 1988; Stamps, 1988). However, the benefit of copying requires that some individuals assess males directly. When a high proportion of individuals copy, copying may yield a male far from the preferred phenotype because there is a risk of copying others that have not assessed males directly (Losey et al., 1986). Opportunities for copying at leks arise when a female can observe the choices of other females that mate before her, either because several females mate within the duration of single lek visit or because a female makes more than one visit to a lek before mating, as is typical of lekking birds (Gibson and Bradbury, 1986; Landel, 1989; Lill, 1974; Pruett-Jones and Pruett-Jones, 1990; Trail and Adams, 1989).

The copying hypothesis is appealing because it could explain why mate choice is highly unanimous even where, as is often the case, correlations with phenotypic or spatial cues are low or absent (Wade and Pruett-Jones, 1990). This point is underscored by computer simulations which show that, unlike copying, independent female choice based on either phenotypic or spatial cues is unlikely to generate such an extreme mating skew as is observed in most field studies (Bradbury et al., 1985). Clutton-Brock et al. (1988) found that female fallow deer entered a lek harem at higher rates when the male began to mount an estrous female. The rate at which females entered harems also increased with harem size in both fallow deer (Clutton-Brock et al., 1989) and Uganda kob (Balmford, 1990). These observations are highly suggestive of copying, but they might also have arisen because both harem size and arrival rates were related to a third variable such as male display rate (see also Jamieson and Colgan, 1989; Ridley and Rechten, 1981).

Among lekking birds, sage grouse are well suited for investigating mate choice. Leks are large and are easily observed due to the species' large size, open habitat, and the predictable timing and location of display (a few hours at dawn and dusk during a 2–3-month period in the early spring). Males typically defend individual mating territories, and females are able to exert choice by entering a male's territory and soliciting copulation. Except where territoriality has broken down, levels of intrasexual interference in courtship and copulation are low (Gibson and Bradbury, 1987), so that differences in mating success must primarily reflect female choice. In a previous study, we showed that differences in mating success at a lek in one season were correlated with male lek attendance (as one might expect) and with differences in the rate and vocal performance of the stereotyped strut display. These results suggest that females base choice on display performance of those males present on the lek they visit (Gibson and Bradbury, 1985). Boyce (1990) has suggested that ectoparasitic lesions may also contribute to male phenotypic differences discerned by females, but such lesions were rare in our population and hence unlikely cues.

Although sage hens appear to use male phenotype to some degree, it remains possible that they also use nonphenotypic cues. Wiley (1973) suggested that spatial cues play an

important role in this species. We were unable to confirm his suggestion that hens prefer centrally located males (Gibson and Bradbury, 1985), but whether hens base choice on topographic cues or exhibit mating-site fidelity has not been adequately tested (but see Hartzler and Jenni, 1988). The possibility of copying was also raised in previous studies (Hartzler and Jenni, 1988; Wiley, 1973). Among hens breeding early in the season, mating is highly synchronized, with 50% of matings at a lek typically occurring within a 5–10-day period (Bradbury et al., 1989) and individual hens typically visiting the lek on 2 or 3 days before mating once on the last visit. Thus, there are opportunities for hens to observe and copy each other's choices both within and between successive visits.

In this paper we use data on mating distributions at two leks collected over four seasons to reexamine the question of choice cues in sage grouse. We provide evidence that hens base choices on male performance of vocal display and on previous mating locations, and that they copy the choices of other hens. We also compare the degree of mating unanimity across leks and years and show that this is linked to the opportunities for hens to copy. We suggest that these data resolve the issue of unanimous mate choice on leks, and we explore their relevance to the problems of lek evolution and the adaptiveness of mate choice at leks.

Methods

We studied a resident population of sage grouse in Long Valley, Mono County, California, USA (118°50'W, 37°40'N), from 1984 to 1989. Data on reproductive success came from two leks: lek 4 was studied intensively from 1984 to 1987 and lek 8 from 1985 to 1987. Data on the movements of hens within the lek were collected at lek 4 in 1989. The study population and general methods have been described previously (Bradbury et al., 1989; Gibson and Bradbury, 1985).

In each year, we recorded male mating success, courtship display, and territory characteristics during daily observations of focal leks between March 15 and late April, the main period of lek display and mating. Observers (2–4 per lek) arrived before dawn and watched the lek from raised vantage points 150–200 m away using ×20–45 zoom telescopes until the birds left the lek 1–3 h later. Individual males were recognized using color bands or, for unbandable individuals, the idiosyncratic patterns of white spots on the under-tail coverts and the shapes and relative lengths of retrices, which we photographed for reference. We trapped birds for banding and measurement using a spotlight, hand net, and chainless chainsaw for acoustic masking ($n = 223$), or with a rocket net ($n = 33$). Using blinds placed on the lek, we also made sound recordings of male displays at ranges of 5–50 m with Sennheiser MKH815 and 816FTU microphones and either reel-to-reel recorders (Nagra IV, Stelavox SP8; 1984–1986) or a Canon VR40A videorecorder (1986–1987). These observations yielded the measures discussed below.

Mating success

Mating success is the total number of females with which a male mated during each morning lek, summed over all days of the season. We watched hens carefully to detect remating within the same morning and are confident that mating counts are not inflated by multiple

matings per hen. Because the entire lek area was monitored continuously, it is unlikely that we missed matings, except during the first 10–15 min of the morning lek when visibility was poor. Unobserved matings may also have occurred at leks in the evening and on moonlit nights, although lek display was sporadic at these times and night sampling suggested that few hens attended. Numbers of males for which mating success was determined at each lek and total copulations are shown in Table 1. Several measures were extracted from mating distribution data and are listed below. We corrected for male attendance at the lek, which we had already found to be an important determinant of overall male mating success (Gibson and Bradbury, 1985). Our focus in this study was to identify components of female choice independent of male attendance.

Table 1. Sample sizes for mating success at leks 4 and 8, 1984–1987

Lek	Year	Days sampled	Total matings	Identified adult males	Males (all ages) attending per day mean (SD)
4	1984	40	23	27	31.9 (7.8)
	1985	41	20	16	23.1 (7.3)
	1986	41	54	16	30.2 (36.6)
	1987	37	38	23	29.7 (9.3)
	1985	29	23	30	35.4 (3.6)
8	1986	27	66	31	28.2 (6.2)
	1987	37	76	36	31.9 (7.8)

1. Adjusted mating success. Adjusted mating success was a measure of a male's attractiveness to females adjusted for differences in both time spent at the lek and the degree of competition for matings. For each male, we computed an expected mating success in which we assumed that females choose at random among the available males. The expected value was computed as the sum over all days that a male was present of the total matings on that day divided by the number of males present. Adjusted mating success was defined as observed divided by expected mating success. To avoid generating spuriously high and low values for males that attended very infrequently, we excluded all individuals that were present for less than 40% of the maximum expected matings for the season. Twenty-seven percent of males monitored fell below this cutoff, which represents the breakpoint in the bimodal distribution of expected mating success. This exclusion did not appear to bias the results because we identified the same correlates of mating success in preliminary analyses using untransformed mating success scores and the entire sample. Adjusted mating success was computed only for adult males; yearlings attended leks infrequently, often visited several leks in a season, and were never observed to mate.

2. Early versus late season matings. To examine site-fidelity effects, we partitioned matings into early season (up to the date of the median mating at the lek) and late season (after that date) and computed an adjusted mating success for each male for each period. The rationale is that most early-season matings are by adult hens (more than 1 year old) with previous breeding experience, whereas most late-season matings involve yearling hens who are in their first breeding season. For example, of 25 early-season lek visits by marked

hens recorded from 1984 to 1989, 75% were by adults and 25% by yearlings, whereas for 26 late-season visits the equivalent figures were 33% and 67% ($\chi^2 = 10.388$, $df = 1$, $p = .0013$).

