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Field Playback of Male Display Attracts Females in Lek Breeding Sage Grouse

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Field Playback of Male Display Attracts Females in Lek Breeding Sage Grouse

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Abstract
Recent correlational studies of lekking sage grouse suggest that male vocal display attracts females. To test this hypothesis further, the natural displays of a territorial male were supplemented with the tape-recorded display of another reproductively successful individual. Significantly, more females approached the speaker's location on days when the recording was played, and also on nonplayback days immediately following a playback, than on other nonplayback days. Analysis of male displays indicated that females were responding to the playback itself rather than to changes in male behavior. The "after-response" following a playback suggests that some females present during a playback remembered its location and approached on a subsequent lek visit. The results provide necessary support for the epigamic function of vocal display, and suggest ways in which female responses to male display may influence lek structure.

Introduction

Conspicuous vocal display (song) by males is characteristic of many avian species during the breeding season. An increasing body of experimental evidence indicates that song frequently serves both intrasexual and epigamic functions (Searcy and Andersson 1986). However, most of the relevant data come from studies of species with resource-based mating systems and relatively little is known of the role of equivalent displays in lek-breeding species. This is unfortunate, for the epigamic role of lek display is of particular interest for theories of sexual selection (Heisler et al. 1987). In the absence of conclusive experimental data, students of lek systems often differ in their assessment of the relative importance of epigamic and intrasexual processes (Bradbury and Gibson 1983; Beehler and Foster 1988).

Lek display in sage grouse *Centrocercus urophasianus* occurs for a few hours at dawn at traditional sites where males defend individual mating territories. While individual males return to the same territory each day, females attend leks on only a few days each and typically move widely among territories before mating with a single male. When females are present, males devote almost all of their time to the repetitive performance of a single, stereotyped display (the "strut") that has a well-defined acoustic structure (Hjorth 1970; Wiley 1973a). Not only is the male display rate strongly affected by female presence (Wiley 1973 b) but a recent study found that male mating success was statistically correlated with both display repetition rate and individually variable acoustic components of strut display performance (Gibson and Bradbury 1985). These results suggest that male vocalizations may both attract females and provide cues on which mate choice is based.

This paper describes a field experiment that examines whether the acoustic component of the sage grouse strut display attracts females. To investigate this question, the displays of a territorial male were supplemented during some morning display sessions with the recorded display of another reproductively successful individual played from a concealed speaker. Movements of females on the lek were monitored to determine whether more were attracted to the territory during playbacks. The results support the notion that male display vocalizations attract females. They also provide evidence for time-lagged female responses that are of potential significance for understanding lek structure.

Methods

The data were collected on 27 days between April 2 and May 12, 1988, in the Crowley Lake area, Mono County, California. The study lek, located in an extensive meadow adjoining sagebrush scrub, was attended by 91–140 males and 1–41 females daily. Mating had begun before the start of the experiment, but females continued to attend, and matings were observed throughout the study period. Supplementary data on lek attendance by marked females were collected during this study and over the previous 4 years at nearby leks.

The playback speaker was placed face up and flush with the ground in a shallow depression within the territory of one of a cluster of 8 males. All attended the lek daily and were individually recognizable using color bands or natural differences in tail shape and patterns of white spots on the under-tail coverts. The surrounding area (200 × 200 m) was gridded at 20-m intervals with numbered wooden stakes to allow mapping of male and female locations. Observations were made (using 10× binoculars and 15–40× zoom telescopes) from a tower erected at the edge of the meadow and 100 m from the speaker location, and from a blind 50 m away from which the playback equipment was operated and male vocalizations recorded. Observers entered the tower and blind in darkness and stayed until the birds left at the end of the morning display period. The speaker could not be seen from either tower or blind and was probably invisible to a grouse > 3 m away. Our activities did not affect the birds' behavior in any discernable way.

Experimental procedure

On 10 mornings a tape recording of single strut display, repeated at approximately 10-s intervals (a typical vigorous display rate when females are present), was played continuously starting ca. 1 h before sunrise and continuing until the birds left the lek 1–2.5 h later. On 17 other mornings no sounds were played. Because of the vagaries of the weather, a planned random sequence of playback and nonplayback days was replaced by the following schedule: playbacks on April 6, 9, 11, 17, and 24–28 and May 2, and nonplayback observations on April 2, 4, 7, 10, 12–16, and 29 and May 3–5, 7, 8, 11, and 12.

