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Sexual Selection in Lekking Sage Grouse: Phenotypic Correlates of Male Mating Success

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Abstract

Mate choice cues in sage grouse were reinvestigated by analyzing relationships between male mating success and a range of suggested cues. Display cues were implicated by significant relationships between mating status (whether or not a male mated) and lek attendance, display rate (corrected for effects of female proximity and time of day), and an acoustic component related to temporal and frequency measure of a whistle emitted during the strut display. Although display rate and the acoustic component were intercorrelated, both exerted significant partial effects on mating success in multivariate analyses. These display measures also differed significantly between males. In contrast, mating success was not significantly related to measures of territory characteristics, including size and proximity to the lek center, or to body size. These results resolve discrepancies between previous studies and provide a basis for experimental analysis of the role of female choice in this lek system.

Introduction

Students of sexual selection hold divergent views about the role of female choice in this evolutionary process. On one side, several workers have developed genetic models demonstrating that female choice for arbitrary male traits can lead to the evolution of both the chosen trait and the preference even if the trait is otherwise disadvantageous (O'Donald 1980; Lande 1981; Kirkpatrick 1982). On the other side, many authors maintain that female choice should favor traits which are not arbitrary but which instead confer advantages on offspring above and beyond the sexual attractiveness of sons (Zahavi 1975;

Borgia 1979; Hamilton and Zuk 1981; Andersson 1982; Kodric-Brown and Brown 1984). The evolution of adaptive female choice is not in doubt for species in which males provide females with resources or paternal care: here, female choice may have clear consequences for fitness (Downhower and Brown 1981; Kirkpatrick 1985). The debate focuses instead on systems, such as lek mating, in which males provide females only with gametes.

In principle the question could be resolved by selecting an appropriate system, identifying the cues by which females choose their mates, and then examining the effects of paternal cue values on components of offspring fitness (Boake 1985). Avian leks appear ideal for this task. In most species matings occur during the day in large male aggregations whose locations are predictable, male mating success is highly variable, and females often appear free to exercise choice with minimal male interference (review: Oring 1982; though see Foster 1983). Differences in mating success are thus easily measured and should reflect the effects of female choice. Despite these advantages, the mate choice cues used by females of avian lek species have proved elusive (review: Bradbury and Gibson 1983). For example, in perhaps the most exhaustive set of studies to date Lill (1974, 1976) was unable to find any male trait that correlated well with mating success in either of two species of manakins.

There are several reasons why identification of mate choice cues may have proved difficult. First there is a wide range of potential cues to consider. For example, females might choose males on the basis of (1) anatomical cues such as color, tail length, or body size, (2) spatial cues such as location within the lek or territorial characteristics, (3) display performance, or (4) agonistic status (Bradbury and Gibson 1983). Any one or some combination of these criteria might be involved. Distinguishing between these alternatives requires that all be measured in the same system and that multivariate statistical methods be used to tease apart the independent effects of each factor from spurious effects due to correlations between them (e.g., Lande and Arnold 1983). Second, several proposed cues are notoriously prone to influences that could create spurious correlations with mating success. For example, mating success and display may become correlated because males display more vigorously when in close proximity to females (Wiley 1973a). Also mating success may become correlated with central location within the lek because unsuccessful males relocate their territories around those of successful males (Bradbury and Gibson 1983). In analyzing the role of mate choice it is necessary to correct measures of the cues for such effects before they are compared to mating success. Sampling all of the requisite cues simultaneously in a large enough sample of males to permit multivariate analysis and with sufficient intensity per male to allow adequate controls is a challenging task. The difficulty of collecting all the relevant data for a single investigator possibly explains why Hartzler (1972), Wiley (1973a), and Lill (1974, 1976), who all worked alone, were either unable to detect correlates of mating success or, if they did, to eliminate the involvement of alternative correlated cues. We thus surmise that using larger teams of observers might overcome these difficulties.

