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Necklace-style radio-transmitters are associated with changes in display vocalizations of male greater sage-grouse

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Radio-transmitters are used widely in wildlife research because they allow researchers to track individual animals and monitor their activity. However, to provide unbiased information about a population, transmitters must be deployed on a representative sample of animals and must not alter the behavior of the individuals. The greater sage-grouse *Centrocercus urophasianus* has been studied intensively using radio-transmitters for the last several decades. A previous study demonstrated that males fitted with necklace-style radio-transmitters could be less likely to attend breeding grounds than those without transmitters. However, how transmitters affect the behavior of males that do attend leks has not been investigated. Therefore, we investigated whether radio-transmitters alter the characteristics of strut vocalizations or display frequency of male sage-grouse. We measured time and frequency characteristics of vocalizations from six collared and seven non-collared adult male sage-grouse on three leks in south-central Idaho, and for two collared and four non-collared males from two leks in northern Nevada. Only one vocalization characteristic (maximum frequency of the primary whistle) differed between collared and non-collared males across both populations. Collared males showed a lower maximum frequency of the primary whistle that typically fell outside the range of variation for non-collared males. This was the only difference found in the sample from Nevada, while in Idaho, collared males also exhibited a narrower bandwidth for the primary whistle (lower maximum frequency and higher minimum frequency), a shorter primary whistle, and a shorter secondary coo than non-collared males. Some acoustic characteristics of sage-grouse strut vocalizations are linked to mate choice by females, and therefore our results suggest that collars could reduce male mating success by altering the production of breeding vocalizations. Therefore, we recommend using alternative attachment techniques for behavioral studies of male sage-grouse.

Radio transmitters are commonly used in wildlife studies, allowing researchers to track individual animals and remotely monitor activities. One fundamental assumption of telemetry is that radio-transmitters do not influence behavior or demographics of marked individuals (Millspaugh et al. 2012). It is important to test this assumption, as a number of studies on various taxa have documented negative effects of transmitters on survival (Theuerkauf et al. 2007, Venturato et al. 2009, Fabian et al. 2015), but other studies have documented no difference in survival between individuals wearing radio-transmitters and those without transmitters (Hagen et al. 2006). However, comparatively few studies have evaluated whether transmitters cause behavioral changes. Transmitters have been associated with detrimental effects on energetics and activity budgets (Godfrey and Bryant 2003, Zenzal et al. 2014, but see also Sedinger et al. 1990), weight loss (Irvine et al. 2007), reproduction (Ward and Flint 1995), and lek behavior (Gibson et al. 2013). Some radio-transmitters may cause irritation or calluses that alter behavior of individuals (Irvine et al. 2007). In some cases, the specific cause of disruption could be traced to the weight of the transmitter, position of the antenna, or attachment method, thus allowing for improvement of future telemetry studies if the problem can be overcome (Millspaugh et al. 2012). Understanding the impacts of monitoring techniques is important when studying sensitive species, as negative impacts on behavior may compound population level declines.

The greater sage-grouse *Centrocercus urophasianus* (hereafter, sage-grouse) is a species of concern throughout western North America due to long-term population declines (Aldridge et al. 2008, Garton et al. 2011, 2015) and

range contractions (Schroeder et al. 2004). The conservation concern for sage-grouse has spurred a large number of demographic and habitat-use studies involving radio-collared birds across the western United States and Canada. Despite widespread use of radio-telemetry, there are few studies evaluating impacts of transmitters on sage-grouse. Initially, Pyrah (1970) expressed concern over the use of collar "poncho-markers" on males because their design interfered with the breeding displays of birds (also see Amstrup 1980). Although poncho-markers are not the same as modern transmitters, the attachment method (collar around the neck) is similar to current 'necklace-style' designs (Fig. 1). Later research suggested that modern necklace-style radio-transmitters (hereafter, collars) were not detrimental to female survival (Caizergues and Ellison 1998). Recent work has shown that radio-collars did not impact the flush order of sage-grouse (Frye et al. 2014), suggesting that necklace-style transmitters may not significantly affect some predator-escape behaviors. However, necklaces were reported to decrease lek attendance by males and sightability at leks (Gibson et al. 2013). Other studies have documented males with necklaces displaying at leks (Baumgardt 2011, Fremgen et al. 2016), although these studies did not compare attendance rates or other measures of behavior between collared and non-collared birds.