3. Solo versus group matings. To investigate copying, we partitioned matings into "solo matings," in which a hen was the only individual to mate with that male on a given day, and "group matings," in which two or more hens mated with the same male on the same morning. A solo mating could not involve copying on the day of observation, although the hen might have copied from an earlier visit; group matings always permit copying, although two females might also choose the same male independently. To determine whether hens that participated in group matings based choices on the same male characteristics as those that chose independently, we converted copulation counts to mating "decisions" and computed an adjusted number of solo and group mating decisions received by each male, using the same approach as for adjusted mating success. We assumed that each solo mating or each group of females mating with a particular male on one morning represented a single mating decision.

4. Unanimity of choice. Unanimity of choice was measured for each lek year as the standardized variance in mating success (variance/mean²; Wade and Arnold, 1980).

5. Opportunity to copy. Opportunities to copy should increase with the numbers of hens that mate during the same morning. To measure this, we computed Lloyd's (1967) index of mean crowding for the distribution of total matings per day in each lek season. Lloyd's index as used here measures the average number of females that mated at the same time as a randomly chosen female. Because few hens were individually recognizable, we were unable to quantitatively characterize the opportunity for hens to copy between lek visits. However, we were able to compare the observed intervals between days on which males mated and the expected intervals if repeat female visits had no effect on mate choice. The computation is described in the Results.

Display rate

The rate at which a male repeated the strut display when females were present was measured by logging the times of 21 successive strut displays on a TRS80-100 portable computer and computing the harmonic mean of the 20 between-strut intervals. Most males elevate display rates when females are nearby (Wiley, 1973). To remove this effect, we recorded the distance from the male to the nearest hen at the start and end of the sample and regressed display rates on mean female distance (square-root transformed). Separate regressions were computed for each male with sufficient data (8–30 samples per season) because the regression slopes differed among individuals in 2 of 4 years (ANCOVAs: $p = .011$ – $.024$). Each male's regression was used to compute an expected display rate at two distances from hens, 5 m (roughly corresponding to a hen in the male's territory) and at 50 m (hens definitely elsewhere on the lek). Note that although the two measures are correlated ($r = .551$, $n = 32$, $p = .0011$), they did not rank males identically because of the differences in regression slopes. Sufficient data for comparisons with mating success were obtained at lek 4 in 1984, 1986, and 1987.

Acoustic display traits

Recordings of strut displays were band-pass filtered to reduce ambient noise and prevent aliasing (Krohn Hite 3550: 0.3–6 kHz), digitized at 22 kHz using a Soundcap AD converter and displayed on a Macintosh computer running Soundwave software. Strut displays of almost all adult males had a similar acoustic structure (Figure 1). Measures of the temporal and frequency structure of displays (Table 2) were made on the Macintosh and with a Uniscan II spectrum analyzer. Amplitudes of struts at 250 and 2000 Hz were also measured at lek 8 in 1986 using a Brüel and Kjær Model 2204 Sound Level Meter and corrected for distance and male orientation using simultaneous videotapes. Videotapes were also used to compare all strut parameters with and without range and orientation corrections. Failure to find any significant correlations between mating success and strut sound amplitudes or between other strut measures and range or orientation persuaded us to omit sound level measures and orientation corrections from subsequent sampling.

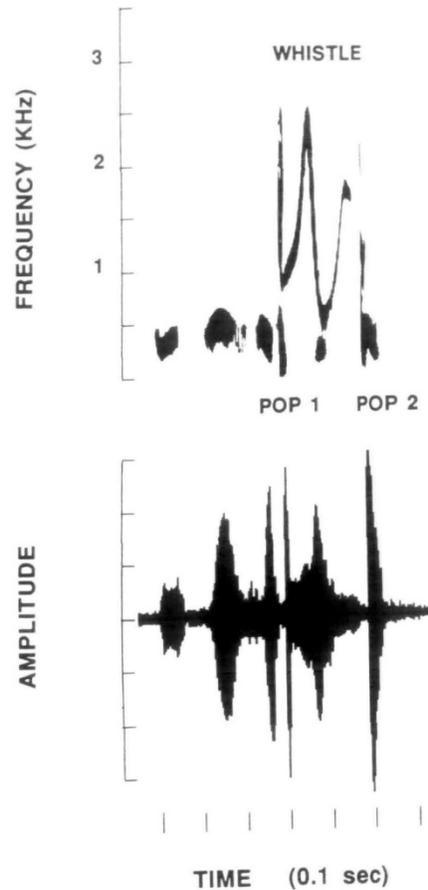


Figure 1. Sonogram and oscillogram of the terminal section of a typical strut display. Three coo notes are followed by the first pop, a frequency-modulated whistle, and finally the second pop.

Table 2. Acoustic measures of strut display structure

1. Pop 1: whistle peak interval*
2. Pop 1: whistle minimum interval
3. Pop 1: pop 2 interval ("inter-pop interval")*
4. Starting frequency of whistle
5. Peak frequency of whistle*
6. Minimum frequency of whistle
7. Upward frequency modulation sweep of whistle (= 5 - 4) (whistle frequency range)*
8. Downward frequency modulation sweep of whistle (= 5 - 6)
9. Rate of upward frequency modulation of whistle (= 7/1)*
10. Fundamental frequency of pop 2
11. Ratio of peak-peak amplitudes of coo 1 : pop 1
12. Ratio of peak-peak amplitudes of coo 2 : pop 1
13. Ratio of peak-peak amplitudes of coo 3 : pop 1
14. Ratio of peak-peak amplitudes of pop 1 : pop 2 (pop amplitude ratio)
15. Ratio of peak-peak amplitudes of minimum frequency to starting frequency point of whistle
16. Ratio of peak-peak amplitudes of minimum frequency to peak frequency point of whistle (whistle amplitude ratio)

All 16 measures were taken at lek 8 in 1987; 5 measures (marked *) were also taken at lek 8 in 1986.

We conducted a systematic search for relevant acoustic cues using a large sample of displays recorded at lek 8 in 1986 (1651 displays) and 1987 (1818 displays). We initially examined all notes in the terminal part of the strut display for individual variation and then focused on a set of measures that showed significant between-male variation (ANOVAs: $p < .05$) and were thus candidates for female discrimination. Five of the 16 measures listed in Table 2 were examined in 1986, and all 16 in 1987. We computed individual mean values for each trait and used stepwise multiple regressions to identify those that were the best predictors of adjusted mating rate in each year at lek 8. Each identified trait was then tested for replicability using ANCOVAs on data from all years except the one in which it was identified. For the latter tests, we used individual mean values based on 10 displays per season (5 per day on 2 days) and included data from 1984–1987 at lek 4.

Morphology

We took three measures from each captured male: unflattened wing-cord length (as a measure of overall body size), tail length from base to the tip of the longest rectrix, and body mass. Lengths were measured to the nearest millimeter and mass to ± 12.5 g.

Age

All males were aged as either yearlings (< 1 year old) or adults (> 1 year). Captured birds were aged using primary molt stage (Eng, 1955). Yearlings could also be distinguished from adults at leks using relative tail length and shape and the degree of development of the esophageal sac (Patterson, 1952). Ages of marked individuals in each year were taken as age at capture plus elapsed time. These were minimum ages for the 81.4% of males first trapped as adults.

Territories

At lek 4 we defined male territories from mapped locations collected during scan samples at 5–10-min intervals. In 1984, scans were supplemented with focal individual observations. Male locations were plotted relative to a grid of numbered wooden stakes placed at 20-m intervals throughout the lek. The grid was positioned in the same location each year by reference to permanent, steel, corner markers. Further details are given in Gibson and Bradbury (1987).

We considered all males that consistently used the same area and aggressively excluded others as territorial, and defined the following measures for each territory.

1. Mating history. Mating history was the proportion of all matings seen at the lek in a previous year that occurred within the current year's territory. Mating history was defined for time lags of 1, 2, and 3 years earlier. To define a male's territory area, we divided the lek into 20×20 -m blocks, ranked blocks by his usage in the current year, and selected the top 75% of the distribution. Although this procedure results in some overlap in areas among territorial neighbors, we prefer it to the more exclusive 50% use areas because it produces more uniformly distributed mating history values. Mating history values (for a 1-year time lag) based on 50% and 75% use areas were highly correlated ($r = .853$, $N = 26$, $p = .001$). We did not compute mating histories for territories occupied by the same male in successive years because in these cases characteristics of site and individual were confounded.