Among avian lek species, sage grouse *Centrocercus urophasianus* appear particularly amenable to cue identification. Lek display occurs for a few hours at dawn and dusk over a three-month period each spring and leks are usually sufficiently stable that the same individual males can be followed throughout the season. The male display repertoire consists of a single motor pattern that is highly stereotyped within and between males (Wiley

1973b). Most matings occur within a three-week period during which each female visits leks for 2 to 3 days before mating once per clutch (Patterson 1952; Dalke et al. 1964; Lumsden 1968). Male mating success is known to be highly variable, an effect usually attributed to female choice (Scott 1942; Patterson 1952; Lumsden 1968; Hjorth 1970; Hartzler 1972; Wiley 1973a). However, the identity of the cues used by females is unclear. Wiley (1973 a) concluded that differences in display were either uncorrelated with mating success or were too invariant between males to be likely cues. He proposed that proximity of male territories to central locations ("mating centers") was used by females in mate choice, though correlations between location and mating success supporting this idea were weak (Gibson and Bradbury in press). In contrast, a concurrent study by Hartzler (1972) indicated that mating centers shifted often enough, both within and between seasons to be unlikely cues for mate choice. Unlike Wiley, Hartzler found that one behavioral measure, display rate, was significantly related to mating success.

In this paper we reanalyze the issue of mate choice cues in sage grouse using new data collected and analyzed with the problems reviewed above in mind. Although so far we have measured all of the relevant cues for only about a third of the males on a typical sage grouse lek, these data have identified significant relationships between mating success and measures of display performance while eliminating several alternative cues.

Methods

Data were collected at a lek in the Crowley Lake area, Mono County, California between February 3 and April 25, 1984. Preliminary studies were conducted in nearby areas from 1980 to 1983. We focused on adult males (over 1 year old) since younger males attend leks irregularly and rarely mate (Wiley 1973a, personal observations). Numbers of adult males attending the Crowley lek fluctuated daily from 18 to 36 and averaged 28. The birds displayed on a 1.2-ha area at one end of a flat alkali meadow surrounded by sagebrush. Vegetation on the meadow (*Carex* spp. and saltgrass) was less than 4 cm high. To facilitate the mapping of male locations, the lek was gridded at 20-m intervals with numbered surveyors' stakes, and additional stakes were placed at 10-m intervals on intensively used areas.

Observations were made daily from first light until the birds left by a team of 2–6 observers located at an elevated vantage point 250 m from the lek. Zoom telescopes (20–45×) enabled us to monitor individual bird's activities over the entire lek without disturbance. Sound recordings were also made from a blind located on the meadow but at least 5 m from the nearest male's territory boundary. 27 males (75% of the maximum daily attendance) were recognized individually: 17 were color banded and a further 10 were identified by differences in tail shape and the pattern of white spots on the under-tail coverts (Wiley 1973a). Males were captured for banding and measurement by spot-lighting or, in 4 cases, rocket-netting. Rocket nets were not used during the period of female visits and copulations.

Data were collected on all the classes of cues mentioned above (see Introduction) except male agonistic status. Levels of male interference vary widely between leks in this species (Gibson and Bradbury in press). We concluded that agonistic status was an unlikely factor at the lek used in this study for three reasons: (a) male interaction rates when near females

were low (1 per 17 min) relative to the time individual females spent in each male's territory (5–7 min), (b) less than 5% of copulation attempts were effectively disrupted, and (c) most interactions (84% of 95) ended inconclusively and we found no evidence for asymmetric dominance relationships between males. To facilitate later analysis, several cue variables were corrected for known biases by regressing sampled values on the biasing variable and using the residuals as a corrected measure. To limit the number of variables to manageable levels we also collapsed correlated measures of the same cue to a smaller set of independent variables using principal components analysis where possible. The following measures were taken from lek observation and capture data. Unless stated otherwise, these were calculated for the period between the first and last recorded mating (March 23–April 20).

Mating success
Numbers of copulations by each male were compiled from focal and ad lib observations. Since the entire lek area could be surveyed continuously, it is unlikely that we missed copulations during the morning display periods. We did not study the shorter display sessions at dusk and on moonlit nights since preliminary observations and previous studies (Hartzler 1972; Wiley 1973a) indicated that few females mated then.

Lek attendance
Lek attendance was the number of days a male was seen at the lek divided by the number of days on which he would have been detected if present. The latter correction is necessary because not all males were recognized at the beginning of the season. Attendance was not calculated for males that could have been recognized on fewer than 5 days.