Figure 1. A modern necklace-style radio-transmitter (collar indicated with arrows) fitted on a displaying male greater sage-grouse *Centrocercus urophasianus* from southern Idaho, spring 2014. Collars were designed for grouse and weighed 17 g. Photos by Natasha Wiggins.

We evaluated the effects of collars on the strut vocalizations of male sage-grouse on leks. During the spring breeding season, male and female sage-grouse gather on leks, where males perform strut displays and females assess male displays to choose a mate (Patterson 1952, Wiley 1973). The strut rate and acoustic quality of the strut display has been linked to mating success of males (Gibson and Bradbury 1985, Gibson et al. 1991, Gibson 1996, Patricelli and Krakauer 2010). There are multiple mechanisms by which collars may interfere with male strutting behaviors. Male strutting includes rapid inflation and movement of an esophageal air sac (Dantzker et al. 1999, Krakauer et al. 2009), which may be constricted by radio-collars. Male display movements are integrally linked to sound production (Koch et al. 2015), which may be altered by radio-collars. The male strut display is also energetically costly (Vehrencamp et al. 1989) and the added weight or stress associated with a radio-collar may result in increased energy expenditure and altered activity budgets. These impacts may, in turn, influence courtship behavior and mating success. Given the movement-intensive display performed by male sage-grouse during courtship, we tested the possibility that radio-collars placed near the esophageal air sac could interfere with the acoustic properties of the strut display of males. We compared the vocalizations of male sage-grouse from Idaho ($n = 6$) and Nevada ($n = 2$) fitted with collars to control males (Idaho $n = 7$, Nevada $n = 4$) from the same leks on the same days to determine whether radio-collars affect strut vocalizations of males on the lek. We also qualitatively compared the range of values for collared males against values obtained from non-collared males in other studies that represent the geographic distribution of sage-grouse.

Methods

Nineteen adult male sage-grouse were fitted with radio-collars in Cassia County, Idaho (42°9′N, 113°24′W) in the spring of 2013, and 23 adult males in Eureka County, Nevada (40°15′N, 116°30′W) were fitted with radio-collars in spring 2011 or earlier. Collars used in Idaho were standard 17-g very high frequency (VHF) transmitters designed for use with grouse (Advanced Telemetry Systems (ATS), Isanti, MN). Collars used in Nevada were 22-g radio collars (ATS, Isanti, MN). All birds were handled using standard capture and marking practices (Geisen et al. 1982, Wakkinen et al. 1992). Vocalizations were recorded in Idaho from six radio-collared males that were observed strutting on leks, and seven non-collared males, on six different days on three leks between 24 March and 14 April 2014, after males had been

