

Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female

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Males in many species have complex, multicomponent sexual signals, and there may be trade-offs between different signal components. By adjusting their signaling behaviors, males may be able to produce more attractive courtship displays in the face of these trade-offs, but this possibility has rarely been tested. In this study, we examined adaptive adjustment of display behaviors during courtship in a lek-breeding bird, the greater sage grouse (*Centrocercus urophasianus*). We measured the potential trade-off between display quantity (display rate) and quality (a temporal feature of displays) in a wild population of sage grouse using controlled approaches of a robotic female to experimentally induce changes in male display rate. We found that males who are more successful in mating can increase quantity without a decline in quality, with only unsuccessful males expressing an apparent trade-off. Male mating success was also positively correlated with responsiveness to changes in receiver distance, suggesting that successful males may avoid a trade-off by tactically adjusting their display rate—saving energy by displaying at low levels when females are farther away and at higher levels as females approach. Alternative explanations for this differential response to female proximity are discussed. Our results suggest that to be successful, males may need both the ability to produce attractive signals and the ability to effectively allocate their display effort by responding to female behaviors. *Key words*: acoustic localization, communication, greater sage grouse, multiple traits, plasticity, sexual selection, trade-off. [*Behav Ecol* 21:97–106 (2010)]

In a wide variety of taxa, negative relationships between 2 or more sexually selected display traits have provided opportunities to investigate how trade-offs can shape individual male displays. For example, mechanical constraints related to vocal tract morphology cause an inverse, triangular relationship between trill rate and bandwidth or amplitude in songs and other vocalizations (Podos 1997, 2001; Ballentine et al. 2004; Illes et al. 2006; Janicke et al. 2008). This mechanical constraint provides an upper limit to the possible trait combinations, and the ability of signalers to approach this limit may be used by receivers to assess potential mates and competitors (Ballentine et al. 2004; Podos et al. 2004; Illes et al. 2006; Cramer and Price 2007). In other cases, the shape of the relationship between display components may vary more widely among signalers. For example, when trade-offs result from allocation of available energy to different display components, signalers with very limited energy may express a negative relationship between traits, whereas signalers with more energy may be able to produce more attractive trait combinations, similar to patterns seen in some life-history trade-offs (Van Noordwijk and Dejong 1986; Dobson et al. 1999). For example, Bertram and Warren (2005) found that exhausted male crickets faced a stronger trade-off between the number of song bouts and song amplitude compared with rested crickets, which were able to increase both factors simultaneously. Similarly, low-ranking chickadees showed a decline in the stereotypy of a key song parameter with a change in pitch, whereas high-ranking males did not, which may be caused by differences in energy resources or singing skill (Christie

et al. 2004). Regardless of whether trade-offs are caused by mechanistic or energetic constraints, or both, signalers may be able to actively adjust their behaviors to produce the most effective signals for the signaling context within the bounds of these constraints. Therefore, sexual traits subject to trade-offs may also provide an opportunity to examine adaptive plasticity in male display behavior.

Many apparent trade-offs between components of sexual displays are between the quality (e.g., bandwidth and amplitude) and quantity (e.g., rate and bout length) of display. These signal features commonly vary over time, especially amplitude and display quantity measures (Gerhardt 1991), but the existence of this variation is puzzling. If females prefer higher quality and quantity signaling, then models of sexual selection predict that males should display at an optimal level, which maximizes their attractiveness given their quality (Grafen 1990). The observed variability in male displays may be random with respect to male traits, or the variability may be informative, reflecting male condition at the time of signaling (Møller and Pomiankowski 1993) or adaptive adjustment of signals in response to the physiological, social, and environmental conditions experienced by the male (Parker 1974; Payne and Pagel 1996, 1997). For example, adaptive plasticity in courtship display behaviors has been described in response to the proximity, interest, and value of the assessing female (Gibson and Bradbury 1985; Kelso and Verrell 2002; Patricelli et al. 2002; Sockman et al. 2006; Byrne 2008; How et al. 2008) and in response to changes in the environment, such as wind, light, or predation risk (Endler 1987; Wiley 2006). These examples show that males in many species adjust their display behaviors over time, but only a few studies have examined how variability in the ability to make these adjustments relates to male fitness (Patricelli et al. 2002, 2006), and we know little about whether males adjust their courtship traits in response to trade-offs between multiple display components.

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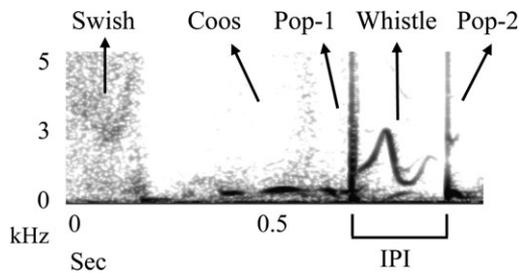


Figure 1
The “strut” vocalization, showing the mechanically produced “swish” of wings against breast feathers, the low-frequency “coo” notes, followed by a pop, a frequency-modulated whistle and another pop. The IPI is the time delay between the 2 pop notes.