Display rates
Display rates were measured in two ways that gave equivalent results. Males were either watched for 5 to 10 min and the number of strut displays per min recorded or exact termination times of 21 consecutive displays were logged and strut rates computed as the inverse of inter-strut intervals. Locations of focal males and the nearest female were noted at one-minute intervals. This appears an adequate measure of female proximity since female lek visits were relatively asynchronous. Average strut rates for each sample (n = 145) were corrected for known effects of time of day and female proximity (Hartzler 1972; Wiley 1973a) by regressing strut rate simultaneously on the distance between the male and the nearest female and time from the start of the sample to sunrise and taking the residuals as a corrected measure. Regressions of corrected strut rate on data for individual males showed no seasonal effects over the mating period.

Acoustic display components
During the strut display males emit a predictable sequence of eight sounds (Fig. 1): two "swishes" generated by rubbing the inner carpal joint against the sides of the esophageal pouch, three low frequency notes, and two intense broad-band popping sounds 200 msec apart separated by a frequency-modulated whistle (Hjorth 1970; Wiley 1973b). Sound re-

cordings of displays by 11 identified males were made under relatively windless conditions and at 5–30 m range using a Sennheiser MKH815T condenser microphone and a Nagra IV tape recorder. The distance between bird and microphone and the bird's orientation were noted. Nine measures were taken from each display. The interval between the first swish and the first pop and the inter-pop interval (see Wiley 1973b), were measured from oscillograms displayed on a Tectronix 5103N storage oscilloscope; reference points were the amplitude envelope peaks of each component. Three measures were extracted from spectrograms using a Unigon model 4512 FFT real-time spectrum analyzer: the starting frequency of the whistle, the highest frequency reached at the end of the first rising frequency phase of the whistle, and the time from the onset of the first pop to the highest frequency of the whistle. Finally, power spectra of 20-msec intervals starting with the onset of each pop were displayed on a Spectral Dynamics SD spectroscope to determine the frequency band at which peak energy registered and the fraction of energy above 500 Hz in each popping sound. None of these measures was related to a male's proximity to females or changed across days.
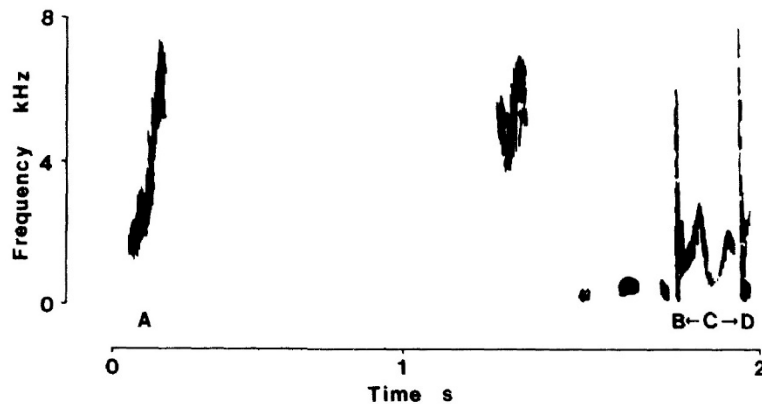
Figure 1. Wide-band sonogram of sounds emitted during the sage grouse strut display. Labeled components are: (A) first wing swish, (B) first popping sound, (C) whistle, and (D) second popping sound.

Because preliminary analyses showed high correlations between several acoustic measures, a smaller number of independent measures was extracted using principal components analysis. The outcome was three components that form the basis of later analyses (Table 1). Spurious correlations between frequency measures might arise as a result of differences in the birds' distance from or orientation to the microphone because frequencies may attenuate differentially with distance or particular frequency components might be emitted directionally. To check that our principal components were not due to such effects, the analysis was repeated using the residuals of frequency measures obtained from multivariate regressions of the original values on range and angle between bird and microphone. The results were unchanged.

Table 1. Rotated Principal Component loadings for 9 acoustic measures of the strut display. Principle components are listed in decreasing order of variance explained and acoustic measures are arranged so that, for each successive component, loadings > 0.5 appear first. The three highest factor loadings for each component are underlined. The variables are: (1) interval from first swish to first frequency peak of whistle, (2) highest frequency of whistle, (3) frequency of energy peak in first pop, (4) fraction of energy above 500 Hz in first pop, (5) interval from first swish to first pop, (6) inter-pop interval, (7) initial frequency of whistle, (8) fraction of energy above 500 Hz in second pop, and (9) frequency of energy peak in second pop.