allowed to adjust to their transmitter for approximately one year. Vocalizations were also recorded in Nevada from two collared males and four non-collared males on two different leks on 29 April 2012, 22 April 2013 and 5 May 2013. All collared birds were adult males, as verified by examination of the plumage during capture the previous year. Non-collared and collared males were recorded on the same day, within several minutes of one another, on the same lek. Separate leks were visited on different days in Idaho and Nevada. We recorded vocalizations for several minutes for each focal bird, which provided an average ± standard deviation of 8.9 ± 4.8 vocalizations to analyze per male for Idaho and Nevada birds. At the Idaho leks, audio was recorded from a blind 30–50 m from the edge of the lek, and at the Nevada leks audio was recorded from the window of a vehicle parked approximately 35 m away from displaying birds. In Nevada, distances were measured using a range-finder, and in Idaho distances were estimated using a 10 × 10 m grid of wooden stakes. At all leks, we recorded vocalizations from males that were within an estimated 15 m of one another, so that males were similar distances from the microphone. We used a Marantz PMD670 portable audio recorder (16 bit, 48 KHz linear PCM), with Sennheiser microphone (K6 with omnidirectional ME62 capsule) and a 22-inch Telinga Pro parabola. For Nevada leks, the identity of strutting males was determined by the observer (DG) and noted on the audio file. For Idaho leks, vocalizations were assigned to the focal male by comparing the timing of struts observed on videos of male lek behavior that were paired with audio recordings of the same bird. For Idaho leks, video recordings were used to calculate strut rates and to verify that there were no obstructions (e.g. sagebrush, rocks) between the recording equipment and the recorded grouse that may have blocked sound transmission. Capture, collaring and lek observations of sage-grouse were approved by the Boise State Univ. Institutional Animal Care and Use Committee (IACUC; permit 006-AC13-010), Univ. of Nevada Reno IACUC (permits A02/03-22, A05/06-22, A07/08-22 and A09/10-22), Nevada Dept of Wildlife permit no. S36652, and Idaho Fish and Game permit no. 110914.

Vocalizations were visualized as spectrograms (FFT size 512; Hann window) and measured in Raven Pro 1.4 (Cornell laboratory of Ornithology, Ithaca, NY U.S.A.) by a single experienced observer (RLE). The sage-grouse display includes six vocally produced notes from each call: three 'coo' notes, two 'pop' notes, and the primary 'whistle' (Fig. 2, 3). We measured time and frequency characteristics of the second coo, the primary whistle and the pop notes. The second coo note is longer and more often identifiable in the recordings so only this coo note was considered for analysis. For the pops, we measured the 'inter-pop interval' (IPI), which is the time delay between the two pop notes (Gibson and Bradbury 1985). For the whistle, which occurs during the IPI, we measured the duration and the maximum and minimum frequency of the primary whistle. The primary whistle rises, falls, and rises again in frequency. The maximum frequency is the highest pitch of the first rise and the minimum is the lowest pitch of the trough (Fig. 2). From these measures, we calculated the ratio of primary whistle duration to IPI, which indicates the fraction of the IPI that is taken up by the whistle. Measurements from individual

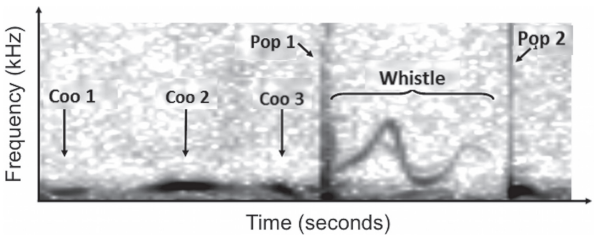

Figure 2. Example of a vocalization from a typical male greater sage-grouse *Centrocercus urophasianus* from a lek in Fremont County, Wyoming. This recording was captured using an on-lek microphone array (Krakauer et al. 2009) instead of the more distant single-microphone recording technique used in this study. This microphone set-up illustrates the full suite of vocal characteristics, some of which are not visible in the spectrograms produced by the microphone used in this study.

notes were discarded if they overlapped with other sounds, such as calls from songbirds or other males. Most male sage-grouse show a secondary whistle that is lower in amplitude

