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RESEARCH ARTICLE

Investigating female mate choice for mechanical sounds in the male Greater Sage-Grouse

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ABSTRACT
Although birds are generally known for their vocally produced songs and calls, some species have evolved alternate means of acoustic communication that do not require the syrinx. While many of these mechanical sounds are used in a courtship context, the importance of among- and within-individual variation in these sounds is almost entirely unknown. We investigated feather-produced sounds in male Greater Sage-Grouse (*Centrocercus urophasianus*), which congregate on leks during the spring breeding season and perform elaborate displays to attract females. Despite decades of research on the vocal components of the display, the frequency-modulated and mechanically generated "swish" sounds remain poorly studied. We used 2 years of acoustic data to evaluate the relationship between the time and frequency characteristics of the swish display and male mating success. Although characteristics of the swish sounds showed individual-specific patterns of variation, neither univariate nor multivariate analyses revealed direct effects of the acoustic qualities of these mechanical sounds on number of copulations. However, we did find that the frequency range of individual notes was correlated with note duration, and that males who successfully copulated showed a larger frequency range for a given duration than unsuccessful males. Furthermore, successful males increased this frequency change more strongly with the approach of a female than did unsuccessful males. These results parallel previous findings that successful and unsuccessful males show different patterns of adjustment with changing courtship conditions. Our results emphasize the importance of considering the interaction among multiple components of displays in analyses of mate choice, and help to broaden our understanding of the function of mechanical sounds in this and other species of birds.

Keywords: mechanical sound, sexual selection, *Centrocercus urophasianus*, display plasticity, mate choice, sonation

Investigación de la selección de pareja por parte de hembras de *Centrocercus urophasianus* basada en sonidos mecánicos

RESUMEN
Aunque las aves son generalmente conocidas por sus cantos y vocalizaciones, algunas especies han evolucionado medios alternativos de comunicación acústica que no requieren de la siringe. Mientras que muchos de esos sonidos mecánicos se usan en un contexto de cortejo, la importancia de la variación en estos sonidos dentro de y entre individuos es casi completamente desconocida. Investigamos los sonidos producidos por las plumas en machos de *Centrocercus urophasianus* que se congregan en asambleas de cortejo durante la temporada reproductiva en primavera y hacen despliegues elaborados para atraer a las hembras. A pesar de décadas de investigaciones sobre los componentes vocales del despliegue, los sonidos *swish* generados mecánicamente y de frecuencia modulada aún son pobremente conocidos. Usamos dos años de datos acústicos para evaluar la relación entre las características de tiempo y frecuencia del despliegue *swish* y el éxito reproductivo de los machos. Aunque las características del sonido *swish* mostraron patrones de variación específicos de cada individuo, ningún análisis univariado o multivariado reveló efectos directos de la características acústicas de estos sonidos mecánicos en el número de cópulas. Sin embargo, encontramos que el rango de frecuencia de las notas individuales estuvo correlacionado con la duración de la nota, y que machos que copularon exitosamente mostraron un rango de frecuencias más amplio en una duración determinada que los machos no exitosos. Además, los machos exitosos incrementaron este cambio de frecuencias más fuertemente que los machos no exitosos cuando las hembras se aproximaban. Estos resultados son paralelos a los de estudios previos que demostraron que machos exitosos y no exitosos presentaron patrones diferentes de ajuste cuando cambiaban las condiciones del cortejo. Nuestros resultados enfatizan la importancia de considerar la interacción entre múltiples componentes del despliegue en

análisis de escogencia de pareja, y ayudan a ampliar nuestro entendimiento de la función de los sonidos mecánicos en esta y otras especies de aves.

Palabras clave: *Centrocercus urophasianus*, escogencia de pareja, plasticidad del despliegue, selección sexual, sonidos producidos por aves, sonidos mecánicos

INTRODUCTION

Studies of syringeally produced songs and calls dominate the research on acoustic communication in birds, but many birds also produce mechanical sounds using their feet, feathers, or bills. A wide array of bird species, including hummingbirds, larks, manakins, honeyguides, doves, grouse, and snipes, communicate with these sounds, termed "sonations" (Bostwick 2006). Most previous research has focused on the mechanism rather than the function of sonations (Bostwick and Prum 2005, Clark and Feo 2008, Bostwick et al. 2010, van Casteren et al. 2010), and the fitness consequences of individual variation in non-syringeal acoustic communication remain largely undescribed (Prum 1998, Hingee and Magrath 2009, Clark and Feo 2010).