Acoustic measure	Principal component		
	1	2	3
1	0.847	−0.063	0.171
2	0.829	0.265	0.042
3	0.604	0.114	−0.025
4	−0.004	0.791	−0.255
5	−0.004	0.791	0.024
6	0.280	0.845	0.297
7	−0.006	−0.129	0.766
8	−0.076	0.466	0.689
9	−0.428	0.466	0.678

Territory size and location

Male territories were sampled by scans of the entire lek and by plotting the location of particular males at 1–2-min intervals for 5 to 20 min. Data for each male were combined across days and territory size computed as the area within the 50% minimum area profile (MAP) of its spatial utilization distribution using the nonparametric method of Anderson (1982). Territory sizes were calculated for those males with at least 10 sample points for the season and then corrected for effects of sampling intensity by taking residuals from the regression of 50% MAP on sample size. Territory location was computed as the distance between the average x and y coordinates of a male's locations and each of two central reference points: the geometrical center of the male aggregation and the "mating center" of the lek. The aggregation center was calculated by taking the mean x and y coordinates for each daily scan prior to the onset of matings and then averaging across days (n = 17 d); the premating period was used to control for relocation of unsuccessful males around mating centers that may take place later in the season (Bradbury and Gibson 1973). The mating center was the average x and y coordinates for all copulations.

Body size and morphology

Four linear dimensions (tarsus length measured from heel to the base of feathering on the middle toe, culmen length, wing length, and tail length) were measured to the nearest mm on captured birds. Since these measures were intercorrelated, principle components analysis was used to extract independent measures. The analysis used data from 36 adult males including the 17 banded birds attending the lek, 5 captured in the same area that did not attend the study lek and 14 captured in a nearby study area in previous years; average

dimensions did not differ significantly between areas or years. The analysis generated 2 components, one related to plumage dimensions (wing and tail) and a second related to skeletal size (tarsus and culmen), that were used as independent variables in later analyses (Table 2). We also weighed all captured males. Although male weights change seasonally (Beck and Braun 1978), there was no relationship between weight and date of capture in our sample *(r = 0.272, n = 22, NS)*.

Table 2. Rotated Principal Component loadings for four measures of size of adult male sage grouse. Components are given in decreasing order of variance explained, and size measures are ordered so that for each successive component loadings > 0.5 appear first.

Size measure	Principal component	
	1	2
Tail	0.791	−0.259
Wing	0.761	0.260
Culmen	−0.179	0.787
Tarsus	0.167	0.708

Multivariate methods were used to analyze effects of each cue variable on mating success wherever possible. Even using a team of observers, samples were not large enough for multivariate analyses of all cues simultaneously. Consequently we first examined bivariate relationships between each factor and mating success and between each pair of cue variables. Then, where cue variables were intercorrelated, multivariate methods were used to dissect their partial effects. Following preliminary analyses of the entire range of mating success variation, we analyzed matings at two levels. First, effects of each cue variable on mating status (whether or not a male mated) were determined using bivariate and multivariate logistical regression (Fienberg 1980; Dixon et al. 1981). Then correlation was used to relate cues to numbers of matings among those males that mated at least once. Because we were unable to measure all of the cues for each of the 27 males, sample sizes vary. However, we detected no significant heterogeneity in mating success between samples used in different analyses.

Results

Variation in mating success
Twenty-three copulations were recorded between March 23 and April 20. All were performed by 13 of the 27 recognized males: 6 mated once, 4 mated twice, and 3 each mated three times. The remaining 14 recognized males did not copulate.

Factors affecting mating success
Although several variables were significantly related either to mating status (whether or not a male mated) or to numbers of matings among males that mated at least once, none was related to mating success over the entire range of values from 0 to 3. Hence we present analyses of the two ranges of variation separately.

Mating status

Table 3 summarizes the results of bivariate logistical regression analyses of each independent variable on mating status. Lek attendance, strut rate, and the first acoustic component were significantly related to mating status while the remaining variables, including all measures of territory characteristics and body size, were not. Males that mated attended the lek more often, strutted at higher rates and scored higher on acoustic component 1 than those that did not mate.

Table 3. Results of bivariate logistic regression analyses between 11 independent variables and mating status. Display rates were corrected for effects of time and female proximity and averaged across sample periods for each male. Acoustic measures are averaged across all displays for each male. Further details are given in the Methods. Tests of significance are based on the chi-square values shown with one degree of freedom. Numbers of males in each sample are also given.