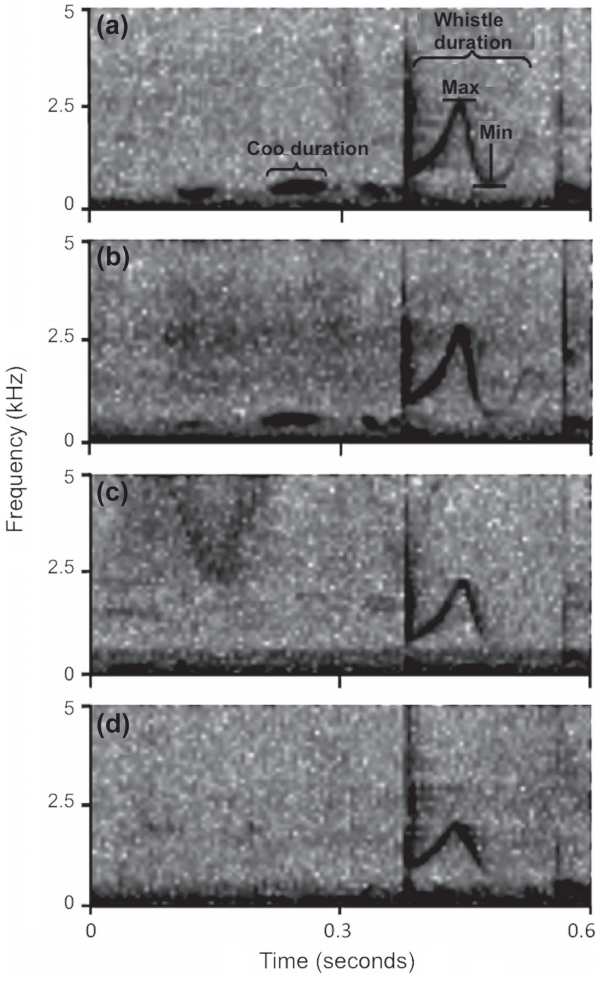

Figure 3. Strut vocalizations recorded from two non-collared (a and b) and two collared (c and d) male greater sage-grouse *Centrocercus urophasianus* in Idaho. The vocalization characteristics found to be significantly different between these groups are labeled in (a): 'max' = maximum frequency of the primary whistle (kHz), 'min' = minimum frequency of the primary whistle (kHz), 'whistle duration' = duration of the primary whistle (s), and 'coo duration' = duration of the second coo (s).

and less frequency-modulated than the primary whistle (Krakauer et al. 2009). These secondary whistles were too quiet on our recordings to measure reliably on the majority of spectrograms and were therefore excluded from this analysis.

We used an ANOVA test to determine if vocalizations differed for birds with collars fitted by different trapping personnel, to see if the individual ($n = 3$ trappers in Idaho, $n = 1$ trapper in Nevada) fitting the collar impacted the vocalization characteristics. For all other analyses, we first tested for normality and then used a Student's t-test (de Winter 2013) to compare the average value of each vocalization characteristic for each collared and non-collared male, and for comparing the average strut rate between collared and non-collared birds in Idaho. Analyses of vocalization characteristics were conducted on birds from both Nevada and Idaho, and because geographic variation exists in vocal characteristics from different populations (Krakauer et al. 2009), analyses were repeated for Idaho and Nevada birds separately. Analyses were performed in JMP 11.0 Pro (SAS Inst.).

To compare display effort between collared and non-collared males, we used the videos of male display from the Idaho leks to measure strut rate. Strut rate is positively correlated with mating success (Gibson and Bradbury 1985, Gibson et al. 1991, Gibson 1996, Patricelli and Krakauer 2010), and birds that have high display rates can expend up to four times basal metabolic rate during displays (Vehrencamp et al. 1989). Therefore, if there is an energetic cost associated with radio-collars it may result in lower strut rates. We calculated strut rate as the inverse of the arithmetic mean of inter-strut intervals (the time period between the end of the first display and the end of the next display) over the observation period, such that higher values reflect faster repetition of struts and/or shorter pauses between consecutive struts – these pauses include variation in the inter-strut-interval (time delay between consecutive struts) as well as the duration of the rest periods between bouts of strutting. Similar to Patricelli and Krakauer (2010), we did not use the harmonic mean used in earlier behavioral studies (Gibson and Bradbury 1985) because it reduces the effect of extreme values, such as extended pauses between bouts of struts, which were of interest in this study. Additionally, we were not able to correct strut rates based on the proximity of the nearest female (Wiley 1973, Gibson et al. 1991, Patricelli and Krakauer 2010) due to high sagebrush cover obscuring hens on the leks in Idaho.