Many examples of avian sonation come from male courtship displays in polygynous species, suggesting that mechanical sounds may evolve by sexual selection (Prum 1998). Yet we have no empirical evidence to indicate whether sonations influence the outcome of mate choice and/or intrasexual competition. One species suitable for investigating the function of sonations is the Greater Sage-Grouse (*Centrocercus urophasianus*). Male sage-grouse congregate in large numbers on leks during the breeding season and perform visual and acoustic displays to attract females. Several studies over the past few decades have examined whether the time and frequency characteristics of male vocal displays are correlated with male mating success in this species. Most of these studies find that 2 aspects of display quantity (number of days on the lek and display rate) and 1 aspect of display quality (a temporal feature of the vocalization called the "inter-pop interval") are correlated with male mating success, though there is some variation among years and among study populations (Wiley 1973b, Gibson and Bradbury 1985, Boyce 1990, Gibson et al. 1991, Gibson 1996, Patricelli and Krakauer 2010). Males that are successful copulators also appear to differ in tactics from non-copulating males: successful males adjust display rate to maximize performance when females are nearby. Additionally, while unsuccessful males show declines in vocal features as display rate increases, successful males appear not to be subject to this quantity–quality tradeoff (Patricelli and Krakauer 2010).

Two components of the Greater Sage-Grouse display that have not yet been analyzed are a pair of mechanically produced sounds, hereafter referred to as the first and second "swishes" of the strut display. They are produced when the male, with his esophageal air sacs fully inflated, strums his wings twice over stiffened feathers on either side of his breast. The 2 swishes precede the syringeally produced coos, pops, and whistle notes in the strut display (Gibson and Bradbury 1985). A spectrogram of the first swish reveals a frequency upsweep; the second swish occurs about 1 s after the first swish and typically begins with a downsweep and increases in frequency in the latter half of the note—i.e. the "downslope" and the "upslope" (Figure 1). These 2 sounds are therefore frequency-modulated, a rare property in mechanically produced sounds (Clark et al. 2011); this acoustic complexity could allow for greater variation in swish sounds among individuals, and higher potential for informative signaling. In this study, we examined whether acoustic qualities of the mechanically produced swishes correlate with male mating success, an important aspect of male fitness (Semple et al. 2001). We also investigated whether components of the swishes might change with variation in courtship conditions, and whether this variation may be related to male mating success.

METHODS

Field Methods

We monitored breeding behaviors of adult male Greater Sage-Grouse on Monument Lek (Fremont County, Wyoming, United States) for the duration of morning lekking activity between early March and late April in 2006 and 2007, except for days when snow prohibited lek access. We focused on the territorial males in the central area of the lek (~100 m by 130 m) whose movements were unobscured by vegetation and topography. We placed 3 high-definition video cameras (Sony HDR-HC1 and HDR-HC3, Tokyo, Japan) in blinds on hills ~200 m from the lek to record all activity occurring on the main portion of the lek throughout the breeding season. During these 2 years, Monument Lek served as a control lek for an experimental noise introduction study (Blickley et al. 2012). For this reason, we avoided capture-related disruptions and instead non-invasively identified males by using individually distinctive patterns of white spots on otherwise black undertails that are highly conspicuous when the tail is erected during lekking. These patterns have been used successfully to distinguish the individual males of a lek within each year, but cannot be used between years because the patterns change as tail feathers are shed and
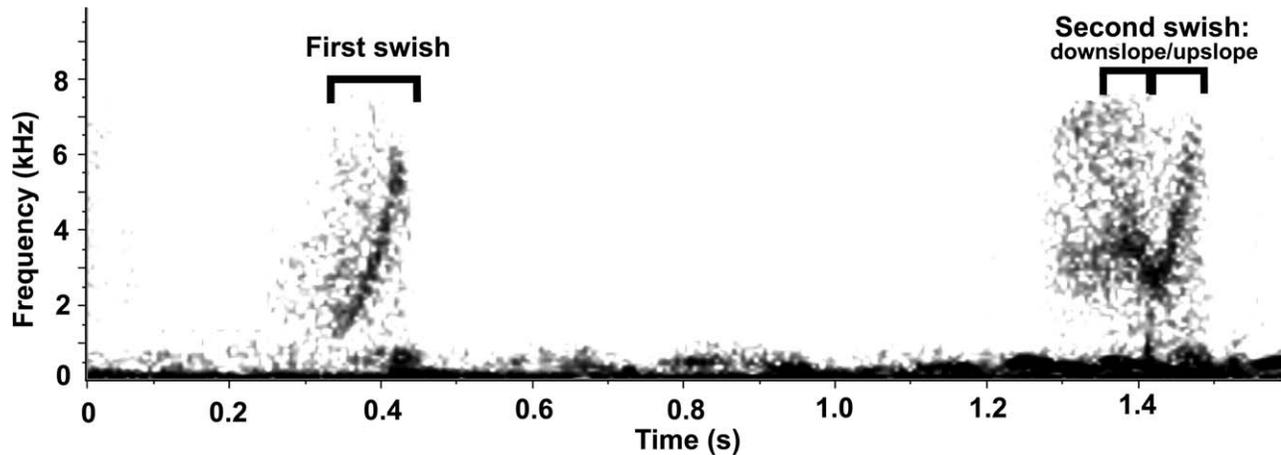
FIGURE 1. Spectrogram of the 2 mechanical swishes in the male Greater Sage-Grouse display. Boxes indicate the selected regions analyzed in Raven.