We examined apparent trade-offs between multiple components of the complex sexual display of greater sage grouse (*Centrocercus urophasianus*) and whether the ability of males to adjust their display traits in the face of these trade-offs relates to mating success. Male greater sage grouse gather on strutting grounds called leks during the spring breeding season and produce spectacular courtship displays (struts) involving both visual and acoustic components. Male sexual displays are visually extravagant, but no morphological or plumage traits thus far measured predict male mating success (Gibson and Bradbury 1985), though the presence of hematomas on air sacs is negatively related to female proximity to males, which may reflect female preference (Boyce 1990). One aspect of the male vocal display is related to male mating success—the interpop interval (IPI), which is the time interval between 2 “pop” notes during which a “whistle” note occurs (Figure 1). IPI is positively related to male mating success, suggesting that females prefer longer intervals (Gibson et al. 1991; Gibson 1996). In addition to this aspect of display quality, the “quantity” of male display is also related to male mating success, with successful males attending the lek more frequently and strutting at a higher rate (Gibson and Bradbury 1985; Gibson et al. 1991; Gibson 1996). High lek attendance may also be associated with lower parasite prevalence (Boyce 1990; but see, Gibson 1990), suggesting that display effort may be an indicator of male quality. Perplexingly, Gibson (1996) also found a marginally significant negative relationship ($P = 0.066$) between strut rate (SR) and IPI among males, suggesting that males have either a high SR or high IPI but not both. Although evidence of a negative relationship is not in itself proof of a trade-off (Stearns 1992; Knops et al. 2007), this result is consistent with a mechanistic or energetic trade-off between SR and IPI.

Here, we look for evidence of a trade-off between the quantity and quality of male display at 2 scales of analysis—covariation between maximum trait values among males and covariation of traits within individual males over time—and test hypotheses about how these traits relate to male mating success and male courtship tactics. We do so in a wild population of sage grouse using controlled approaches of a robotic female on the lek to measure how males adjust their SR in response to robot proximity and how IPI covaries with SR within individual males. We begin by examining whether there is a negative relationship between maximum SR and maximum IPI among males, similar to the relationship found in another population of sage grouse (Gibson 1996). Next, we test 2 alternative hypotheses about the relationship between SR and IPI within individual males, as males adjust their SR in response to changes in proximity with the robotic female. First, we test the hypothesis that all males will be constrained to express a negative relationship between display traits (the fixed relationship hypothesis); this predicts that all males will show a similar decline in their IPI as

their SR increases, such that individual males mirror the negative relationship Gibson (1996) found among males. Second, we test the hypothesis that the relationship between display traits will differ among males, as we would expect if this relationship was influenced by differences among males in the resources they have available to produce costly displays (the differential constraint hypothesis). This predicts that there will be significant differences among males in the slope of their relationship between SR and IPI. Further, we predict that this slope will be positively related to male mating success, with preferred males able to increase their SR with lesser or no decline in IPI, consistent with female preference for males better able to produce costly displays.

In addition to testing these hypotheses about the relationship between display components, we examine how individual males adjust their signals according to female proximity. Observers of sage-grouse courtship have long noticed that male display rate increases with proximity to females (Hartzler 1972; Wiley 1973a, 1973b; Gibson and Bradbury 1985). If females prefer higher SRs, then why don't males display at their maximum rate at all times? One possibility is that courtship display is energetically costly (Vehrencamp et al. 1989) and that males could mitigate this cost by reducing SR when potential receivers are more distant and are less likely to be assessing the male (Taigen and Wells 1985; Bertram and Warren 2005; How et al. 2008). We test whether variation in how males adjust their SR in response to robot proximity explains the observed relationships between display components. Because males may differ in both the overall levels of display and the relationship between display components, we use multivariate analysis to examine how maximum display levels, the relationship between traits, and response to proximity all relate to male mating success.

MATERIALS AND METHODS

We monitored breeding behaviors of 41 territory-holding adult male greater sage grouse on Monument Lek (Fremont County, Wyoming, United States, 42°49'44.42" N, 108°30'24.08" W) daily from first light until all birds left the lek, between 3 March and 30 April 2007 (excepting 5 days when snow prohibited lek access). In 2007, Monument Lek contained a maximum of 103 adult and juvenile males, including a peripheral group of males who are dispersed in the sagebrush around the main portion of the lek; the view of these males is obscured by vegetation and topography, so we focused on the males in the main open portion of the lek, which included 41 territory-holding males. Robot experiments were conducted between 9 April and 28 April 2007, after the peak in female visitations and copulations for the season (83% of copulation occurred before this interval) to avoid interference of and by real females. Trials were conducted in the morning between 0645 and 0820, when males were actively strutting; this encompasses the average time of maximum male (mean = 0725, standard deviation [SD] = 38 min) and female (mean = 0722, SD = 41 min) daily attendance on this lek and is well before birds typically depart from the lek (mean = 0920, SD = 41 min). Observers in blinds on a hill ~200 m from the lek used spotting scopes to identify males individually by plumage patterns (Wiley 1973b) and note their locations ± 1 m relative to the grid of survey stakes placed at 10 meter (m) intervals on the main area of the lek (ca. 100 m \times 130 m). Identified males were observed on average 2.1 ± 0.8 times per day, with the regular territory-holding males seen as many as 10 times per day. We used 3 high-definition video cameras (Sony HDR-HC1 and HDR-HC3, Tokyo, Japan) placed in the observer blinds overlooking the lek to capture the activity of all males in the main

portion of the lek throughout the breeding season; an additional camera was used to capture behaviors during experiments (Sony HDR-FX1). During video analysis, observers used field identifications to assign an ID to a bird on the video and then track the bird over time to score behaviors (male mating success and SR). We also used the field record and video to assign IDs to localized vocalizations (see below). This research was approved by the Wyoming Game and Fish Department (permit 405) and UC Davis Animal Care and Use Committee (protocol 11662).