Results

Vocalization characteristics did not differ depending on the person that fitted the collar (ANOVA: primary whistle maximum frequency $F_{2,3} = 0.572$, $p = 0.616$; primary whistle minimum frequency $F_{2,3} = 3.11$, $p = 0.185$; primary whistle duration $F_{2,3} = 0.451$, $p = 0.674$; secondary coo duration $F_{2,2} = 0.984$, $p = 0.504$), but sample sizes for each trapper were low and may therefore prevent adequate testing of this effect.

When comparing vocalizations from all recorded birds in both states, the only acoustic measurement to differ between collared and non-collared birds was the maximum frequency of the primary whistle ($t = 6.596$, $df = 8.687$, $p < 0.001$), with collared males having a lower maximum frequency than non-collared males. For other acoustic characteristics, comparisons between collared and non-collared birds in both Idaho and Nevada were non-significant ($p > 0.05$; Table 1). There was no significant difference between the collared and non-collared birds in the estimated distance between the bird and the microphone during recording ($t = –0.667$ $df = 18$, $p = 0.513$), which suggested that differences in vocal features between the groups was not an artifact of differential transmission of the sounds.

Maximum frequency of the primary whistle was also the only characteristic that differed between collared and non-collared males from the Nevada population alone ($t = 9.987$, $df = 3.926$, $p < 0.001$; Table 1). For other acoustic characteristics, comparisons were non-significant ($p > 0.05$), though the sample size for these comparisons is low (two collared and four non-collared males) because few collared males attended leks in the Nevada study area (Gibson et al. 2013). There was no significant difference between the collared and non-collared birds in the estimated distance between the bird and the microphone during recording ($t = –1.309$, $df = 4$, $p = 0.261$).

When comparing vocalizations from birds from Idaho only, four characteristics of vocalizations differed between males with and without radio-collars (Fig. 4, Table 1). Whistles in non-collared males had a higher maximum frequency ($t = 4.854$, $df = 12$, $p = 0.003$), a lower minimum frequency ($t = –2.539$, $df = 12$, $p = 0.031$), and a longer duration ($t = 2.288$, $df = 12$, $p = 0.042$) than whistles in collared males. Non-collared males also had longer second coos than collared males ($t = 3.004$, $df = 11$, $p = 0.019$). We were not able to measure second coos on all spectrograms, therefore resulting in a smaller sample size for this vocalization characteristic. For other acoustic characteristics, comparisons were non-significant ($p > 0.05$). There was no significant difference between the collared and non-collared birds in Idaho in the estimated distance between the bird and the microphone during recording ($t = –0.249$, $df = 12$, $p = 0.808$).

The strut rate (inverse of mean inter-strut-interval) of displaying males from Idaho did not differ between collared and non-collared males ($t = 0.999$, $df = 10$, $p = 0.341$).

Discussion

Previous studies have found that the strut rate and acoustic quality of the strut display is critical in determining which males are chosen by females as mates (Wiley 1973, Gibson and Bradbury 1985, Gibson et al. 1991, Gibson 1996, Patricelli and Krakauer 2010). The inter-pop interval (IPI, the time delay between the pop notes during which the whistle note occurs) is the most consistent acoustic correlate of male mating success in studies of sage-grouse from the California Mono Lake Basin population, with females preferring males that produce an IPI with a longer duration (Gibson and Bradbury 1985, Gibson et al. 1991, Gibson 1996). These previous studies also suggested that the amplitude of the whistle may be positively correlated with the

Table 1. Univariate tests (two-sample t-tests), mean ± SEM, and sample sizes for vocalization and display characteristics of male greater sage-grouse *Centrocercus urophasianus* with and without radio-collars for vocalization characteristics of birds from the Idaho and Nevada populations ('both'), Nevada only ('Nevada'), or Idaho only ('Idaho'), spring 2012 and 2013. Inter-pop interval also designated as 'IPI'. Some characteristics could not be measured on all spectrograms, so some sample sizes are lower than the number of recorded birds, and characteristics that could not be measured for enough birds to compare are denoted with a "---". Significant results are in bold.