regrown during annual molt (Wiley 1973a, Gibson and Bradbury 1985, Patricelli and Krakauer 2010).

Observers in blinds continuously recorded each male's position relative to a grid of survey stakes placed at 10 m intervals. We captured the acoustic portion of male displays with an array of 24 omnidirectional microphones (Sennheiser K6/ME62, Wedemark, Germany) recording simultaneously across the main portion of the lek (Krakauer et al. 2009, Patricelli and Krakauer 2010).

Acoustic Analyses

Sound localization and identification. We viewed all 24 channels of recorded sound simultaneously using program Syrinx (John Burt, University of Washington), and selected vocal displays with minimal interference from other calls or background noise. We passed the selected calls through MATLAB code (ArrayBatchGUI, John Burt, University of Washington) that performed spectrogram cross-correlation to generate time-of-arrival differences at each microphone to localize the origin of the call. Calls were then assigned to males by matching the time and location of sounds with the time and position of male displays visible on video recordings of the lek (Krakauer et al. 2009, Patricelli and Krakauer 2010). We collected data from 29 males in 2006 and 38 males in 2007, and approximated mating success for each male from total number of copulations observed in the field and all-occurrence sampling from the videos of lekking behavior. The positions of females during male lekking were also recorded from video in 2007, and we used additional MATLAB code to calculate the distance of the nearest female to each recorded male display (Patricelli and Krakauer 2010).

Sound measurement. We analyzed the acoustics of at least 3 swish displays from each male included in our study. When more than 3 recordings for 1 male were

identified, we randomly selected up to 12 displays to measure per day on the lek. Though not all males were present on the lek every day, we measured males on multiple days when possible to account for variability in recording conditions. This sampling scheme was shown to be effective in a previous study of vocal behavior in sage-grouse (Patricelli and Krakauer 2010). We used Raven Pro version 1.4 (Cornell University) to measure the temporal and frequency aspects of the 3 main components of the swish display visible in spectrograms: 1) the first swish, 2) the second swish downslope, and 3) the second swish upslope (Figure 1; Table 1). A single observer (R. Koch) conducted all of the measurements, and temporal and frequency limits of the sounds were estimated by eye from the spectrograms (Hann type, with a grid size of 86.1 Hz and a discrete Fourier transform size of 512 samples).

For each display, we produced 9 measurements (Figure 1): duration (D1), low frequency (LF1), and frequency range (FR1) of the first swish; duration (D2), low frequency (LF2), and frequency range (FR2) of the second swish downslope; duration (D3) and frequency range (FR3) of the second swish upslope; and time between the end of the first swish and start of the second (TB). Because the low frequency of the second swish is represented by the low frequency of its downslope as well as its upslope, we excluded the low frequency of the upslope from our analysis to avoid redundancy. Measurement of minimum and maximum frequency from spectrograms could lead to error with changes in spectrogram parameters or signal amplitude (Zollinger et al. 2012). We reduced this source of error by measuring only recordings in which the boundaries of the swishes were clearly defined as high-intensity (high-amplitude) regions that were distinguishable to the observer. We could not measure all parts of some swish displays because of interference with other

TABLE 1. Description of acoustics and variation in: 1) the first swish, 2) the downslope, and 3) the upslope of the second swish. F statistics are reported for one-way ANOVAs comparing variation within and among acoustic traits; all $P < 0.001$ except where otherwise noted.