Male mating success

Male mating success was used as an estimate of male fitness and was scored from videos as the total number of copulations by the male (e.g., Gibson et al. 1991). Female choice is a major determinant of male fitness in sage grouse, because females are free to sample and mate with any male on the lek (Gibson et al. 1991; Gibson 1996). Females receive no direct benefits from males (males provide no parental care and females nest off the lek); thus, the resource quality of territories does not influence female choice. Previous paternity studies indicate that mating success predicts actual male reproductive success (Semple et al. 2001). We observed 75 copulations in 2007, 91% of which were attributable to a male of known identity. We did not adjust mating success values for the number of days on the lek (Gibson and Bradbury 1985; Gibson et al. 1991; Gibson 1996); instead, we included the number of days on the lek as a variable in the principle components analysis (PCA; see Table 1 and Figure 5).

Array recording and the acoustic localization system (ALS)

We used acoustic localization to reconstruct the locations of sound sources using the time delay of the same sound reaching multiple microphones (Spiesberger and Fristrup 1990). Acoustic localization has been used primarily to track marine mammals (e.g., Clark and Ellison 2000) and only more recently in studies of terrestrial ecology (e.g., Langemann et al. 2000; Mennill et al. 2006). We used an array of 24 omnidirectional microphones (Sennheiser K6/ME62, Wedemark, Germany) to record the strut vocalizations of all males on the main portion of the lek simultaneously. Audio was acquired (16 bit, 44.1 kHz, WAV format) through three 8-channel digitizing preamplifiers (Mark of the Unicorn [MOTU] 896 and 896HD) on a Macintosh Powerbook G4 laptop running MOTU digital performer and recorded on external hard drives. We used Word Clock time code from a MOTU MIDI TimePiece AV to ensure sample-accurate synchronization among our 24 audio channels. We used Syrinx (John Burt, University of Washington) to display our 24-channel audio recordings and choose vocalizations for analysis. Localization was performed on annotated audio files using the program ArrayBatchGui (John Burt) in MATLAB (Mathworks). We used the time and location of male displays collected from videos to determine which individually identified male was the source of each localized call.

We tested the ALS in Spring 2007 by playing back multiple recordings of sage grouse and other local bird species from 3 locations within the array and 1 location at the array edge; accuracy at the 3 playback sites within the array ranged from 0.37 ± 0.18 m ($N = 88$) to 0.48 ± 0.20 m ($N = 85$) (unpublished data). Accuracy at the edge of the array was slightly lower (1.08 ± 0.43 m, $N = 51$) but still sufficient to identify the source of a display in most cases. We localized male courtship displays recorded on the microphone array during the experiment and used the time and location of male displays collected from video recordings of the experiments in order to

Table 1
PCA of 5 measures of male display effort and quality

	PC1	PC2	PC3
% Var explained	37	23	18
Eigenvalue	1.87	1.14	0.88
Component score: Max SR ^a	0.81	0.07	-0.14
Component score: Max IPI ^a	-0.11	0.01	0.99
Component score: slope proximity ^b	-0.8	-0.12	0.02
Component score: slope IPI-SR ^c	-0.05	0.91	-0.07
Component score: days on lek ^d	0.39	0.74	0.1
R_s with mating success ^e	0.5	0.33	0.18
P of correlation	0.008	0.098	0.37

^a Maximum SR (Max SR) and maximum IPI (Max IPI) are measures of display effort and quality.

^b The slope of SR on proximity is a measure of the degree to which the male adjusts his SR in response to female proximity.

^c The slope of IPI and SR is the slope of the relationship between SR and IPI within individual males.

^d The number of days spent on the lek is a season-long measure of display effort.

^e " R_s with mating success" is the Spearman rank correlation between the factor and male mating success. $N = 27$ for all correlations.

determine which male was the source of a given call. Video and audio time codes were synchronized to within 1 s to an atomic digital clock. All microphones and survey stakes were georeferenced using a surveyor-grade GPS (Ashtech Promark II) to improve accuracy of acoustic localization.

Robot and experimental protocol

We used a robotic female to provide a controlled female stimulus to displaying males (Figure 2). Robots are increasingly common in behavioral research, as they allow playback experiments with a visual stimulus in a natural setting (Webb 2000). The robot was enclosed in real female sage-grouse skin (Patricelli et al. 2006) and was moved along G-scale model train tracks (for video, see Online Supplement). The robotic female sage grouse (Figure 2a) has 2 axes of movement, each radio remote controlled by servo motors (Futaba T9CAP remote controller, 1024 8-channel 74-MHz transmitter, and servo motors): 1) the head moves side to side to appear more realistic and 2) the body rotates 360° to face the displaying male. The electronics were enclosed by a metal- and plastic-mesh armature on which sage-grouse skin is attached (see Methods in Patricelli et al. 2006). Skins were collected in Lander, WY, United States, by federal sage-grouse managers during the hunting season. To measure male display from a female's perspective (Figure 2b), the robot is equipped with a wireless video camera, as well as a microphone and audio recorder (these audio recording were not used in the current experiment). Video was acquired with a mini-video camera (Supercircuits PC182XS) emerging from the front of the robot and transmitted wirelessly (Supercircuits AVX434 transmitter and receiver) to the blind where it was viewed and recorded on a Sony GV-D1000 Mini-DV recorder. The live video feed was used to navigate the lek without collision and find experimental stop locations (see below). Noise produced by the robot (mainly the servos) was approximately 40.4 dBA at 1 m (re 20 μ Pa, measured with a Larson-Davis 824 sound level meter); equivalent to the typical noise level of a quiet room (Singal 2005). The mean distance between the robot and courting males was 16.6 m (SD = 8.4), predicting <16 dBA at the average courting male, which is quieter than ambient (ca. 34 dBA with no males vocalizing, unpublished data).