Playbacks were broadcast from a Nagra DSM speaker-amplifier driven by a Sony TC-DSM cassette recorder. The playback level was adjusted initially to a level judged to be as intense or slightly more so than the males displaying nearby and kept at the same setting in subsequent sessions. To maximize the chance that the experimental display would be attractive to females and to ensure that it differed from those of males at the lek, I used a display recorded from a male that obtained the most matings at another lek in 1986 and 1987.

Female responses

Female responses were assessed by the proportion of individuals on the lek that both came close to the speaker's location and moved directly toward it (details following). These criteria excluded individuals that came close to the speaker but gave no indication that they were responding to its location.

Females attending the lek were counted during a 30-min period before sunrise, when numbers typically peaked. Each female that entered a 100 × 100-m area centered on the speaker was mapped at 1-min intervals until she left the area. As far as possible, individuals were also followed after they left the mapped area to ensure that they were not counted twice. Female tracks yielded 2 measures: (1) the minimum distance between female and speaker location, and (2) the mean vector angle of movement, expressed as an angular deviation from a direct approach to the speaker, and calculated as follows: For each mapped location along the female's path, the compass bearing from that point to the speaker was subtracted from the bearing to the next mapped location. This procedure was repeated for successive points from the female's first mapped location to the location prior to her closest approach to the speaker. The mean vector (Batschelet 1981) of the angles was then computed. Birds that came within 15 m of the speaker and whose mean vector angle deviation from a direct approach by $< 22.5°$ were classified as "responding."

Because there was a danger that response measures might be chosen to confirm experimental expectations, the preceding measures were extracted from a data set in which each female's identify, and hence information about date and experimental treatment, had been replaced by a random code. Afterward the code was broken to match individual females to particular days. Also, to ensure that results were not arbitrarily dependent on the specific distance and angular criteria used, the analyses were repeated with other reasonable values; essentially the same results were obtained.

Male responses

On all playback and most nonplayback days, we also monitored the locations of all 8 territorial males, plus the display rates and acoustic display parameters of the three males whose territories were closest to the speaker. Male locations were plotted at 10-min intervals. Numbers of displays were counted for 5 min every 15 min. The distance between each male and the nearest female was also noted at the beginning and end of each 5-min sample. For analysis display rate samples were partitioned into cases where females were "absent" (no female < 200 m) or present (female < 200 m). Sound recordings of male displays were made using a Sennheiser MKH 816TFU microphone and Canon VR40A hi-fi video recorder and were digitized using a Macintosh computer running Soundwave software. We took four measures that were correlated with mating success in a previous study: (1) interpop interval, the interval between the amplitude peaks of two "popping" sounds at the end of the display; (2) relative pop amplitude, the ratio of the peak amplitude of the second pop divided by that of the first; (3) whistle range, the frequency sweep between the start and the highest frequency section of a frequency modulated whistle that occurs between the two pops; and (4) relative frequency amplitude, the ratio of the amplitude of the lowest frequency section of the whistle to the amplitude of the highest frequency section. The latter two measures were made on a Uniscan II spectrum analyzer. Where possible we obtained measures from 5 displays per day per male. In the previous study, male mating success was correlated positively with all measures except pop-amplitude ratio, with which it was negatively correlated.

Statistical analysis

To analyze female responses, data were combined across days of similar experimental treatment, and each female lek day was treated as an independent observation. The latter assumption is made with the proviso that lack of independence could arise because some females visit the lek on more than one day and behave similarly on each occasion, or because a female's movements on the lek are influenced by those of other females. The latter did not appear to be true of most "responders" in this study (see Results). Analyses followed the recommendations of Fienberg (1980) in the use of χ^2 instead of G and in omission of Yate's correction. For post hoc comparisons, critical χ^2 values were adjusted to maintain an experiment-wise error rate of 0.05 (Everitt 1977, p. 45). Data on display rates, sound measures and male-speaker distances were transformed where necessary to meet the assumptions of parametric analysis of variance. Where there were sufficient data, nested ANOVAs were used to separate the effect of experimental treatment from inherent day-to-day variability in display parameters. Otherwise data were pooled across days within each treatment class and treatment effects tested by one-way ANOVAs. Analysis of covariance was used to control for the influence of female proximity when analyzing effects of playbacks on male display in the presence of females (Wiley 1973b).