2. Relative location. The degree to which a territory was central versus peripheral was measured by computing the harmonic mean distance between a male's activity center and those of all other territorial males at the lek. This measure weights short distances more heavily than long ones so that central males, which are close to several others, will have shorter harmonic mean distances than peripheral individuals. It does not assume that there is a single lek center (cf. Höglund and Lundberg, 1987). Individual activity centers were defined based on a 10-m grid using the harmonic mean method of Dixon and Chapman (1980).

3. Territory area. Territory area was measured as the 50% utilization area [MAP (.50)] using Anderson's (1981) Fourier transform method.

Female movements

In 1989, we mapped the locations of all females present within a gridded 2-ha area of lek 4 at 1-min intervals to investigate whether hens responded to each other's movements. The area included 9 male territories. Observations were made on 13 days between 5 and 20 April, with 1–4 hens present at any time. We mapped 28 hen visits for a total of 683 hen min on the grid.

We defined nine "arbitrary territories" as 20×20 -m grid blocks within which territorial males displayed regularly. These overlapped the areas occupied by male territories, although the real territories varied considerably in area. Each block accumulated at least 15 hen min in the pooled sample. We pooled the data across days and computed the rate at which other hens present on the grid entered each arbitrary territory under two conditions: with no other hen present in the "territory" and with one or more (1–3) present. To control for

opportunities for hens to approach, rates were normalized by the number of available hens outside the block.

Statistical analysis

In testing relationships between mating success and other traits, we attempted to maximize power by using parametric tests where appropriate and employing the largest homogeneous samples available. Distributions of all mating success measures were right skewed and so were $\log(1 + Y)$ transformed for tests. Proportions were arcsine (\sqrt{P}) transformed. Non-parametric Spearman rank correlations (r_s) were used in a few cases. Where possible, we combined data across different leks and years to maximize sample sizes. Differences in annual lek means were removed by scaling trait values as deviations from the annual mean for the lek. Where variances differed greatly, trait values were further divided by the annual standard deviation, converting them to z scores. We used analyses of covariance (ANCOVAs) to test for differences in the relationship between mating success and traits before combining samples and did not pool data if the year versus trait interaction was significant at $\alpha = .05$. Sample sizes for tests vary among traits due to differences in sampling emphasis among leks and years, as described above.

Finally, although we report only tests for directional effects of traits on mating success, we also used second-order polynomial regressions to test for the possibility that females exerted normalizing or disruptive selection on male traits (Lande and Arnold, 1983). The results provided no support for this idea and so will not be presented.

Results

Phenotypic correlates of adjusted mating success

Our analyses showed that adjusted mating success was related to differences in strut display performance, but not to morphology or age, as discussed below.

Courtship display

Adjusted mating success increased with the duration of the inter-pop interval of the strut display (Figure 2). Initial surveys using stepwise regression on samples from lek 8 in 1986 and 1987 identified four different acoustic predictors of adjusted mating success, including inter-pop interval (Table 3). However, when we tested each trait by correlating it with adjusted mating success in other years, only inter-pop interval was repeatable (Table 3). The relationship of inter-pop interval to adjusted mating success was not statistically heterogeneous across the six samples (ANCOVA interaction: $p = .299$); however, the proportion of the variance in adjusted mating success it explained varied widely, from 0 at lek 8 in 1987 to 95% at lek 4 in 1984 (Table 3). Two traits that we had identified as correlates of mating success on lek 4 in 1984 (Gibson and Bradbury, 1985), peak frequency and rise time of whistle, were not significant correlates in subsequent years. However, they were both correlated with whistle frequency range (WFR in Table 3), which showed high Pearson coefficients on lek 4 in 1984 and lek 8 in 1986, but low values in other lek years. The overall

impression generated by these examples and the data in Table 3 is that the relative importance of specific vocal traits varies markedly from year to year and from lek to lek.

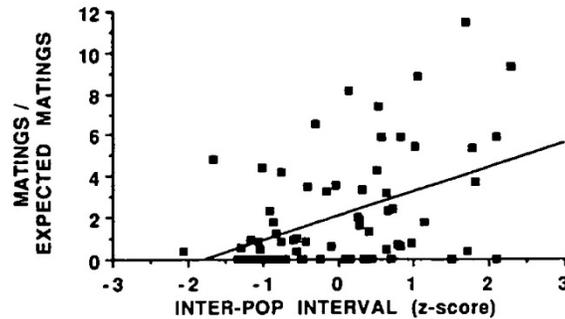


Figure 2. The relationship between adjusted mating success and mean inter-pop interval [73 males from lek 4 (1984–1987) and lek 8 (1986–1987)]. The regression is $Y = 2.041 + 1.172X$.

Lek-year	$r(n)$	Trait ^b			
		IPI	PAR	WFR	WAR
4-84	$r(n)$.973 (5)	.712 (5)	.675 (3)	.948 (3)
4-85	$r(n)$.627 (9)	.161 (9)	.210 (10)	-.584 (8)
4-86	$r(n)$.303 (10)	-.550 (10)	.058 (10)	.514 (10)
4-87	$r(n)$.494 (12)	.000 (12)	.130 (12)	-.460 (12)
8-86	$r(n)$	<u>.469</u> (19)	.051 (19)	<u>.469</u> (19)	-.356 (17)
8-87	$r(n)$	-.008 (19)	<u>.441</u> (18)	.190 (19)	<u>.360</u> (19)
ANCOVAs					
	Covariate (p)	.008	.826	.153	.940
	Interaction (p)	.292	.920	.486	.032

- a. Pearson correlations (r) between each cue and adjusted mating success in each year are shown; (n) = sample size. The sample in which each measure was identified is underlined. ANCOVAs test the effect over all years excluding the sample in which the trait was identified.
- b. IPI = inter-pop interval, PAR = pop amplitude ratio, WFR = whistle frequency range, WAR = whistle amplitude ratio

Adjusted mating success was positively correlated with the rate at which males displayed (display rate uncorrected for female proximity: $r = .594$, $n = 30$, $p = .0003$). This correlation was generated partly by the facts that most males inflated display rates when hens were nearby and successful males were more often close to hens. However, after correcting for female proximity, successful males still displayed at higher rates when hens were distant (Figure 3; hens at 50 m: $r = .424$, $p = .020$) but not when hens were nearby (at 5 m: $r = .051$, $p = .788$). This could mean either that distant hens were more likely to approach males that displayed at high rates or that males that were more attractive for other reasons displayed more vigorously to distant hens. The former alternative should be accepted cautiously because the effect of display rate when hens were at 50 m was not independent of

inter-pop interval: when both measures were included in a multiple regression, inter-pop interval remained closely linked to mating success (partial $r = .892$, $p = .0044$), whereas the effect of strut rate weakened and became marginally nonsignificant (partial $r = .385$, $p = .0599$).

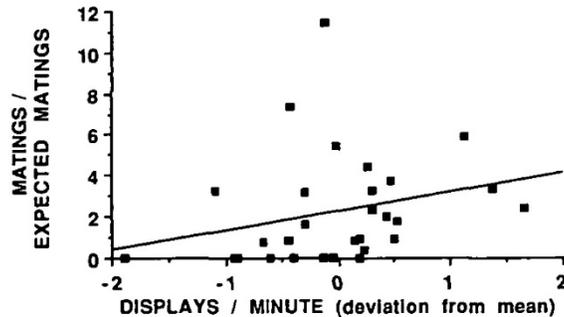


Figure 3. The relationship between adjusted mating success and mean strut rate when hens were at 50 m (30 males at lek 4, 1984 and 1986–1987). The regression is $Y = 2.245 + 0.946X$.

Morphology

There were no relationships between adjusted mating success and wing length ($r = .051$, $n = 38$), tail length ($r = -.087$, $n = 36$), or body mass ($r = -.168$, $n = 39$). Data were pooled across four years at lek 4. We also found no relationships between morphological traits and either inter-pop interval or display rate (hens at 50 m).