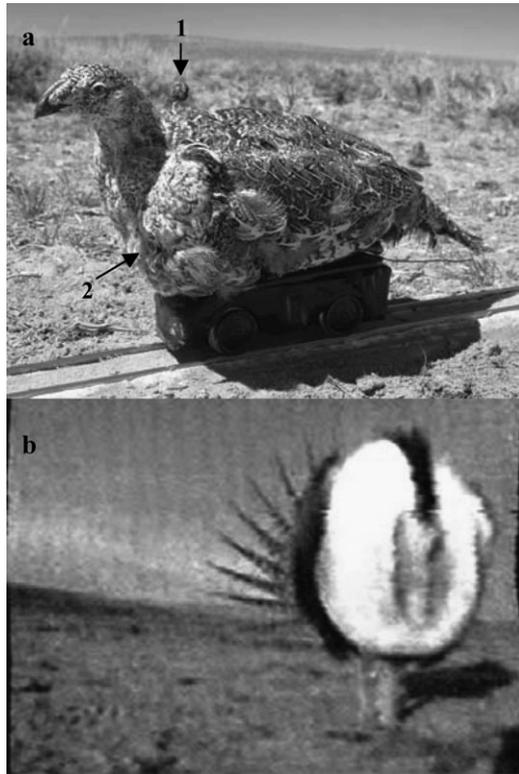


Figure 2

(a) The robotic female sage grouse, showing the on-board microphone (arrow 1) and the mini-video camera (arrow 2). By remote control, the robot can look side to side and rotate to face the focal male. During experiments, the robot was moved along camouflaged G-scale train tracks, stopping at 3 locations with increasing proximity to the focal male. (b) A still image from the on-board video camera of a male courting the robot. See Online Supplement for video of the robot and male courtship.

Tracks were placed on the lek on the afternoon before the experiment, when no birds were present on the lek. Tracks approximately 20 m in length emerged from a blind on the lek (from which the robot was controlled) and ran straight toward the favored display site of the focal male. The tracks were camouflaged with cloth and dirt from the lek, leaving only the brass rails visible; the grouse showed no aversion to the tracks, crossing them readily (personal observation). Tracks are present during the pretrial periods of the experiments, so any undetected effects of the tracks on male behavior were controlled in comparisons of male behavior in the presence and absence of the robot. Immediately before each experiment, we used speakers in the blind to play “quacking” sounds often made by females arriving at the lek (Hartzler 1972); vocalizations were recorded on the microphone array earlier in the season. During experiments, we stopped the robot for 3 min at each of 3 points along straight tracks: 16, 6, and 1 m from the end of the tracks, then returned to the blind. Stops were marked by a small flag near the tracks, which was visible from the robot video camera. At each stop, the robot was rotated by remote control to face the focal male; the head was turned side to side at a moderate pace throughout the experiment to appear more realistic. For each experiment, we chose a focal male randomly with respect to male mating success, but surrounding males also courted the robot and are included in the experimental analysis. Focal males were not necessarily the closest male to the robot and responded similarly to nonfocal males (there were no significant differ-

ences in response variables between focal and nonfocal males; mean SR $t = 1.01$, $P = 0.39$; mean IPI $t = 4.43$, $P = 0.13$; slope of SR on proximity $t = 0.38$, $P = 0.6$; slope IPI–SR $t = 0.42$, $P = 0.63$). We tested 28 males with the robot during 9 trials (3–8 males courted the robot in each trial). To avoid multiple stimuli for males during experiments, we performed experiments when no females were present on the main portion of the lek (i.e., $\gg 50$ m from the target males). This simulates the visit of a single female to the lek, which is not uncommon; 21% of 2007 lek-attendance counts in which female(s) were present involved only 1 female.

The behavior of male and female sage grouse toward the robot was not qualitatively or quantitatively different from behavior toward real females. Males noticeably increased their SR when the robot exited the blind, and adjusted their SR in response to robot proximity (see Results, Figure 4), which are the main behavioral responses of males to real females (e.g., Wiley 1973a). We are currently examining the details of male strut behaviors in 2007 in response to real females to test the same hypotheses described here in natural courtships; preliminary results suggest that there is no difference in mean distance-corrected SR (at 5 m, calculated as described in Gibson et al. 1991; Gibson 1996) between courtships with the robot and courtships with real females (mean SR toward the robot = 0.096 ± 0.007 , $n = 28$, mean SR toward the real females = 0.098 ± 0.016 , $n = 21$; $t_{50} = 0.06$, $P = 0.96$), and for males measured in both situations, SR toward the robot significantly predicts SR toward real females ($R_s = 0.6$, $n = 14$, $P = 0.03$). Further, in 2 attempted trials where females arrived on the lek during experiments, the females aggregated near the robot as they would with a real conspecific female (Gibson et al. 1991); these trials were dropped from the analysis.

Our experimental design has 2 unavoidable limitations. First, a single robot was used for all of the experiments, due to ethical concerns and the difficulty of obtaining additional skins. Thus, there was pseudoreplication (sensu Kroodsma 1986) of one aspect of the playback stimulus (the robot), though not the robot’s behaviors. Partly mitigating this effect, the robot armature was composed of taxidermied parts from 3 females and thus did not represent a single individual female (similar to combined or synthesized playbacks, McGregor et al. 1992). A study on bowerbirds found no difference in male response to different robotic models that were similarly made from multiple skins (Patricelli 2002; Patricelli et al. 2006). A second limitation of this experimental design is that multiple males responded to the female in each treatment, and their behavior may not be completely independent (a problem in most observation or experimental lek studies). We are currently investigating this possibility.