Variable	Chi-square	P	n (No. males)
Lek attendance	7.64	0.006	22
Display rate	16.90	< 0.00005	19
Acoustic component 1	7.11	0.008	11
Acoustic component 2	0.49	NS	11
Acoustic component 3	1.06	NS	11
Territory size	1.12	NS	15
Distance to aggregation center	1.70	NS	24
Distance to mating center	0.21	NS	24
Size component 1	0.54	NS	17
Size component 2	1.66	NS	17
Body weight	0.06	NS	17

To determine whether the effects of attendance, strut rate, and acoustic component 1 were independent, bivariate correlations between them were computed. Attendance was not significantly correlated with either strut rate ($r = 0.105$, $n = 17$, NS) or acoustic component 1 ($r = 0.151$, $n = 11$, NS), suggesting that its effect was independent of these measures. However, there was a significant positive correlation between strut rate and acoustic component 1 ($r = 0.676$, $n = 11$, $P < 0.05$). To separate their effects of multivariate logistic regression was run for the sample of 11 males for which both measures were available. Attendance was not a factor since it was not significantly related to mating status within this sample (logistic regression: chi-square = 2.11, $df = 1$, NS). Both strut rate and acoustic component 1 showed significant partial effects, tested by the improvement in the goodness of fit chi-square when each was added to the model after inclusion of the other (strut rate: chi-square = 8.05, $df = 1$, $P < 0.005$; acoustic component 1: chi-square = 4.92, $df = 1$, $P = 0.027$). These data indicate that strut rate and acoustic component 1 each contributed independently to mating status. In addition the fitted model discriminated between breeders and non-breeders without misclassifications, suggesting that threshold effects of each variable were sufficient to account for variation in mating status in this sample.

To pinpoint effects of specific acoustic features, the preceding analysis was repeated replacing acoustic component 1 in turn by each of the three measures that loaded heavily

on it (Table 1). All three showed significant effects on mating status in bivariate analyses (frequency of energy peak in pop 1: chi-square = 6.39, P = 0.011; interval from first pop to whistle frequency peak: chi-square = 7.22, P = 0.007; highest frequency of whistle: chi-square = 6.78, P = 0.009, all with df = 1). However, when each was included with strut rate in multivariate logistic regression analyses, only the last two measures had significant partial effects (first pop to whistle peak: chi-square = 4.04, P = 0.044; whistle frequency peak: chi-square = 5.045, P = 0.025). This suggests that the pattern of frequency modulation of the whistle is a critical feature affecting mating success. The initial rising frequency phase of the whistle (Fig. 1) was longer and the peak frequency reached higher in breeders than in nonbreeders. These two measures were also correlated with each other (r = 0.540, n = 72 displays, P < 0.01).

Although none of the remaining independent variables was significantly related to mating success, two relationships between these and display rate were found. First, males that strutted at higher rates tended to be further from the center of the aggregation (r = 0.609, n = 17, P < 0.01). This raises the possibility that a small effect of proximity to the lek center on mating success might have been obscured by a larger effect of display rate. However, after controlling for strut rate the partial effect of distance from the aggregation center on mating status was not significant (Chi-square = 0.21, df = 1, NS). Second, males that strutted at higher rates tended to be skeletally smaller as measured by tarsus and culmen lengths (strut rate vs. size component 2: r = 0.675, n = 12, P < 0.05). Again there was no evidence of a partial effect of size on mating status after controlling for display rate (Chi-square = 0, df = 1, NS).

Numbers of matings among successful males

Only one of the independent variables was significantly related to differences in numbers of matings among males that mated at least once: acoustic component 3 was positively correlated with mating success (r = 0.911, n = 6, P < 0.05). This is interesting because it suggests that one set of factors is necessary for mating status whereas another may be invoked in choosing between acceptable males. Such combined criteria for mate choice might have contributed to the difficulty of identifying mate choice cues in prior studies. The result should be accepted cautiously for two reasons. First, given the number of traits correlated with mating success, the chance of falsely rejecting the null hypothesis when using a critical probability level of 0.05 is appreciable. Second, because sample sizes were small (only half of the males mated) we may have erroneously rejected other traits.