	Both Years			2006				2007			
	Mean $\pm$ SD	Min	Max	$F_{22,201-223}$	CV_b	CV_w	PIC	$F_{31,289-303}$	CV_b	CV_w	PIC
D(1)[a]	0.09 $\pm$ 0.02	0.04	0.21	1.49[b]	28.52	26.35	1.08	4.13	29.04	23.99	1.21
LF(1)	1476 $\pm$ 369	625	3620	1.65[c]	29.05	25.38	1.14	2.87	22.22	20.82	1.07
FR(1)	5490 $\pm$ 881	2382	7647	6.17	16.73	14.23	1.18	4.89	15.70	13.82	1.34
D(2)	0.04 $\pm$ 0.01	0.01	0.09	3.58	27.90	25.17	1.11	6.38	30.48	24.14	1.26
LF(2)	3117 $\pm$ 510	1934	4949	19.06	15.49	10.03	1.54	21.11	16.68	9.73	1.71
FR(2)	2268 $\pm$ 638	25	4862	2.76	24.00	19.66	1.22	5.07	29.16	25.68	1.14
D(3)	0.05 $\pm$ 0.01	0.02	0.08	4.48	14.86	11.01	1.35	7.48	17.20	13.78	1.25
FR(3)	4275 $\pm$ 871	1722	6284	8.02	20.14	14.63	1.38	8.20	20.81	16.62	1.25
TB	1.01 $\pm$ 0.05	0.89	1.21	16.74	4.74	2.81	1.69	25.52	4.59	9.06	0.51

[a] D and TB are in units of seconds; LF and FR are in units of hertz.
[b] $P = 0.079$
[c] $P = 0.038$

sounds, such as other male displays or the songs of non-target species.

Statistical Analysis

We first computed descriptive statistics (mean, standard deviation, minimum, and maximum) for the 9 swish measurements. We performed these calculations on a pooled data set of all measurements accumulated from both years of the study to best capture average values for the swish displays in this population. We also created a correlation matrix to investigate multicolinearity among variables in each year. To assess whether our 9 swish measurements were individually distinctive, we performed one-way ANOVAs and PIC (potential for information coding) calculations to compare within- and among-male variation in these sounds within each year. A PIC value is the ratio of the coefficient of variation among all males (CV_b) to the mean coefficient of variation within each male (CV_w); a PIC >1 indicates a trait that can potentially communicate individual-specific information because the variation among males exceeds the variation within each male (Robisson et al. 1993, Garcia et al. 2012). Bonferroni corrections for multiple comparisons were not applied to ANOVAs in order to avoid the possibility of type II error (Moran 2003, Nakagawa 2004). Descriptive statistics and PIC values were calculated using Microsoft Excel 2008 for Mac (version 12.3.1; Microsoft 2008) and ANOVAs were performed in R version 3.0.2 (R Core Team 2014).

We tested for a relationship between the acoustic measurements and mating success using a generalized linear mixed model (GLMM) with a binomial error distribution using the lme4 package version 1.1-7 (Bates et al. 2014, R Core Team 2014). We conducted separate GLMMs on the 2006 and 2007 data sets because males were not permanently marked and could not be identified

between years, so an unknown number of males recorded in 2007 were also represented in the 2006 sample. We used only the subset of data in which all measurements for a given display could be made; 2 males were therefore excluded from this analysis because they lacked at least 3 fully measured swish displays. The full model included all 9 swish measurements as fixed effects and Male ID as a random effect; the response variable was a binomial term for mating success (1 = at least one copulation, 0 = no copulations). We conducted stepwise term reduction of fixed effect terms, but no reduced model showed a significant relationship between any fixed effect and mating success, so only the full model results are described here. We also ran Principal Components Analyses for each year, but the analyses failed to provide components that explained much of the total variation in acoustic measurements (approximately 25% or less for PC1) or showed consistent patterns of variation across years. For these reasons we did not include these analyses in the manuscript.

One pair of variables showed consistently high correlations in both 2006 and 2007 for all 3 swish components: duration (D) and frequency range (FR). We used the nlme package version 3.1-117 (Pinheiro et al. 2014) to investigate how these 2 swish characteristics varied with copulation success and social context. First, to assess the relationship between FR and D in the 3 swish components (first swish, second swish downslope, and second swish upslope), we ran GLMMs testing the effects of D, copulation success (a factor designating males that obtained at least one copulation vs. those with no copulations), and their interaction on FR, with male identity as a random effect. Second, we calculated the ratio of FR:D to capture variation in that relationship for each swish component for each measured display, and

performed further mixed model analyses to assess how the FR:D ratio of each swish component varied with log-transformed distance to the nearest female, copulation status (copulated vs. did not copulate), and their interaction, with male identity as a random effect. We limited these analyses to the 2007 data because female positions were not documented in 2006. In addition, to determine whether amplitude variation may have influenced our measurements, we used mixed models to examine the relationship between FR:D and the distance between the male and the closest microphone in the array on a subset of data from 2006, with male identity as a random effect.