Age

Minimum ages of males in our sample ranged from 2 to 4 years. Adjusted mating success did not increase or decrease with age, either across different males within seasons ($r = .154$, $n = 45$, $p = .312$) or within individuals followed from year to year (paired $t = 0.061$, $df = 15$, $p = .953$). Mean success peaked at 3 years of age, but this was not significant when tested with a second-order polynomial regression ($p = .229$). There were also no significant relationships between age and either inter-pop interval or display rate.

In short, we identified one individually variable component of the strut display, inter-pop interval, that was consistently related to mating success across all samples. Strut display rate when hens were distant was also correlated with mating success, but we could not demonstrate this effect independently of inter-pop interval. Mating success did not appear to be affected by gross measures of body size or, among birds more than 1 year old, by age.

Territory characteristics

As in our earlier work, we found no evidence that adjusted male mating success was correlated with either proximity to a lek center (harmonic mean distance to other males: $r = .079$, $n = 45$; 1984–1987 at lek 4) or with territory size ($r = -.061$, $n = 44$). We did, however, find evidence that hens returned to sites where they had mated in a previous year. In 1987, the mating success of males that were in their first season on a territory at lek 4 increased with

the proportion of matings occurring at that site in the previous year (Figure 4, upper panel; $r = .755$, $n = 10$, $p = .012$), although this relationship was absent in the 2 preceding years (1985: $r = -.241$, $n = 8$; 1986: $r = -.168$, $n = 7$; 1985–1986 versus 1987 year versus territory history interaction: $F_{1,19} = 6.19$, $p = .021$). A more consistent effect was found when we compared changes in individual mating success across years. Among individuals that shifted their territories between seasons, adjusted mating success increased by an amount proportional to the mating history of the new territory (Figure 4, lower panel: $r = .744$, $n = 8$, $p = .014$). This suggests that either topographic features of the territory or female-site fidelity affected the locations where hens mated.

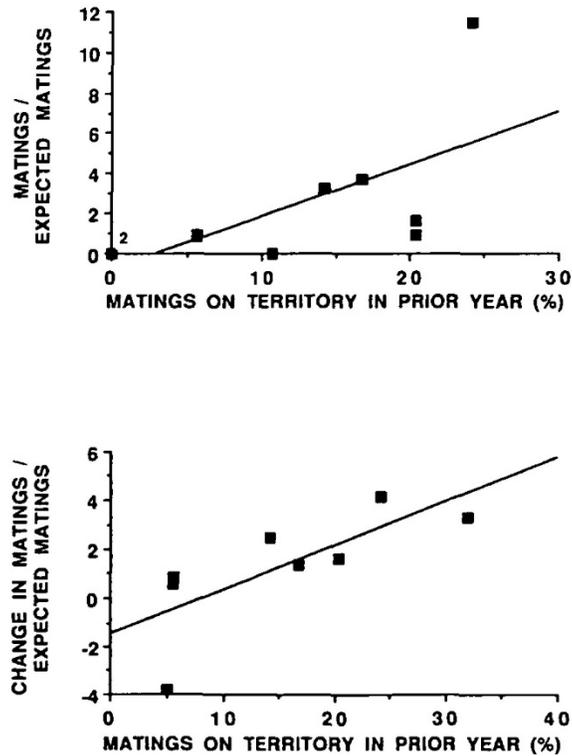


Figure 4. The relationship between adjusted mating success and territory history in the previous year. Upper panel: cross-sectional comparison for 10 males occupying new territories at lek 4 in 1987 (regression $Y = -0.792 + 0.260X$). Lower panel: change in adjusted mating success from year 1 to year 2 for all males at lek 4 that moved their territories between years (1984–1987) in relation to mating history of the new territory (regression $Y = -1.502 + 0.182X$).

To separate these possibilities, we tested two predictions of the site-fidelity hypothesis (Table 4). First, if site effects are due to returning hens, the effect should decline over longer time lags because of the mortality of hens. As predicted, both mating success of males in 1987 and changes in mating success of males that moved their territories between years were significantly correlated with the mating history of their territorial site in the previous

year, but not 2 or 3 years earlier. Second, because older hens breed earlier (see Methods), a territory's mating history should be more closely related to mating success measured during the first half of the mating period than during the second half. As expected, correlations with both mating success in 1987 and changes in mating success across years were significant for early but not late season success (Table 4). Correlations of inter-pop interval with early and late season success were of similar magnitude, suggesting that younger hens were as proficient as adults at assessing male vocal display. Because we did not measure topographic features of territories, we cannot exclude that they play an additional role, although the absence of long-term effects of a territory's mating history on mating success suggests that this is unlikely.

Table 4. Tests of the female site-fidelity hypothesis at lek 4

	Measure of mating success	
	Adjusted mating success in 1987 $r(n)$	Change in adjusted mating success year 1 to year 2 $r(n)$
Time lag (years) ^a		
1	.755 (10)*	.744 (8)*
2	.676 (10)	-.028 (7)
3	-.046 (10)	-.615 (6)
Period ^b		
Early	.755 (10)*	.859 (8)*
Late	.602 (10)	.128 (8)

a. Pearson correlations between adjusted mating success and territory history at three time lags

b. Pearson correlations between mating history of a territory in the previous year and adjusted early- and late-season mating success of males taking new territories

* $p < .01$

Territory history versus phenotypic traits

Inter-pop interval and a territory's mating history tended to covary ($r = .295$, $n = 25$, males on new territories at lek 4, 1985–1987, $p = .152$). This suggests that the effect of each variable on mating success might have been inflated by its association with the other. To check this, we computed both simple and partial correlations between adjusted mating success and each measure. We split the sample into two periods (1985–1986 and 1987) because territory history affected mating success only in 1987 (see above). In 1985–1986, inter-pop interval and adjusted mating success were positively correlated both in a simple comparison ($r = .568$, $n = 16$, $p = .027$) and with mating history partialled out (partial $r = .592$, $p = .026$), but in 1987 the partial correlation was no longer significant (simple $r = .661$, $n = 10$, $p = .038$; partial $r = .572$, $p = .108$). By contrast, territory history and adjusted mating success were still significantly correlated in 1987 when inter-pop interval was partialled out ($r = .697$, $n = 10$, $p = .037$). Thus, females based choice on both inter-pop interval and previous mating locations with the relative emphasis varying annually.

Neighbor effects

We also found evidence for neighbor effects on mating success (Table 5). When we compared the mating success of territorial males as a function of distance between their activity centers, spatial correlations (Moran's I) were positive for males located within 25 m of each other in all years and were significant in 2 years. By contrast, there were no significant correlations between the mating success of males separated by greater distances.

Table 5. Moran's I correlations between mating success and trait values of males with activity centers separated by 25 m or less at lek 4

Variable	1984 I(n)	1985 I(n)	1986 I(n)	1987 I(n)
AMS ^a	.501 (9)	.630 (11)*	.193 (10)	.802 (13)***
Inter-pop interval	.149 (10)	.654 (9)*	.698 (11)**	.933 (13)***
Territory history	—	.786 (7)	.518(8)	.941 (10)**
Residual AMS	—	.356 (9)	.319(10)	.719 (10)*

a. AMS = adjusted mating success. Residual AMS is the residual of adjusted mating success regressed on inter-pop interval (1985–1986) and both inter-pop interval and territory history (1987).

* $p < .05$

** $p < .01$

*** $p < .001$

This pattern would be predicted if particular males or their territories are focal points for female attraction, and there is some "spillover" onto the mating success of neighbors. But two alternatives are that neighbors were phenotypically similar or that neighboring territories had similar mating histories. Males located within 25 m of each other had inter-pop intervals that were positively correlated in all 4 years and significantly correlated in 3 years. Similarly, mating histories of territories were positively correlated in 3 years and significantly in 2 years. However, when we removed these effects by using residuals from the regression of adjusted mating success on inter-pop intervals (1985–1986) and both inter-pop intervals and territory history (1987), the correlation between neighbor mating successes was still positive and significant in 1 year (1987). This suggests that, at least in 1987, neighboring males exhibited similar mating success because of spatial spillover.