Measuring SR, IPI, and response slopes

At each of the 3 robot stopping points and during a 3-min pretrial period (before the trial and when no females were present within 50 m of the male), we calculated for each male the mean SR, IPI, and distance between the male and the robot. There was no relationship between the minimum distance between the male and the robot and male mating success that could bias estimates of male traits ($R_s = 0.005$, $n = 28$, $P > 0.98$). To measure SR, we recorded the time at which each strut occurred from videos of experimental courtships. SR for each male (at each robot stop) was measured as the inverse of the arithmetic mean of interstrut intervals over the observation period. We did not use the harmonic mean of strut intervals (e.g., Gibson and Bradbury 1985), because we do not want to minimize extreme values (i.e., occasional longer rests between struts) given the controlled nature of the female stimulus and

our interest in changes in male display effort with proximity to the robot. The duration of the IPI is small compared with the time interval between struts; thus, even the extreme values of IPI we observed on the lek would not significantly affect the SR (mean among males of interstrut intervals during each male's fastest bout of strutting = 9.74 s, SD = 2.6, $n = 28$, min = 5.5 s; mean IPI among males = 0.2 s, SD = 0.004, $n = 28$, max = 0.2112). Three of the tested males were not visible during the pretrial period, so we could not calculate an SR in the absence of the robot or real females. IPIs were measured as the time delay between the center of the first and second pops (see Figure 1; Gibson and Bradbury 1985); IPIs were measured in Syrinx on the audio channel with the clearest spectrogram (fast Fourier transform size = 512, Hanning window). Measurements were made prior to acoustic localization and thus were blind to the identity of the male and the distance to the robotic female. A mean IPI was calculated at each robot stop as the mean IPI of all vocalizations that were free of overlapping vocalizations from other males and could be localized and assigned to the male during the stop period; the mean number of struts per male per robot stop was 10.9 ± 0.5 and the mean number of IPIs that could be measured from these struts was 3.52 ± 0.3 . "Maximum SR" and "maximum IPI" are the maximum values for each male among the robot stops and pretrial periods (the highest value among average these sample-period averages). A "response to proximity" slope was calculated for each male as the slope of SR on the mean distance between the robot and the male (calculated using the "slope" function in Microsoft Excel). Similarly, a slope was calculated for each male between IPI and SR ("slope of IPI on SR"). For one male, we were only able to localize vocalizations at one of the robot stops; thus, we were unable to calculate a slope for IPI on SR.

Statistics

Spearman rank correlations (R_s) were used when variables, such as male mating success, could not be transformed to meet assumptions of normality for parametric statistics. We used repeated-measures regression to test for significant differences among males in the slopes of SR on IPI, using an SR-by-male interaction term; male ID was included a random block effect (MIXED procedure, SAS version 9). PCA, performed in SPSS (version 16), was used to analyze the relationship between 5 measures of male display traits and male mating success. We included in the PCA 2 measures of display effort and quality: maximum SR (Max SR) and maximum IPI (Max IPI). In addition, we included the response slope of SR on female proximity and the relationship between SR and IPI within individual males. Finally, we included the number of days spent on the lek, a season-long measure of display effort. Variables were rotated to maximize loadings using the varimax method with Kaiser normalization; we present results for the first 2 factors, which had eigenvalues greater than one (Quinn and Keough 2002), and the third factor, which had an eigenvalue close to one and loaded strongly with a variable of interest, maximum IPI (see Figure 5 and Table 1). All probability values are 2-tailed. Means are presented \pm standard error, unless otherwise noted.

RESULTS

We found a positive relationship between maximum SR toward the robot and male mating success ($R_s = 0.39$, $n = 28$, $P = 0.042$), suggesting a female preference for males who strut at a faster maximum rate. However, we did not find a significant relationship between maximum IPI and male mating success ($R_s = 0.11$, $n = 28$, $P = 0.6$). Similar to Gibson

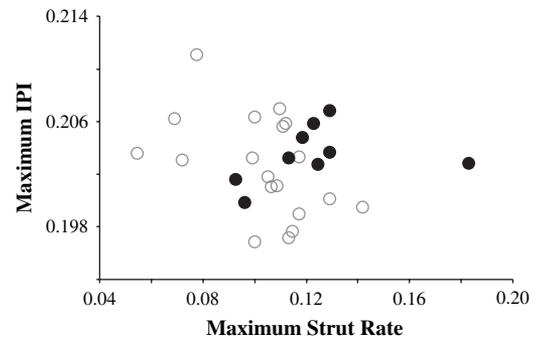


Figure 3

There is no significant relationship between maximum SR (1/mean duration of interstrut intervals) and maximum IPI in seconds (Max IPI) among all males combined ($R_s = -0.12$, $n = 28$, $P > 0.5$). However, examining only unsuccessful males, there is a significant negative relationship between these traits (open circles; $R_s = -0.46$, $n = 19$, $P = 0.048$), and in successful males the relationship is of approximately equal strength but reversed, though not statistically significant (closed circles; $R_s = 0.48$, $n = 9$, $P = 0.2$). These correlation coefficients are significantly different from each other (Fisher's $Z = 2.13$, $P = 0.0331$).