Results

Over the 27 days of the study, 174 female lek visits were recorded. Fifty-four females were tracked through the experimental area. Of these, 17 came within 15 m of the speaker's location, and 10 did so by approaching the speaker's location directly (see Methods). The 10 "responses," which form the basis of the following analysis, occurred on six days between April 9 and May 2. Although more than one female approached the speaker on three days, no other female was within 50 m of the speaker during the responder's approach in all but one case, in which two hens approached together.

Six of the responses occurred on playback days and the remaining four on nonplayback days that immediately followed a playback (Fig. 1). Relative to numbers of females attending the lek, more females approached the speaker on playback days, and also on nonplayback days following a playback, than on other nonplayback days (overall $\chi^2 = 12.10$, $df = 2$, $P < 0.005$; post hoc comparisons: playback vs. other days $\chi^2 = 9.02$, $P < 0.05$, next vs. other days: $\chi^2 = 14.06$, $P < 0.01$). When playback and immediate post-playback days, which did not differ significantly from each other, were combined and contrasted with other nonplayback days, the difference was also highly significant ($\chi^2 = 10.86$, $df = 1$, $P < 0.001$). Although almost three times as many females (as a proportion of those on the lek) approached the speaker during playbacks than on all other days combined, the difference was not quite significant ($\chi^2 = 2.90$, $df = 1$, $P = 0.09$), due to masking by the post-playback "after response."

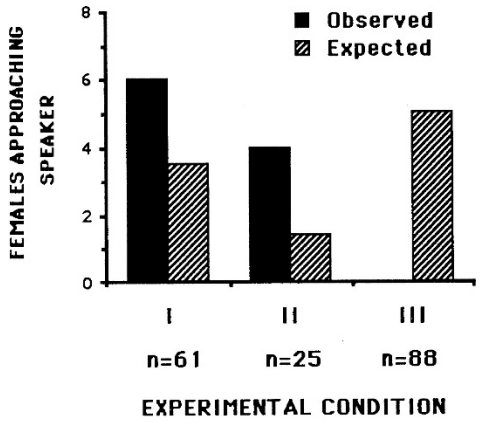

Figure 1. Observed and expected numbers of females approaching the speaker's location under three conditions: I – playback days, II – nonplayback days preceded by a playback day, and III – nonplayback days preceded by a nonplayback day. Numbers of female lek days for each condition are indicated. Further details are given in the text.

The playbacks may also have affected the mating success of the male in whose territory the speaker was located. Although this bird had not mated and rarely attracted females before the playbacks began, he obtained two matings (1 and 2 days post-playback) toward the end of the study. No other male in the monitored group of eight mated during this period, though two had obtained several matings earlier in the season.

Although the data suggest that females were attracted by the playback, an alternative hypothesis is that the speaker affected the displays of the male in whose territory it was located, making him more attractive. To investigate the latter possibility, display rates, acoustic measures, and male-speaker distances for this individual were compared among the three "experimental treatment" classes (see Fig. 1) used in the female response analysis.

There was little evidence that male display explained female response patterns. No significant effect of experimental treatment was found for display rate (females absent: one way ANOVA $F_{2,28} = 2.26$; females present: ANOVA, $F_{2,37} = 2.307$). Among the acoustic measures, inter-pop interval, whistle range, and pop amplitude ratio all varied significantly across days ($P < 0.005$), but none of these measures exhibited a significant added treatment effect (nested ANOVAs). Whistle amplitude ratio varied significantly with experimental treatment (one way ANOVA: $F_{2,27} = 6.632$, $P < 0.005$). However, the direction of the effect (lower whistle amplitude ratio on days following a playback) does not explain the pattern of female response. The male was also significantly closer to the speaker on playback and immediate post-playback days than on other days ($F_{2,63} = 7.895$, $P < 0.001$). This raises the possibility that, if females approached this individual at similar rates regardless of his location, more would have been spuriously classified as responding to the speaker during and immediately after playbacks. However, the male was never approached by a female except when close to the speaker. Analyses of the displays and locations of two nearby males also failed to provide evidence of behavioral changes that could have spuriously generated playback-correlated female responses. In addition, although one individual disappeared mid-season, there were no changes in the occupancy or locations of the eight male territories located near the speaker that correlated with patterns of female response. Thus overall the data suggest that females were attracted by the sound playback itself rather than by changes in male behavior.