Copying*Within days*

If hens copy others mating on the same day, mating choice should become more unanimous as the numbers of hens mating at the same time increase. We examined this prediction using data from 56 days on which two or more hens mated across 7 lek years.

Figure 5 (upper panel, filled symbols) confirms the prediction: as the number of hens mating per day increased, hens became more likely to choose a male chosen by other females on the same day ($r_s = .589$, $n = 56$, $p < .00001$). To test whether this could have arisen if hens chose independently of each other, we computed an expected number of group

matings for each day in the sample assuming independent choice. For each day we simulated 103 trials in each of which the observed number of hens selected mates independently, with each male's probability of being chosen set by the observed proportion of matings he accumulated over all other days of the season. These simulations showed that the expected proportion of group matings also increases with the number of hens mating (Figure 5, upper panel, open symbols: $r_s = .926$, $p < .00001$). However, comparison between observed and expected levels of group mating shows that independent choice is insufficient to explain the level of group mating observed when many hens mated on the same morning: the proportion of days with more group matings than expected increased with the numbers of hens mating per day (Figure 5, lower panel; logistic regression: $\chi^2 = 22.24$, $df = 1$, $p < .0005$). Thus, as the number of hens mating per morning increased, hens became more likely to choose a male also chosen by others, both absolutely and relative to levels predicted by independent choice.

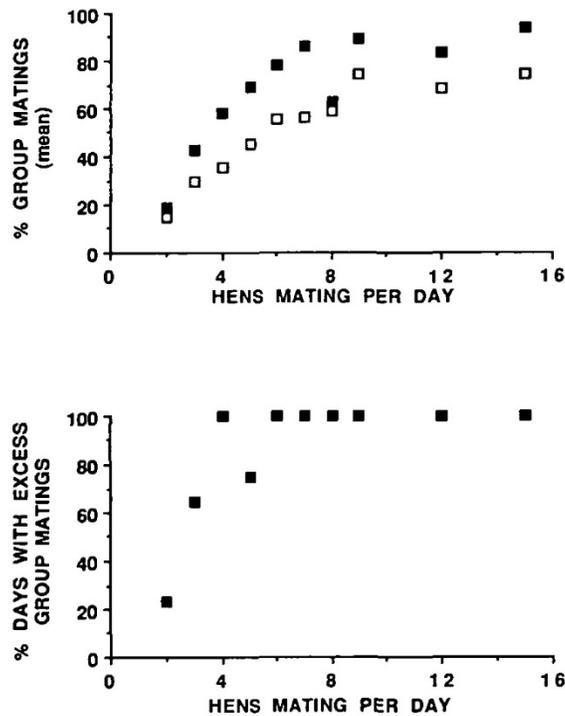


Figure 5. Upper panel: the mean proportion of hens that chose a male also chosen by other hens (group matings) in relation to the numbers of hens mating per day across 56 days in 7 lek seasons. Filled symbols are observed values, and open symbols are those expected if hens chose independently of each other (see text). Lower panel: the proportion of days with more group matings than expected with independent mate choice in relation to the numbers of hens mating per day.

We identified one process that may contribute to this effect: Hens appeared to be attracted to territories where others were already present. The rate at which hens present on

the lek arrived at individual "arbitrary territories" (see Methods) increased from 0.012 min^{-1} when no hen was initially present in the "territory" to 0.131 min^{-1} when at least one other hen (range, 1–3) was there already (paired $t = 4.134$, $df = 8$, $p = .0025$; there were insufficient data to test whether arrival rates increased further with additional hens on the territory).

Between days

Sage hens typically visit leks for 2 to 3 days only a few days apart and mate once on the last visit (see Introduction). Therefore, if hens copy the choices of others that mated on a previous visit, short intervals between days on which a male mates should be more frequent than expected if a male's probability of mating were independent of when he last mated. This prediction is unlikely to be confounded by remating: Records of marked hens indicate that they do not return to a lek after mating unless a clutch fails and then only after a lengthy interval.

To test this idea, we compared the pooled distribution of intervals between successive mating days ($n = 99$) by each male that mated on more than 1 day ($n = 42$), with an expected distribution, computed as follows. We first computed an expected probability distribution of days between copulations for a male that mated on a particular number of days in a given season ($n = 2, 3, \dots, 8$). In each of 10^3 simulated trials, a male was assigned n days chosen at random from a distribution of the number of mating decisions per day, subject to the constraint that he could not be assigned the same day twice. We weighted each probability distribution by the number of intervals contributed to the sample by all males with the same n in that year and then summed the weighted distributions over all values of n and all 7 lek years to yield an expected distribution.

Figure 6 confirms the predicted pattern. The observed and expected distributions differ significantly (Kolmogorov-Smirnov one-sample test: $p < .01$, $n = 99$ intervals) due to an excess of short (2-day) intervals in the former. Comparison with the distribution of 12 intervals between successive visits by 7 marked hens seen at leks on more than 1 day shows that 2 days is the modal interval between successive lek visits (Figure 6, lower panel). This close correspondence suggests that the choices of some hens were influenced by matings observed on a previous visit.

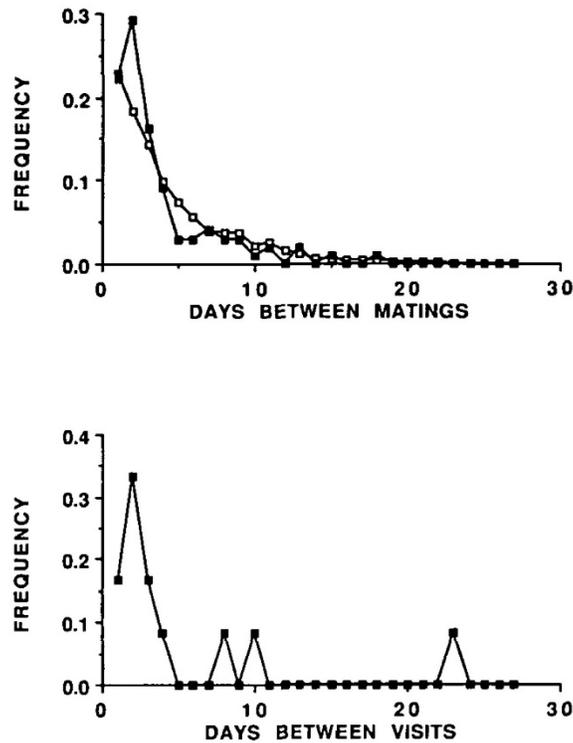


Figure 6. Upper panel: observed distributions of intervals between successive mating days (filled symbols) and the distributions expected if mating probabilities are determined independently on each day (open symbols). Lower panel: the frequency distribution of intervals between successive lek visits by banded hens. Lines connect adjacent frequency classes.

Copyjing or changes in male display?

A possible alternative interpretation of both within- and between-day patterns is that they were due to changes in male display performance rather than or in addition to copying. However, when we compared the mean display performance of a male on days when he mated versus days in the same season when others mated, we found no significant changes in basal display performance. A male's inter-pop interval tended to be longer on days when he mated than on days when other males mated, but the mean difference was small (0.86 ± 1.62 ms) and not significant (for 11 males recorded at lek 8 in 1986–1987, paired $t = 1.755$, $df = 10$, $p = .1098$). Display rates adjusted for female proximity also tended to be slightly, though not significantly, higher on days when a male mated (0.27 ± 0.78 struts min^{-1} : $t = 1.642$, $df = 21$, $p = .116$). This shows that the temporal distribution of matings across days cannot be explained solely by changes in basal display performance. However, it is still possible that within days a male's mating success might have been inflated if he escalated display performance after attracting the first female. It is suggestive that display rate uncorrected for female proximity was higher on days when a male mated compared to days when others mated (7.10 ± 0.60 versus 6.20 ± 0.87 struts min^{-1} ; paired $t = 4.328$, $df = 21$,

$p = .0004$ for 22 males at lek 4, 1984–1987). However, whether increased display rate enhances a male's attractiveness to hens is unclear (see above).