All values reported as Mean ± SD except where otherwise noted.

RESULTS

We observed a total of 50 copulations among our focal males in 2006 and 62 in 2007; 12 out of 29 males in 2006 and 8 out of 38 males in 2007 achieved at least 1 copulation. Mating success in both years was dominated by 1–2 males, with 55% of copulations in 2006 achieved by 2 males and 69% of the copulations in 2007 attributed to 1 male. We analyzed a total of 766 swish displays in the 2 years of our study.

Most one-way ANOVAs (12/14) comparing variation among males in each measurement were highly significant ($P < 0.001$) and most PIC values (13/14) were >1, indicating that the swish measurements we took tended to vary more among than within males (Table 1). The low frequency of the second swish had the greatest PIC value across both years, although no PIC value exceeded 2. Interestingly, the single measurement with a PIC value less than 1 (time between swishes, 2006) had a value well over 1 in the subsequent year (2007; Table 1). Because no single measurement scored as consistently uninformative in either ANOVA or PIC calculations, we included all 9 measurements in subsequent analyses.

To investigate the relationship between mating success and swish characteristics, we performed a GLMM analysis for 2006 and 2007. We assessed an average of 8.9 calls (± 6.6) from each of 28 males in 2006 and 11.3 calls (± 5.7) from 37 males in 2007. $P > 0.05$ for all fixed effects and the intercept in both years; the lowest P-values were for D2 and FR2 in 2007 ($P = 0.08$ and 0.05, respectively), but these terms were nonsignificant in 2006 (both $P > 0.9$).

We created a correlation matrix of swish measurements to examine multicolinearity among variables, which revealed that frequency range (FR) and duration (D) were correlated for all swish components in both years (all $r = 0.5$–0.6). We examined this further using GLMM, which confirmed that in both 2006 and 2007, the D of all swish components (first swish, second swish downslope, first swish upslope) had significant positive relationships with the FR of that swish component (all $P < 0.01$; Table 2), such that longer swish durations tended to also have larger frequency ranges. Copulation status did not have a significant effect on FR in any swish component in either year in the GLMMs (all $P > 0.10$; Table 2), consistent with the ANOVA results. However, the interaction between D and copulation status for the second swish downslope had a significant effect on FR in both 2006 and 2007 ($P < 0.05$; Table 2, Figure 2). These results indicated that successful males tended to have larger FR for a given D in the second swish than did unsuccessful males.

To determine whether individual males varied these characteristics of their swishes with changes in social environment, we assessed the effects of log-transformed distance to nearest female, male copulation status, and their interaction on the ratio FR:D, and we again found significant effects only for the second swish downslope ($P < 0.05$; Table 2). As predicted by the earlier analyses, the second swish downslopes of successfully copulating males had significantly larger FR relative to D (a larger FR:D ratio) than those of noncopulating males. Further, there was a significant interaction between distance to female and copulation status, such that copulating males *increased* the magnitude of this ratio with *decreasing* distance to nearest female (i.e. when females were closer). This interaction term was not significant for the first swish or the second swish upslope, though plots are suggestive (Figure 3). When we investigated the effect of microphone distance on FR:D measurements for a subset of 2006 data, we found a significant effect for the first swish (FR:D vs. microphone distance: slope = 2050, SE = 400, $t = 5.14$, $P < 0.05$), but not for either the second swish downslope (slope = 156, SE = 392, $t = 0.40$, $P = 0.69$) or the second swish upslope, which in fact had a nonsignificant trend in the *opposite* direction (slope = −531, SE = 344, $t = −1.54$, $P = 0.13$); it is therefore unlikely that variation in the distance of a displaying male from an array microphone was responsible for the significant effects we observed in the second swish downslope.

DISCUSSION

To investigate whether female Greater Sage-Grouse use mechanical swish sounds as criteria for choosing mates, we tested whether male mating success varied according to the spectral and temporal characteristics of his sonations. We found that swishes tended to vary more among males than within males. Our analyses did not indicate any direct relationship between the acoustic components of swish displays and male mating success in our population. However, we found evidence that successful males had a larger frequency range per unit duration in at least one component of their display—the second swish downslope. Further, we found that males may have adjusted this rate

TABLE 2. Results of 2 general linear mixed models assessing the relationships between components of the male Greater Sage-Grouse swish display and copulation success.