Discussion

Despite much interest in the epigamic function of bird song (Searcy and Andersson 1986), experimental evidence that male song attracts distant females is sparse (Eriksson and Wallin 1986). The data presented here provide further evidence for such an effect. Hens approached the playback speaker's location both when it was playing and, unexpectedly, on silent days immediately preceded by a playback. Although they might have been responding to playback-induced changes in male behavior, there was little indication that this occurred. Instead, it appeared that the playback itself was attractive.

While responses during a playback are readily understood, the cause of the after-response is less obvious. The most likely explanation is that some birds present on the lek during a playback remembered its location and approached when visiting the lek the next day. These individuals might either have approached the speaker on the first day or merely been present within auditory range. Although neither possibility could be directly confirmed because none of the responding females was individually marked, data from 22 banded females seen at leks over a 5-year period suggest that both are plausible. In the latter sample, repeat visits were common (68% of females) and most (62%) successive visits occurred either on consecutive days or after a one-day absence. Similar observations were

reported in earlier studies (Lumsden 1968; Petersen 1980). Marked females have also been observed to return to the same location within the lek on successive visits. A possible objection is that although nonconsecutive visits should have produced some responses time-lagged more than one day post-playback, none was observed. However, this could be explained either as a sampling effect or, if directionality of responses wanes with time, by the stringent response criterion. Consistent with the latter possibility, 2 of 26 females that attended the lek 2–7 days post-playback came within 15 m of the speaker. These questions can be resolved only by data from marked females. Nevertheless, while the current evidence is indirect, it is entirely consistent with the return-visit hypothesis.

The demonstration that the acoustic component of display is attractive to females provides further support for the hypothesis that vocal display plays an epigamic role in this species (Gibson and Bradbury 1985). Sufficient evidence would include a demonstration that females respond differentially to call variants that correlate with mating success. Although the experimental design used here does not reveal which components of the call are most attractive, the previous correlational studies have identified a number of possible variables whose effects could be investigated by a modified experimental design.

The results are also relevant to recent discussions of factors that structure leks. The experiment suggests that exposure to females is increased by proximity to the present or recent location of a source of attractive display. These effects could justify aggregation by individuals attempting to increase proximity to females by exploiting the displays of others (Arak 1988; Beehler and Foster 1988). Such behavior would not be unexpected in this species given the apparently high energetic costs of display (Vehrencamp et al., in press) and the existence of individual differences in acoustic display quality. However, whether it is actually important must also depend on the competitive costs of close proximity. These are clearly not mimicked by the present experiment and warrant further study.

A related issue is the suggestion that spatial cues, though not the primary basis of mate choice (Wiley 1973b; cf. Bradbury and Gibson 1983; Gibson and Bradbury 1986; Hartzler and Jenni 1988), might be used by females to relocate a potential mate chosen previously by other criteria (the "rendezvous" site hypothesis: Gibson and Bradbury 1987). This possibility receives support from the "after-response" to the playbacks. It is of interest because any tendency for females to delay approaching, or to pay return visits to, sites from which males display should select for site fidelity by males and hence help to stabilize male dispersions. Leks might alternatively or in addition be stabilized by the occurrence of sites within the lek that for topographic reasons are better for encountering females or by reduced competitive costs of territoriality over wide-ranging search (Courtney and Anderson 1986; Poethke and Kaiser 1987). The experimental results suggest that female responses may be lagged over only a day or so, justifying day-to-day lek stability. This may be relevant to understanding the changes in lek stability through the breeding season (Gibson and Bradbury 1987). But females also return to leks at longer intervals, between first and second nesting attempts within a season (Petersen 1980) and from year to year. Rendezvous-site effects over these longer intervals could provide a rationale for the longer term stability of lek structure typical of this, and other, lekking species (Warner 1988).

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