Do copiers always copy hens that assessed males directly?

If hens that copy always copy others that have assessed males directly, males should be ranked identically by both the choices of solo mating hens and by group decisions (see Methods). By contrast, if some copiers copy others that have not assessed males directly, the rankings should be poorly correlated and solo mating decisions would be more closely related to male phenotypic traits. To investigate this, we split mating decisions into solo versus group decisions, computed an adjusted mating success for each male in each situation (details in Methods), and compared these two measures of male attractiveness.

Two results supported the latter hypothesis. First, although there was a positive correlation between adjusted mating successes under solo and group decision conditions, the relationship was weak and reached significance only when data were pooled across all lek years ($r = .293$, $n = 69$, $p = .015$; both leks from 1985–1987; no male at lek 4 in 1984 received group matings). Second, whereas solo mating success was significantly correlated with inter-pop interval and (in 1987 at lek 4) territory mating history, correlations between these male traits and group mating decisions, although still positive, were not significant (Table 6). We considered the additional possibility that group-mating hens might have chosen different traits, but group mating success was not significantly correlated with any other measure of male courtship display, morphology, or territory.

Table 6. Pearson correlations of inter-pop interval and territory mating history (previous year) with adjusted mating success measured by solo and group mating decisions

Variable	Lek	Year	Solo decisions $r(n)$	Group decisions $r(n)$
Inter-pop interval	4	1984	.951 (5)*	—
	4	1985	.810 (8)*	.051 (9)
	4	1986	.388 (10)	.133 (10)
	4	1987	.595 (12)*	.207 (11)
	8	1986	.596 (18)**	.312 (19)
	8	1987	.058 (17)	.072 (19)
	4 and 8	1985–1987	.425 (65)***	.180 (68)
Territory history	4	1987	.763 (10)*	.495 (9)

n = number of males

* $p < .05$

** $p < .01$

*** $p < .001$

In summary, distributions of matings among males both within and across days suggest that some hens copied the choices of others. There was little support for an alternative interpretation based on changes in male display performance across days. Some hens apparently copied the choices of others that had not assessed males directly, as indicated by low correlations between the mating success of males measured by group mating decisions compared to success based on solo decisions and by low correlations between male traits

such as inter-pop interval and territory history and adjusted mating success when females make group decisions.

Copying and the variance in mating success

To test whether unanimity of choice was enhanced by copying, we compared the standardized variance in mating success with the mean number of hens that mated at the same time as an average female (Lloyd's index of crowding) across the 7 lek seasons. As shown in Figure 7 (upper panel), the variance in mating success increased with the opportunity to observe other hens mating ($r_s = .873$, $n = 7$, $p = .02$).

As opportunities to copy increase, phenotypic or spatial cues would be predicted to explain a smaller proportion of the variance in mating success both because some hens copy others that have not assessed males directly (see above) and because day-to-day variation in the number of hens involved in group mating decisions adds noise to the underlying relationship. To test this, we compared the variance explained by inter-pop interval with the standardized variance in mating success (Figure 7, lower panel). As expected, the two were negatively related ($r_s = -.943$, $n = 6$, $p = .035$). We also considered an alternative possibility that the effect of inter-pop interval might depend on changes in its mean and/or variance across seasons, but found no significant relationships.

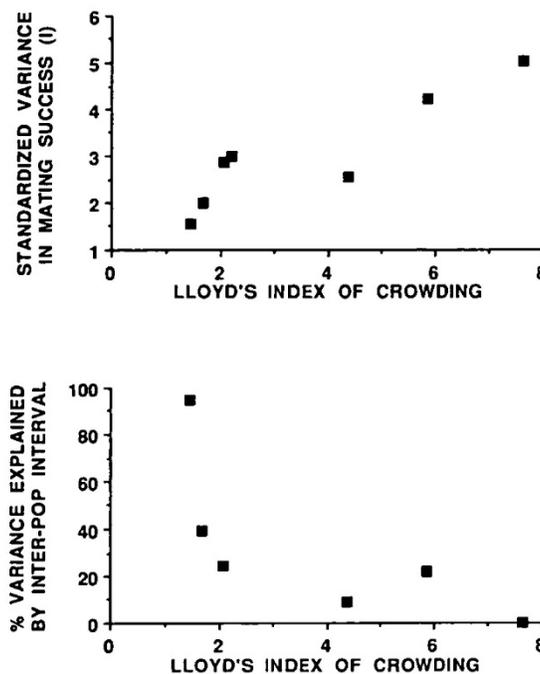


Figure 7. Relationships between the mean number of hens that mated at the same time as a random hen (Lloyd's index of mean crowding) and the standardized variance in male mating success (upper panel) and the proportion of the variance in adjusted mating success explained by inter-pop interval (lower panel). Each point represents a lek in a single year.

Discussion

Our data suggest two main conclusions. First, we have confirmed our earlier finding (Gibson and Bradbury, 1985) that mate choice in this species is based in part on female assessment of male phenotypic traits and have shown that at least one of these traits is invoked in a repeatable way in successive mating seasons. Second, our analysis indicates that females also resort to secondary mate choice strategies such as fidelity to territories in which they mated previously and copying other females' mate choices. The frequency of copying increases with the opportunity to do so: In years with high synchrony of female visits, copying appears to be very prevalent. Both secondary processes tend to reduce the correlations between male phenotypic traits and mating success. These results have important consequences for four issues concerning lek evolution and sexual selection, as discussed below.

Identification of cues used by lek females

The last two decades of research on mate choice by lek females have produced a heterogeneous set of results. Because many lek species are markedly sexually dimorphic, the initial assumption was that strong correlations between male phenotypic traits (including display performance) and mating success should be easily demonstrable. While some studies have found such correlations (Andersson, 1989; Gibson and Bradbury, 1985; Höglund and Lundberg, 1987), other results have brought this proposition into question. These include the presence of extreme mating skew in the absence of evident cues (Lill, 1974; Wiley, 1973), the inability to replicate the effects of particular cues between different years of the same study (Hartzler and Jenni, 1988; this study), and the observations of levels of mating unanimity in excess of those predicted by independent female choice for identified cues (Bradbury et al., 1985).

These divergent results have generated a variety of hypotheses about the factors determining mating success on leks, making synthesis difficult. Among the factors suggested as determinants of differential male mating success are: (1) male attendance at leks, (2) dominance and interference between males, (3) female choice of particular male phenotypes, (4) female preference for particular territories, and (5) female copying of other females' mate choices. Based on our studies, we believe that all of these factors play some role in sage grouse, and that they probably play a role, with perhaps different weightings, in other lek species. It is not surprising that male attendance has repeatedly been associated with mating success. Although male interference is generally low in our populations, a severe winter in 1983 led to the establishment of much smaller and less stable leks in which there was substantial male interference (Gibson and Bradbury, 1987). The existence of traits that are repeatably correlated with female choice, particularly that of females making solo visits, argues strongly for female choice of particular male phenotypes. And finally, this study shows that both site fidelity and female copying can strongly affect male mating success in sage grouse. We suggest that much of the debate among lek researchers about favored cues can be resolved by recognizing that some combination of these factors is likely to be present in any lek system.

One intriguing but unresolved issue is whether there are shifts between leks or years in the weight attached by females to different aspects of display. The magnitude and even the direction of the correlations for several traits vary markedly among years and leks. For example, inter-pop interval was not significantly correlated with mating success at lek 4 in 1987 after territory history had been partialled out (Table 3), nor was it correlated with mating success at lek 8 when group mating decisions were excluded (Table 6). Similarly, three other vocal traits were correlated with mating success in 1 year but not in others (Table 3). These shifts might reflect changes in the weight given by females to particular traits. However, they could alternatively be explained by temporal changes in the roles of copying or site fidelity, both of which tend to reduce true correlations between mating success and the cues used by females for direct male assessment, or as type-one errors generated by the stepwise regression procedure (for the case of single-season correlates). Resolution of this issue will require manipulations of male cues.