			Model 1[a]			Model 2[b]			
	Effect	Year	Coefficient (SE)	t	P	Effect	Coefficient (SE)	t	P
First swish:	Intercept	2006	4100 (320)	12.8	<0.001	Intercept	65000	14.4	<0.001
		2007	4500 (180)	24.7	<0.001				
	Duration	2006	14100 (3450)	4.1	<0.001	Log(Male–Female distance)	550 (1500)	0.37	0.71
		2007	10800 (1860)	5.8	<0.001				
	Copulation status	2006	85 (420)	0.2	0.84	Copulation status	15600 (9800)	1.6	0.13
		2007	−300 (370)	−0.82	0.42				
	Interaction	2006	−2000 (4200)	−0.49	0.63	Interaction	−3900 (3000)	−1.29	0.2
		2007	6170 (3730)	−0.48	0.1				
Second swish downslope:	Intercept	2006	1300 (160)	8.6	<0.001	Intercept	54000 (4100)	13.3	<0.001
		2007	970 (110)	8.6	<0.001				
	Duration	2006	22900 (3550)	6.4	<0.001	Log(Male–Female distance)	2000 (1350)	1.5	0.15
		2007	31600 (2500)	12.5	<0.001				
	Copulation status	2006	−290 (230)	−1.3	0.21	Copulation status	21800 (8900)	2.4	0.02
		2007	−260 (220)	−1.2	0.24				
	Interaction	2006	10700 (5400)	2	0.05	Interaction	−5600 (2700)	−2.04	0.04
		2007	12400 (5100)	2.45	0.01				
Second swish upslope:	Intercept	2006	2300 (470)	4.9	<0.001	Intercept	80900 (4300)	18.6	<0.001
		2007	1700 (300)	5.8	<0.001				
	Duration	2006	39300 (8900)	4.4	<0.001	Log(Male–Female distance)	1300 (1300)	0.97	0.33
		2007	50600 (5600)	9.1	<0.001				
	Copulation status	2006	−960 (600)	−1.6	0.12	Copulation status	12100 (9300)	1.3	0.2
		2007	−570 (560)	−1.0	0.32				
	Interaction	2006	14700 (11200)	1.3	0.19	Interaction	−1950 (2600)	−0.74	0.46
		2007	16900 (10500)	1.6	0.11				

[a] Model 1 tested the effects of duration, copulation success (copulated vs. did not copulate), and their interaction on frequency range.
[b] Model 2 tested the effects of log-transformed male–female distance, copulation success, and their interaction on the frequency range:duration ratio, for 2007 data only.

according to changes in their social environment (in this case, the distance to the female they courted), with successful males adjusting their mechanical sound production more than the unsuccessful males.

Our finding that successful males may have adjust their displays to increase the frequency range of the second swish downslope when females were near echoes the findings of a concurrent 2007 study of display behaviors and vocalizations on this lek. Patricelli and Krakauer (2010) found that successful males adjusted their display rate more strongly with female proximity, displaying at a high rate only when females were close. These successful males were able to increase their display quantity without a decline in the quality of vocalizations. In contrast, unsuccessful males adjusted their display rates less and showed a quantity–quality tradeoff. These results suggested that males tactically allocated their signaling effort to produce high-performance displays during close courtship, when they were most important in influencing female choice (Gibson 1996). Consequently, successful males may have displayed both at a faster rate and with larger frequency ranges for at least one component of the swish display when close to females. It is possible that the kinematics of producing the swish sounds could drive a performance tradeoff such that only some males could both accelerate display rate and optimize frequency range for a given duration. To test this possibility, further work is needed to understand how frequency modulation in the swish is achieved, such as whether modulation is due to changes in the rate of wing movement across the chest or by stimulating feathers with a broader range of resonant frequencies (K.S. Bostwick and L. Louis, personal communication). Interestingly, the closely related Gunnison Sage-Grouse, a sister species to the Greater Sage-Grouse with a similar strut display and habitat, has acoustically simple swishes with no frequency modulation (Young et al. 1994). Frequency sweeps are therefore not a necessary consequence of strumming feathers to produce swish sounds in these taxa and instead appear to be unique characteristics of the Greater Sage-Grouse sonations.