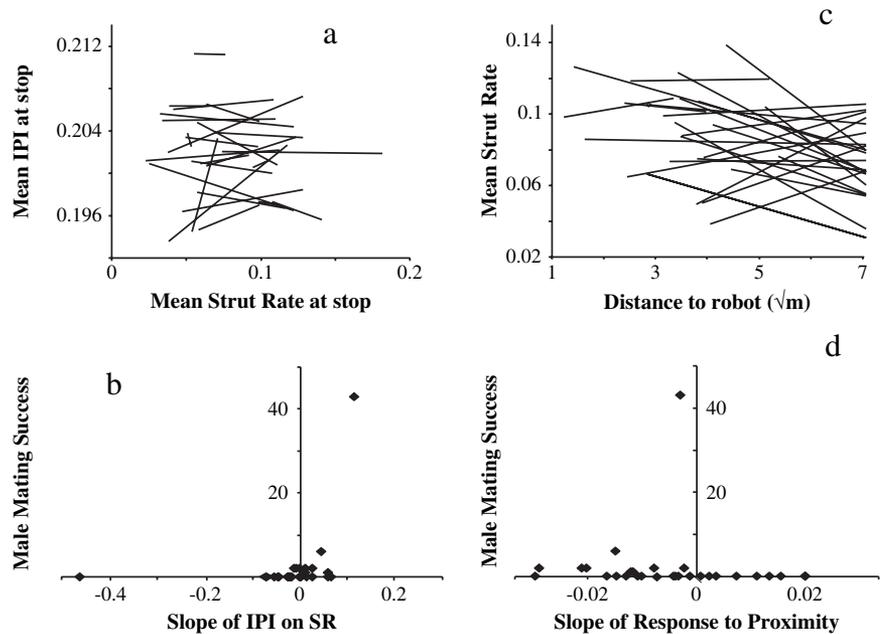
(1996), we found a negative relationship between maximum SR and maximum IPI among males, but only when we examine males who were not successful in copulating (Figure 3). When we examine males who were observed to copulate, we find a positive, but not significant, relationship between trait values. We found a significant difference in the correlation coefficients between successful and unsuccessful males (Figure 3).

In addition, we examined how SR and IPI covary within individual males, as males adjust their SR to proximity with the robotic female. Consistent with the differential constraint hypothesis, we found variability among males in the relationship between SR and IPI (clearly visible in Figure 4a); the average slope of the within-male relationship between these traits did not significantly differ from zero, and a mixed-model Analysis of covariance revealed significant differences in the relationship between SR and IPI among males, with a significant interaction between SR and male identity (dependent variable = mean IPI per male per robot stop, independent variable = mean SR per male per robot stop; fixed effects: SR = $F_{1,42} = 0.42$, $P = 0.52$, SR*male interaction = $F_{27,42} = 11.6$, $P < 0.0001$). Further, we found a positive relationship between male mating success with real females and the slope of each male's relationship between SR and IPI (Figure 4b), with unsuccessful males having more negative slopes between SR and IPI. Males who strut at a high rate do not do so at the expense of regular attendance; indeed, we found a weak, nonsignificant tendency for males with a higher maximum SR to spend more days on the lek (Pearson $R = 0.29$, $n = 28$, $P = 0.14$).

To determine how successful males can increase their SR without causing a decrease in their IPI, we measured how male mating success relates to the slope of male response to robot proximity (the slope of male SR on distance to the robot). We found that the average slope among males was negative and differed significantly from zero (Figure 4c), suggesting that males typically respond to robot proximity by increasing their SR. We then examined how variation in these slopes relates to male mating success, finding a significant negative relationship (Figure 4d), which suggests that successful males adjust their SRs more strongly than unsuccessful males in response to proximity. Moreover, male SR in the pretrial period (with no robot on the lek and no real females within 50 m) was not

Figure 4

The fitness consequences of within-male variation in male display. In the upper plots (a and c), each line represents an individual male in the study; in the lower plots (b and d), the slopes of these lines are used as independent variables against mating success. (a) The average slope of the within-male relationship between IPI and SR does not significantly differ from zero ($t_{26} = 0.17$, $P = 0.86$). (b) There is a positive relationship between the slope of IPI on SR and male mating success with real females ($R_s = 0.39$, $n = 27$, $P = 0.043$), with unsuccessful males disproportionately facing a trade-off between SR and IPI. Note that rank correlations (R_s) are used here to avoid undue influence of the outliers on the statistical tests. (c) Males on average respond to robot proximity by increasing their SRs—the average slope among males is negative and differs significantly from zero ($t_{27} = 2.56$, $P = 0.0164$). (d) There is a negative relationship between the slope of SR on proximity to the robot and male mating success ($R_s = -0.42$, $n = 28$, $P = 0.027$), with successful males adjusting their SRs more strongly than unsuccessful males in response to proximity.



positively related to mating success ($R_s = -0.31$, $n = 25$, $P = 0.14$). Thus, successful males did not display at a higher rate than unsuccessful males in the absence of females—indeed there is a weak tendency to display at a lower rate in the absence of females.

We used PCA to examine how 5 measures of male display effort and quality relate to each other, and to male mating success (see Table 1). In a factor plot of the first 3 principle components (Figure 5), males that copulated can be seen to cluster in the region of the plot representing relatively high values of PC1 (on which maximum SR loads positively and the slope of proximity on SR loads negatively), high values of PC2 (on which slope of IPI–SR and days on the Lek load positively), and moderate values of PC3 (on which Max IPI loads positively).