Individual differences in display measures

One question raised by these results is whether differences in average display measures that correlate with mating success represent consistent individual differences or are a product of sampling. As described in the Methods, display measures were corrected for known biases prior to analysis. However, it is still possible that differences between males might have been caused by inadequate sampling. To investigate this, one-way ANOVAs were performed on strut rate, acoustic components 1 and 3, and the two critical measures of the whistle that loaded on component 1. Analyses included all males for which at least

4 samples were available. Data were transformed where necessary to meet the assumptions of normality and equal variances. Table 4 shows that for all measures individual differences were highly significant. The strut rate values used were averages for 5–10-min samples and thus already eliminated some short-term variability. We also investigated whether male display rates differed significantly over shorter periods (3–6 min) by comparing inter-strut intervals within groups of 3 to 4 adjacent males sampled simultaneously when a female was within 20 m and approximately equidistant from each male. Kruskal-Wallis ANOVAs were used since distributions of inter-strut intervals resisted normalization. Significant between-male variability was found within each of the five samples ($P <$ 0.001–0.02). Overall this suggests that there were consistent individual differences in all of the display measures that correlated with mating success.

Table 4. Analyses of variance of individual differences in 5 display measures in adult male sage grouse. Strut-rate data were means of single samples corrected for effects of time of day and proximity to females (see Methods) and pooled for the entire mating season. Data for acoustic measures are individual displays.

Variable	F	df	P
Strut rate	6.24	11,122	< 0.001
Acoustic component 1	24.30	5, 39	< 0.001
Interval from 1st pop to whistle frequency peak	8.85	5, 39	< 0.001
Highest frequency of whistle	63.79	5, 39	< 0.001
Acoustic component 3	14.64	5, 39	< 0.001

Discussion

Our data provide evidence that mating success was related to the time males spent on the lek, and to individual differences in display rates, and in temporal and frequency characteristics of the whistle emitted towards the end of the strut display. Despite evidence that the sage grouse strut is one of the most highly stereotyped avian displays (Wiley 1973b), there is still enough variation between males, and consistency within each male's performance, to account for much of the observed variation in male mating success.

Although the literature on lek mating both in sage grouse and other avian lek species has been dominated by the view that females choose to mate with centrally located males (Kruijt et al. 1972; Wiley 1973a; Lill 1974), we did not find any evidence that territory location or size affected mating success. Is it likely that some spatial cues affect mate choice but we overlooked them because of small sample sizes? While this remains a possibility, it is important to note that tests for spatial correlates of mating success involved our largest samples. In contrast, samples were generally smaller for display and morphological measures. Despite the advantage of larger samples, no spatial variables emerged as significant correlates of mating success whereas several display measures did. This suggests that if spatial cues play a role, their effects must be much weaker than those of the display cues that emerged despite the smaller samples. It is reassuring that these results agree with those of Hartzler (1972) not only in the absence of spatial effects but also in the presence of a significant relationship between display rate and mating success.

While it is encouraging to have identified significant correlates of mating success, it would be premature to conclude that these are the critical cues. We did not measure some potential cues, e.g., visual components of display. It is therefore possible that some un-measured correlate of strut rate or the acoustical components is the focus of female choice. In addition, some effects (e.g., acoustic component 3) are based on small samples and thus require confirmation. However, these results immediately suggest experimental manipu-lations that would test the effects of the identified cues on female choice directly.

The implication that mate choice is based on display performance rather than spatial or anatomical cues raises several issues. If females choose between males on the basis of strut rate, sound production and lek attendance, what prevents all males from performing at successful levels? There is some circumstantial but intriguing evidence that energetic fac-tors may play an important role. Male, but not female, sage grouse lose weight and most of their prebreeding fat reserves during the display season (Beck and Braun 1978; Hupp 1983). We have also found that males are less likely to attend leks after periods of cold weather that increase their thermoregulatory requirements, even though receptive females are present. Thus regular lek attendance may entail higher energetic expenditure. Meta-bolic constraints may also explain the curious result that smaller males displayed at higher rates. This is interesting both because Searcy (1979) reported a similar relationship in red-winged blackbirds and because it runs counter to the expected effect of size on mating success in this highly dimorphic species. Apparently the evolution of sexual size dimor-phism in polygynous birds is more complex than is often assumed.

In conclusion, our finding that male mating success in sage grouse is more closely re-lated to individual differences in display effort and sound production than to territorial or morphological characteristics appears to resolve discrepancies between previous studies of mate choice in this species. The implication of performance cues makes sense of both the effort committed to lek display and the apparent associated energetic costs. It also pro-vides a basis for further analysis of the operation of sexual selection in this avian lek sys-tem.

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