Another potential explanation for the increase in frequency range we detected is that successful males could adjust swish amplitude depending on distance to the female, and that the increased frequency range during close courtship was a byproduct of detecting a broader range of frequencies from a louder display. We used
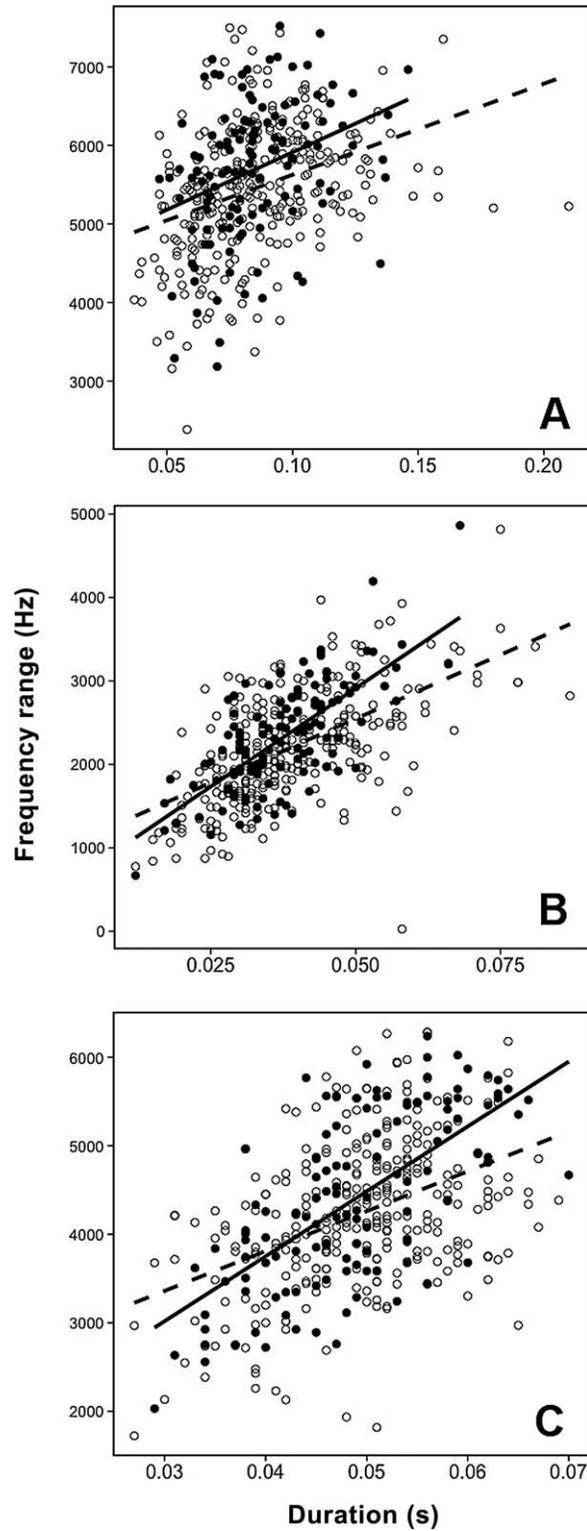
FIGURE 2. Scatterplots of frequency range versus duration with linear regression lines for (**A**) the first swish, (**B**) the second swish downslope, and (**C**) the second swish upslope for 2007. Open circles and dashed lines represent data from males that did not copulate during the lekking season; closed circles and solid lines represent data from males that copulated at least once.
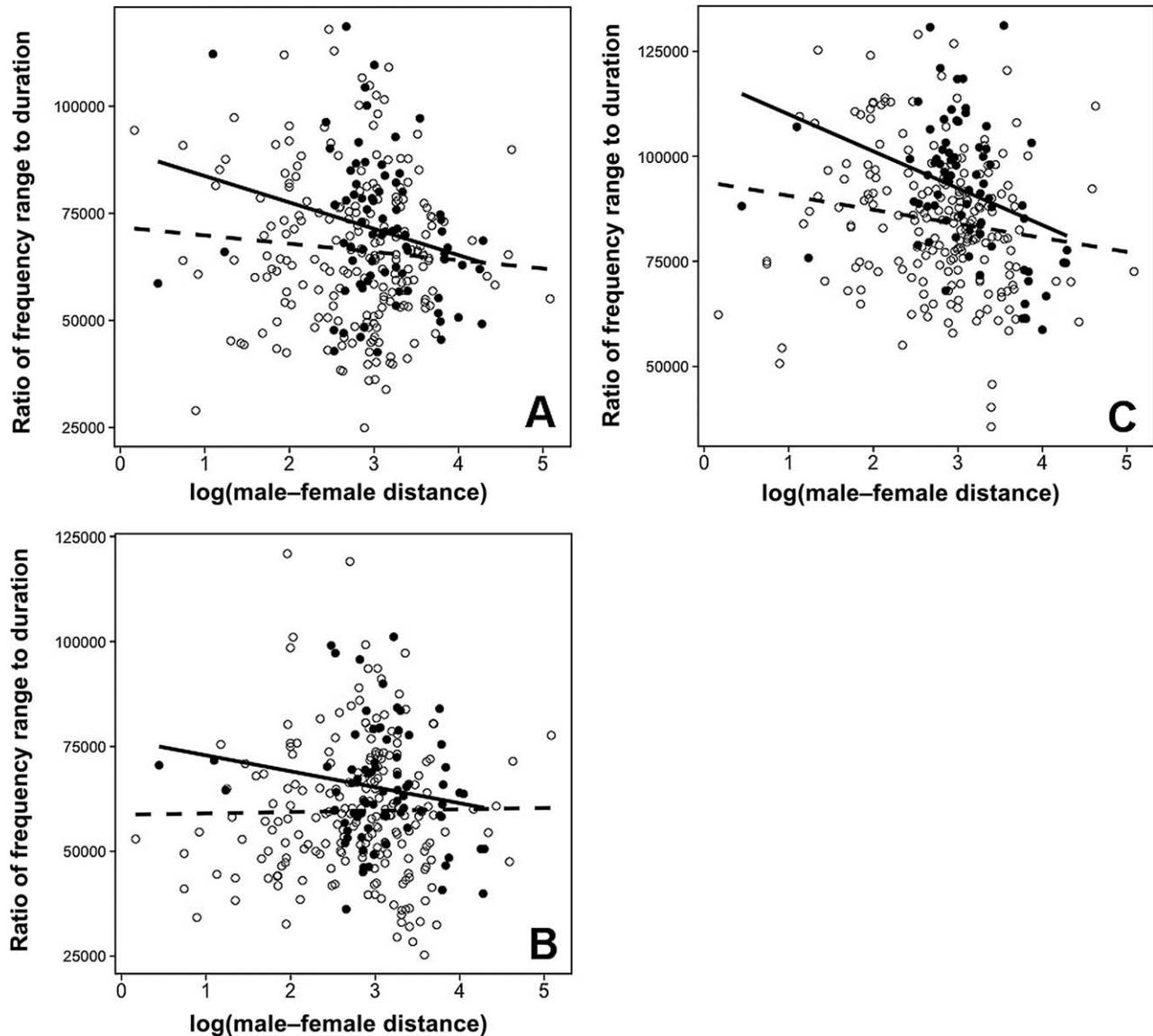
FIGURE 3. Scatterplots of the ratio of frequency range to distance (FR:D) versus log-transformed distance to nearest female with linear regression lines for (**A**) the first swish, (**B**) the second swish downslope, and (**C**) the second swish upslope for 2007. Open circles and dashed lines represent data from males that did not copulate during the lekking season; closed circles and solid lines represent data from males that copulated at least once. We added one to the raw female distance measurements prior to log transformation to eliminate negative values.