DISCUSSION

In this study, we find patterns at multiple scales of analysis—among and within individual males—that are consistent with a trade-off mediated by energetic constraints. At the larger scale, looking among individuals, we found a negative relationship between maximum SR and IPI among males, similar to Gibson (1996). However, we only found this negative relationship in males who were not successful in copulating (Figure 3). Males who were observed to copulate had a significantly different relationship between their display traits, indeed, there is a nonsignificant trend toward a positive relationship

between trait values in this small sample of males. Previous studies finding positive correlations among males in multiple sexually selected traits (Badyaev et al. 1998; Thornhill and Moller 1998; Patricelli et al. 2003; Coleman et al. 2004) have been interpreted as evidence that multiple traits are redundant indicators of male quality or have synergistic effects on signal efficacy (Hasson 1989; Møller and Pomiankowski 1993; Hebets and Papaj 2005). Studies finding negative relationships between traits (Ballentine et al. 2004; Illes et al. 2006) have been interpreted as evidence of a trade-off (e.g., the multitasking hypothesis, Hebets and Papaj 2005). Our results highlight that these may not always be mutually exclusive alternatives—successful males may be those with sufficient resources to produce multiple signals, whereas unsuccessful males may specialize in one trait or another (Hebets and Papaj 2005). Further study on a larger sample of successful males, and further information about how traits relate to underlying male quality, is needed to examine this possibility in greater sage grouse.

We found further evidence consistent with energetic constraints when we examined the covariation between SR and IPI within individual males over time. We found that males differ significantly in the slopes of the relationship between SR and IPI, supporting the differential constraint hypothesis. Further, we found a positive relationship between male mating success with real females and the slope of this relationship (Figure 4b), suggesting that successful males can increase display rate without decreasing their IPI (and in some cases

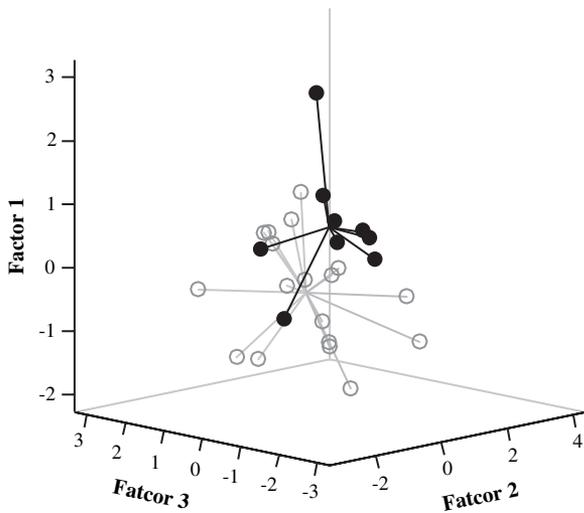


Figure 5
 A factor plot of the relationships between principle components 1, 2, and 3. Maximum SR loaded positively and the slope of proximity on SR loaded negatively on PC1 (see Table 1), the slope of IPI–SR and Days of the Lek loaded positively on PC2, and the maximum IPI loaded strongly on PC3. Males who did not copulate are shown in open circles with gray lines; males who copulated are shown as filled black circles with black lines. Lines converge on the mean point (centroid) for each group.

increase both simultaneously), whereas unsuccessful males have a negative relationship between them. Taken together, these results suggest that within the range of SR and IPI values observed on the lek, males do not face a fixed constraint that cannot be overcome. Instead, the negative relationship between these traits is expressed disproportionately by unsuccessful males.

Why do unsuccessful males express a more negative relationship between IPI and SR? One possible explanation is that courtship display is costly, and males differ in their ability to bear these costs (Ryan 1988; Grafen 1990; Stearns 1992). There are a number of potential costs to male strutting behavior. Vehrencamp et al. (1989) measured the metabolic cost of displaying in sage grouse and found that strutting is energetically costly and that these costs affected males differently. Males that displayed actively (i.e., more attractive males) were found to forage further from the lek and maintain their body weight, whereas less active (i.e., unattractive) males foraged more closely and lost weight. Display behaviors may also incur costs by inciting aggression from neighboring territory holders (Westcott 1997; Pryke et al. 2001) or by increasing the risk of predation via increased conspicuousness, reduced vigilance or reduced ability to escape (Endler 1987; Cooper 1999; Koga et al. 2001). We do not have information about the condition of males in this study to directly test the possibility that successful males are in better condition and are thus better able to produce an attractive combination of traits. However, we found that both the slope of SR on IPI and the number of days spent on the lek, a season-long measure of effort, loaded together in a PCA (Figure 5 and Table 1).

Alternatively, or additionally, successful males may be better at tactical adjustment of their display rate. Gibson (1996) found evidence that SR is more important in influencing female choice during close courtship. Thus, males may benefit from displaying at a lower rate when females are farther away, to reduce their costs, and allocating more effort to display as females approach. Supporting this explanation, we found that successful males adjust their SR more than unsuccessful males

in response to proximity (Figure 4d). Both maximum SR and responsiveness to proximity load together and correlate with male mating success, suggesting that males who more strongly adjust their SR in response to proximity are able to display at a higher maximum rate (see Figure 5 and Table 1). Moreover, we found a nonsignificant tendency for unsuccessful males to strut at a faster rate than successful males in the absence of females. Taken together, these results suggest that males tactically adjust their display traits as females approach, reducing costs by displaying at a lower rate when females are far away and that the tendency to do so is positively related to male mating success. Such differences in male tactical abilities may arise due to genetic and/or environmental differences in the ability to learn or respond to environmental stimuli (Koolhaas et al. 1999; Sih and Bell 2008) and/or differences in prior experience with courtship (King and West 1983; Trainer et al. 2002). We do not have sufficient information about the age and other characteristics of males in this study to address these possibilities here.