Male settlement strategies

Previous studies suggest that ideal free settlement of males on "hotspots" of female range overlap predicts both the distribution of males across lek sites within this population (Bradbury et al., 1989; see also Pruett-Jones, 1985) and also the major differences between species in lek dispersions (Bradbury et al., 1986), but not the precise locations of leks or the intensity with which males cluster their territories. Several authors have proposed complementary mechanisms by which the unanimity of female choice within a lek might act to intensify the clustering of male territories at particular locations (Arak, 1988; Beehler and Foster, 1988; Höglund and Robertson, 1990; Wiley, 1973). Our data support the assumptions of two of these proposals.

In the "hotshot" model, male clustering is driven by spatial spillover of matings from an attractive male to his close neighbors (Beehler and Foster, 1988). This provides a rationale for centripetal clustering by less successful males, but not for the behavior of the attractive male who loses matings to those around him. As suggested by models of kleptoparasitism (Parker and Sutherland, 1986; Pulliam and Caraco, 1984), some additional benefit must be invoked to explain why an attractive male stays in the same location rather than moving on. Our data support the assumption of spillover in mating success among close territorial neighbors. Our data also provide evidence for long-term site fidelity by hens that could provide the necessary benefit for a male to remain at a site where he has previously mated. Site fidelity by hens within a season, for example, resulting from hens returning to the same territories either across successive visits to the lek before mating or between nesting attempts, is also possible and could reinforce this effect (Gibson, 1989).

A second model suggests that the combination of highly skewed mating in each season with site fidelity by hens across seasons causes males to compete intensely for previously successful territories. This leads to smaller territories or clumps of males queueing for accession to a favored location (Wiley, 1973). Our observations suggesting site fidelity by hens across years support the underlying assumption of this "temporal spillover" model. The situation, however, appears more complex than was suggested previously. First, several factors, and particularly copying, are implicated in the generation of mating skew within seasons. Second, female site fidelity appears to predict the locations of matings only

between successive years and not over longer periods. Finally, site effects are evident only in some years. This suggests that males should use the copulation distributions of the previous year only as an initial predictor of settlement locations and that the locations at which males cluster within a lek should shift over periods longer than a year as the locations of popular males change. Observations of male settlement that test the predictions of both the hotshot and temporal spillover hypotheses will be presented elsewhere (Gibson RM, submitted).

Unanimity of mate choice versus intensity of sexual selection

Because of the extreme unanimity of female choice, and hence high variance in male mating success, it is often assumed that preferred male traits are under intense sexual selection on leks. In fact, the variance in male mating success has been proposed as a useful measure of sexual selection intensity (Wade and Arnold, 1980), although it actually only measures the opportunity for sexual selection (Lande and Arnold, 1983; Clutton-Brock, 1983). Whether that opportunity is exploited or not depends on the strength of the covariation of relative male mating success and the values of specific male traits.

Female sage grouse can either choose males by direct assessment or fall back on secondary processes such as site fidelity and copying. Although these secondary processes are effective rules of thumb in the sense that they do better than chance, they identify males with preferred traits with lower accuracy than does direct assessment. Of the two secondary processes identified here, copying has the greatest potential to increase the unanimity of female choice. As we have shown, the greater the opportunity to copy other hens, the greater the variance in male mating success and the lower the correlations between specific male trait values and male reproductive success. This leads to the unexpected conclusion that, to the extent that copying is responsible for the increased variance, the variance in male mating success on leks is inversely related to the strength of sexual selection on male traits.

Costs of female choice and theories of sexual selection

Recent debate concerning the relative roles of Fisherian (nonadaptive) versus adaptive sexual selection has raised the possibility that mate choice may be costly to females (Kirkpatrick, 1987; Pomiankowski, 1988): If mate choice is costly, female preferences for ornamental traits in males are unlikely to evolve unless females benefit from exercising choice either directly or via "good genes" effects (see Introduction). Our finding that sage hens readily adopt secondary strategies of mate choice suggests that direct assessment of males may indeed be costly to females.

How might sage hens benefit from the adoption of secondary mating tactics? An obvious advantage would be a reduction in sampling or search costs. Site fidelity might reduce sampling costs both because previously successful territories are more likely to be resettled in the following year and because the density of settlement increases (and hence intermale spacing decreases) with the previous occupant's mating success (Gibson RM, submitted). It is possible also that site fidelity provides an indirect way of assessing male phenotype,

as we found a positive (although not significant) correlation between territory mating history and inter-pop interval. If secondary strategies reduce mate search times, this would free females for greater investments in foraging and nest-site defense.

Secondary strategies could of course incur costs as well as benefits. We have already discussed the lower accuracy in identification of preferred male traits when secondary processes are used. This should reduce any benefits of choice when compared to direct assessment. The fact that solo and group rankings of males are positively correlated, although weakly, implies that copying is still better than choosing males at random. Copying could also lead to large accumulations of females within a single male's territory and, because males tend to copulate with such females at lengthy intervals, any time savings of copying might be reduced by lengthy waiting times: The apparently slow mating rates of males under these conditions might be related to sperm depletion (each female must obtain enough sperm to fertilize her entire clutch several days after visiting the lek) or be a male strategy to facilitate copying by females that arrive at the lek at different times during the morning.

In conclusion, the finding that sage hens frequently resort to secondary strategies suggests that direct male assessment is costly and that copying or site fidelity have average payoffs as high or higher than direct assessment. Given the pivotal role that mate choice economics are now seen to play in understanding sexual selection, it will be important to test these interpretations in subsequent work.

Acknowledgments – Collection of these data would not have been possible without the dedicated assistance of 30 undergraduate students from the University of California, Los Angeles, and the University of California at San Diego. Jessica Young and LaReesa Wolfenbarger shouldered the mammoth task of taking multiple acoustic measurements on several thousand displays. Dan Dawson provided facilities at the University of California's SNARL Reserve. R.M.G. is particularly grateful to Gwen Bachman for help in all phases of this study and to Joel Berger, Robert Boyd, David Hirschleifer, and Stephen Pruett-Jones for discussion and comments on the manuscript. Data collection was supported by National Science Foundation grants BNS-8215426, BNS-8516737, and BNS-8719342.

References

- Alcock J, 1987. Leks and hilltopping in insects. *J Nat Hist* 21:319–328.
- Anderson DJ, 1981. Home range: a new non-parametric estimation technique. *Ecology* 63:103–112.
- Andersson S, 1989. Sexual selection and cues for female choice in leks of Jackson's widowbird *Euplectes jacksuni*. *Behav Ecol Sociobiol* 25:403–410.
- Arak A, 1988. Callers and satellites in the natterjack toad: evolutionarily stable decision rules. *Anim Behav* 26: 416–432.
- Avery MI, 1984. Lekking in birds: choice competition and reproductive constraints. *Ibis* 126:177–187.
- Balmford AP, 1990. Lekking in Uganda kob (PhD dissertation). Cambridge: Cambridge University.
- Beehler BM, Foster MS, 1988. Hotshots, hotspots and female preference in the organization of lek mating systems. *Am Nat* 131:203–219.
- Borgia G, Collis K, 1990. Parasites and bright male plumage in the satin bowerbird (*Ptilonorhynchus violaceus*). *Am Zool* 30:279–285.