variation in distance between the male and closest array microphone to examine this possibility: for the second swish there was no relationship between distance and FR, and the trend went in the opposite direction as predicted for the second swish upslope, with slightly higher frequency ranges at greater distances from the microphone rather than when closer to the microphone as we would expect if received amplitude were influencing detectability. We are currently working to calculate amplitude of the acoustic displays directly from our array recordings to test this possibility more rigorously, but results to date suggest

that amplitude was not a significant determinant of frequency range in this study.

We did not find evidence for selection acting on any one feature of swishes, but rather a combination of multiple features—the rate of change in frequency and the adjustment of frequency range with proximity to females. Females might have assessed these traits directly, or judged how these traits covaried with display rate or another trait. Swishes could also function as signals in male–male competition or as amplifiers to attract attention to a different trait, such as the bright yellow vocal sacs

prominently displayed during the swish motions, the pop-whistle display that the swishes precede, or even the strummed breast feathers themselves (Hasson 1989, Boyce 1990, Saether et al. 2005, Ord and Stamps 2008, Takahashi et al. 2008). Experimental manipulation or ablation of the swish display would help to test these alternative functions. Unfortunately, such manipulation would prohibitively interfere with other aspects of male sage-grouse display and was not possible during our study. We are currently investigating seasonal patterns in swish acoustics, and whether the swishes may interact with other components of the sage-grouse display.

To our knowledge, this study is the first to describe the acoustic components of the swish sonation in male Greater Sage-Grouse and investigate the fitness consequences of individual variation in a mechanically produced sound in birds. Additional studies among the widespread populations of Greater Sage-Grouse and in other species with prominent sonations will be necessary to enhance our understanding of the functions of these behaviors.

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