Are successful males more skilled in tactically allocating their courtship effort or do other factors cause the difference in display adjustment between successful and unsuccessful males? The patterns observed here are unlikely to be caused by successful males being more exhausted than unsuccessful males on the day of the experimental trial—real females (1–2 per morning) were present on the lek prior to robot trials on 3 of 9 trial mornings, but no males tested copulated with these females. However, successful males would certainly have engaged in more courtships earlier in the season and have a higher probability of future courtships; therefore, the conservation of courtship effort may be more important for these males, favoring stronger display adjustment. The optimal tactics for successful and unsuccessful males may thus differ. In addition, struts are used in agonistic context as well as a courtship context (Wiley 1973a, 1973b); therefore, unsuccessful males may need to maintain a higher SR to defend their territories. We are currently analyzing natural fighting behavior to address this possibility. Regardless of whether these differences in how males adjust their display effort with female proximity are mediated socially, by differences in favored tactics or by differences in the skill at which these tactics are executed, our results suggest that the tactical allocation of display effort allows males to produce a more attractive combination of display traits during courtship.

Our finding that successful males adjust their SRs more strongly with female proximity appears to contradict results in another population of sage grouse. Gibson et al. (1991) found the reverse of our results—correcting for female proximity, they found a positive relationship between male display rate at 50 m and male mating success but not display rate at 5 m. This would suggest that the slopes of male SR on proximity would not have negatively correlated with male mating success, as we found in our study population, and indeed that the opposite may have been true. Although a later study (Gibson 1996) found that corrected SR at 5 m was positively correlated to the probability that a female would mate during close courtship, SR at a distance is not reported in that study; therefore, we cannot directly compare our results with these. It is unclear whether the difference between the 1991 study and the present study reflect a difference in behavior between these populations, differences in the time of the season in which the study was conducted (our study was conducted later in the season, which may affect male strutting behaviors, as discussed above) or a difference between the experimental and observational nature of these studies. Supporting the first explanation, Hartzler (1972) found results more similar to ours in an observational study of a Montana population—he found that SR in close courtship is higher for breeding males,

but he found no relationship between breeding status and SR when no females were present on the lek. Similarly, a significant reversal in the relationship between display rate and mating success in the presence and absence of females was found in an observational study of closely related greater prairie chickens (Noaker and Sandercock 2008).

Similar to previous studies on other populations of greater sage grouse (Hartzler 1972; Gibson and Bradbury 1985; Gibson et al. 1991; Gibson 1996), we found that males who display at a higher maximum rate have higher mating success. However, we did not find a positive relationship between IPI and mating success, which was found in most, but not all, years in previous studies (Gibson and Bradbury 1985; Gibson et al. 1991; Gibson 1996). It is currently unclear whether 2007 was a year in which the correlation between IPI and mating success was too weak for us to detect, whether females in our study population (Wyoming, United States) assess traits differently than females in the previously studied population (California, United States) or whether the larger size of our study lek affects female mate-choice behaviors (Gibson et al. 1991). Analysis of the correlates of mating success in additional years is underway to examine these possibilities. Here, we examined the relationship between IPI and other traits based on strong previous evidence that IPI is assessed by females during mate choice or related to a trait that is assessed by females (e.g., amplitude, Dantzker et al. 1999; Gibson 1996).

Taken together, our results provide evidence consistent with a trade-off mediated by energetic constraints. But although there is evidence (discussed below) that strutting is energetically costly, further study is needed to examine how both quality and quantity are linked to available energy to demonstrate an energetic trade-off between them. In addition, further information is needed about how males allocate their energy on these different scales. The window during which we measured male display traits was narrow (2–12 3-min periods sampled per male), but males may face energetic trade-offs that play out at life-long, season-long, day-long, and courtship-long scales (Stearns 1992). The relationship between a male's energy resources and his tactical use of these resources at all of these scales may be complex. For example, if males are in good condition, they may have less need to tactically adjust their traits. This predicts a pattern opposite to the one observed here but nonetheless highlights the complexity of how animals might respond to energetic constraints. In addition, male display traits in this study were measured with an experimentally controlled female stimulus but were not experimentally manipulated; thus, the correlations we observed between male traits and mating success may be caused by other factors, as is generally true for observational studies.

Although further study is needed to understand the causes of the observed relationships between display traits, these results show that examination of the covariation between display components can elucidate how both the trait space available to a male, as well as his adjustment within this space, may contribute to male fitness. To be successful, males may need the ability to produce attractive signals, as well as the ability to respond to female behaviors and tactically allocate their limited display effort. Researchers have considered short-term tactical allocation of effort in sequential assessment during variable or escalating contests among males (e.g., Clutton-Brock et al. 1979; Payne and Pagel 1997; Price et al. 2006; Cardoso et al. 2009). Tactical allocation of effort has less often been considered within courtship displays (Parker 1974; Payne and Pagel 1996). Because males in a wide range of taxa increase their courtship display rate or other call features when females are close (e.g., Collins 1994; Byrne 2008; How et al. 2008), such fine-scale adjustments of display effort are

likely to be widespread. In addition, energetic and/or mechanistic trade-offs between different components of multicomponent displays appear to be common (e.g., Lambrechts and Dhondt 1988; Podos et al. 2004; Bertram and Warren 2005). If there are benefits to emphasizing different signal features in different contexts, or producing less costly signals when the potential benefits are low, then tactical adjustment of signaling behaviors may allow males to maximize the attractiveness of their sexual displays in the face of these trade-offs (Wells and Taigen 1986; Bertram and Warren 2005; Price et al. 2006; How et al. 2008; Cardoso et al. 2009). However, this hypothesis has not yet been tested in other species, nor have the fitness consequences of variation in the ability to make these adjustments been measured. For sage grouse, our results suggest that there is plasticity in both the quantity and quality with which male strut signals are produced—despite their description as a “fixed-action pattern” (Wiley 1973a)—and that the ability to adjust these displays tactically may itself be a trait favored by sexual selection.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.beheco.oxfordjournals.org/>.

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