- Boyce MS, 1990. The red queen visits sage grouse leks. *Am Zool* 30:263–270.
- Boyd R, Richerson PJ, 1985. *Culture and the evolutionary process*. Chicago: University of Chicago Press.
- Bradbury JW, Gibson RM, 1983. Leks and mate choice. In: *Mate choice* (Bateson P, ed). Cambridge: Cambridge University Press; 109–138.
- Bradbury JW, Gibson RM, McCarthy CE, Vehrencamp SL, 1989. Dispersion of displaying male sage grouse: II. The role of female dispersion. *Behav Ecol Sociobiol* 24:15–24.
- Bradbury JW, Gibson RM, Tsai IM, 1986. Hotspots and the evolution of leks. *Anim Behav* 34:1694–1709.
- Bradbury JW, Vehrencamp SL, Gibson RM, 1985. Leks and the unanimity of female choice. In: *Evolution: essays in honour of John Maynard Smith* (Greenwood PJ, Harvey PH, Slatkin M, eds). Cambridge: Cambridge University Press; 301–314.
- Clark CW, Mangel M, 1984. Foraging and flocking strategies: information in an uncertain environment. *Am Nat* 123:626–641.
- Clutton-Brock TH, 1983. Selection in relation to sex. In: *Evolution from molecules to men* (Bendall DS, ed). Cambridge: Cambridge University Press; 457–481.
- Clutton-Brock TH, Green D, Hiraiwa-Hasegawa M, Alban SD, 1988. Passing the buck: resource defence, lek breeding and mate choice in fallow deer. *Behav Ecol Sociobiol* 23:281–296.
- Clutton-Brock TH, Hiraiwa-Hasegawa M, Robertson A, 1989. Mate choice on fallow deer leks. *Nature* 340: 463–465.
- Dixon KR, Chapman JA, 1980. Harmonic mean measure of animal activity areas. *Ecology* 61: 1040–1044.
- Eng RL, 1955. A method for obtaining sage grouse age and sex ratios from wings. *J Wildl Manage* 19:267–272.
- Gibson RM, 1989. Field playback of display attracts females in lek breeding sage grouse. *Behav Ecol Sociobiol* 24:439–443.
- Gibson RM, Bradbury JW, 1985. Sexual selection in lekking sage grouse: phenotypic correlates of male mating success. *Behav Ecol Sociobiol* 18:117–123.
- Gibson RM, Bradbury JW, 1986. Male and female mating strategies on sage grouse leks. In: *Ecological aspects of social organization* (Rubenstein DI, Wrangham RW, eds). Princeton: Princeton University Press; 379–398.
- Gibson RM, Bradbury JW, 1987. Lek organization in sage grouse: variations on a territorial theme. *Auk* 104:77–84.
- Gosling LM, Petrie M, 1990. Lekking in topi: a consequence of satellite behavior by small males at hotspots. *Anim Behav* 40:272–287.
- Gratson MW, 1989. *Sexual selection on sharp-tailed grouse leks* (PhD dissertation). Victoria, British Columbia: University of Victoria.
- Hartzler JE, Jenni DA, 1988. Mate choice by female sage grouse. In: *Adaptive strategies and population ecology of northern grouse*, vol. 1 (Bergerud AT, Gratson MW, eds). Minneapolis: University of Minnesota Press.
- Heisler L, Andersson MB, Arnold SJ, Boake CR, Borgia G, Hausfater G, Kirkpatrick M, Lande R, Maynard Smith J, O'Donald P, Thornhill AR, Weissing FJ, 1988. The evolution of mating preferences and sexually selected traits group report. In: *Sexual selection: testing the alternatives* (Bradbury JW, Andersson MB, eds). Chichester: Wiley-Interscience; 97–118.

- Höglund J, Eriksson M, Lindell LE, 1990. Females of the lek-breeding great snipe, *Gallinago media*, prefer males with white tails. *Anim Behav* 40:23–32.
- Höglund J, Lundberg A, 1987. Sexual selection in a monomorphic lek-breeding bird: correlates of male mating success in the great snipe *Gallinago media*. *Behav Ecol Sociobiol* 21:211–216.
- Höglund J, Robertson JGM, 1990. Female preferences, male decision rules, and the evolution of leks in the great snipe *Gallinago media*. *Anim Behav* 40:15–22.
- Jamieson IG, Colgan PW, 1989. Eggs in the nests of males and their effect on mate choice in the three-spined stickleback. *Anim Behav* 38:859–865.
- Kermott LH, 1982. Breeding behavior in the sharp-tailed grouse (PhD dissertation). Minneapolis: University of Minnesota.
- Kiester AR, Slatkin M, 1974. A strategy of movement and resource utilization. *Theor Popul Biol* 6:1–20.
- Kirkpatrick M, 1982. Sexual selection and the evolution of female choice. *Evolution* 36:1–12.
- Kirkpatrick M, 1987. Sexual selection by female choice in polygynous animals. *Annu Rev Ecol Syst* 18:43–70.
- Lande R, 1981. Models of speciation by sexual selection on polygenic traits. *Proc Natl Acad Sci USA* 78:3721–3725.
- Lande R, Arnold SJ, 1983. The measurement of selection on correlated characters. *Evolution* 37:1210–1226.
- Landel H, 1989. A study of female and male mating behavior and female mate choice in the sharp-tailed grouse *Tympanuchus phasianellus* (PhD dissertation). West Lafayette, Indiana: Purdue University.
- Lill A, 1974. Sexual behavior of the lek-forming whitebearded manakin, *M. manacus trinitatis*. *Z Tierpsychol* 36:1–36.
- Lloyd M, 1967. Mean crowding. *J Anim Ecol* 36:1–30.
- Losey GS, Stanton FG, Telecky TM, Tyler WA, 1986. Copying others, an evolutionarily stable strategy for mate choice: a model. *Am Nat* 128:653–664.
- McDonald DB, 1989. Correlates of male mating success in a lekking bird with male-male cooperation. *Anim Behav* 37:1007–1022.
- Parker GA, Sutherland WJ, 1986. Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Anim Behav* 34: 1222–1242.
- Patterson RL, 1952. *The sage grouse in Wyoming*. Denver: Sage Books.
- Petrie M, Halliday TR, Saunders C, 1991. Peahens prefer males with elaborate trains. *Anim Behav* 41:323–332.
- Pomiankowski AN, 1988. The evolution of female mate preferences for male genetic quality. *Oxford Surv Evol Biol* 5:136–184.
- Pruett-Jones SG, 1985. The evolution of lek mating behavior in Lawes' parotia Aves: *Parotia lawesii* (PhD dissertation). Berkeley: University of California.
- Pruett-Jones SG, Pruet-Jones MA, 1990. Sexual selection through female choice in Lawes' parotia, a lek-mating bird of paradise. *Evolution* 44:486–501.
- Pulliam HR, Caraco T, 1984. Living in groups: is there an optimal group size? In: *Behavioral ecology, an evolutionary approach* (Krebs JR, Davies NB, eds). Sunderland, Massachusetts: Sinauer; 122–147.
- Ridley M, Rechten C, 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour* 76:152–161.

- Shields WM, Crook JR, Hebblethwait ML, Wiles-Ehmann SS, 1988. Ideal free coloniality in swallows. In: The ecology of social behavior (Slobodchikoff CN, ed). San Diego: Academic Press; 189–228.
- Stamps JA, 1988. Conspecific attraction and aggregation in territorial species. *Am Nat* 131:329–347.
- Trail PW, 1984. The lek mating system of the Guianan cock-of-the-rock: a field study of sexual selection (PhD dissertation). Ithaca, New York: Cornell University.
- Trail PW, 1985. Courtship disruption modifies mate choice in a lek-breeding bird. *Science* 104:496–507.
- Trail PW, Adams ES, 1989. Active mate choice at cock-of-the-rock leks: tactics of sampling and comparison. *Behav Ecol Sociobiol* 25:283–292.
- Wade MJ, Arnold SJ, 1980. The intensity of sexual selection in relation to male sexual behavior, female choice and sperm precedence. *Anim Behav* 28:446–461.
- Wade MJ, Pruett-Jones SG, 1990. Female copying increases the variance in mating success. *Proc Natl Acad Sci USA* 87:5749–5753.
- Warner RR, 1987. Female choice for sites vs. mates in a coral reef fish *Thalassoma bifasciatum*. *Anim Behav* 35: 1470–1478.
- Warner RR, 1988. Traditionality of mating site preferences in a coral reef fish. *Nature* 335:719–721.
- Wiley RH, 1973. Territoriality and non-random mating in sage grouse *Centrocercus urophasianus*. *Anim Behav Monogr* 6:85–169.
- Wiley RH, 1991. Lekking in birds and mammals: behavioral and evolutionary issues. *Adv Study Behav* 20:201–291.