Vocal or display characteristic	Population	n collared males	Mean (SEM) for collared males	n non-collared males	Mean (SEM) for non-collared males	t	p
IPI (s)	both	7	0.189 (0.002)	12	0.186 (0.001)	–1.234	0.241
	Nevada	2	0.186 (0.007)	4	0.184 (0.004)	–0.257	0.823
	Idaho	5	0.191 (0.002)	7	0.188 (0.003)	–1.700	0.134
Maximum frequency of primary whistle (Hz)	both	8	2162.4 (65.4)	12	2618.4 (22.5)	6.596	**<0.001**
	Nevada	2	2158.3 (25.5)	4	2616.2 (38.1)	9.987	**<0.001**
	Idaho	6	2163.7 (89.0)	7	2605.2 (30.2)	4.854	**0.003**
Minimum frequency of primary whistle (Hz)	both	8	1049.7 (78.9)	12	909.5 (85.9)	–1.202	0.254
	Nevada	2	1124.1 (313.4)	4	1099.3 (229.2)	–0.063	0.955
	Idaho	6	1024.9 (67.7)	7	810.4 (54.8)	–2.539	**0.031**
Duration of primary whistle (s)	both	8	0.108 (0.006)	12	0.124 (0.007)	1.736	0.099
	Nevada	2	0.116 (0.024)	4	0.121 (0.018)	0.196	0.860
	Idaho	6	0.105 (0.005)	7	0.125 (0.008)	2.288	**0.042**
Maximum frequency of secondary whistle (Hz)	both	2	1823.8 (51.2)	8	1935.6 (42.2)	1.684	0.203
	Nevada	1	1772.9	1	1968.8	---	---
	Idaho	1	1875.0	6	1932.3 (57.3)	---	---
Minimum frequency of secondary whistle (Hz)	both	1	1031.2	2	890.7 (46.8)	---	---
	Nevada	0	---	0	---	---	---
	Idaho	1	1031.2	2	890.7 (46.8)	---	---
Duration of secondary whistle (s)	both	2	0.106 (0.025)	8	0.089 (0.006)	1.684	0.203
	Nevada	1	0.081	1	0.080	---	---
	Idaho	1	0.132	6	0.092 (0.008)	---	---
Maximum frequency of second coo (Hz)	both	6	490.2 (26.8)	12	541.5 (9.2)	1.811	0.118
	Nevada	1	468.8	4	521.5 (24.1)	---	---
	Idaho	5	494.5 (32.4)	7	550.0 (6.24)	1.735	0.154
Duration of second coo (Hz)	both	6	0.061 (0.004)	12	0.073 (0.004)	1.912	0.0768
	Nevada	1	0.068	4	0.064 (0.011)	---	---
	Idaho	5	0.0598 (0.004)	7	0.078 (0.003)	3.004	**0.019**
Ratio of duration of primary whistle to IPI	both	7	0.612 (0.033)	12	0.689 (0.040)	1.482	0.157
	Nevada	2	0.642 (0.128)	4	0.660 (0.085)	0.116	0.919
	Idaho	5	0.599 (0.023)	7	0.704 (0.053)	2.006	0.073
Ratio of duration of secondary whistle to IPI	both	2	0.559 (0.136)	7	0.477 (0.041)	0.579	0.653
	Nevada	1	0.422	1	0.427	---	---
	Idaho	1	0.696	5	0.498 (0.056)	---	---
Strut rate	both	NA	NA	NA	NA	NA	NA
	Nevada	0	---	0	---	---	---
	Idaho	6	0.068 (0.008)	6	0.079 (0.008)	0.999	0.341

IPI and that the amplitude of the whistle may be more important for mating success than IPI per se (Gibson and Bradbury 1985, Gibson 1996, Dantzker et al. 1999). We did not find a difference in IPI between collared and non-collared males in the Idaho or Nevada populations, suggesting that collars may not influence at least one major acoustic predictor of mating success. However, several characteristics of the primary whistle did differ between collared and non-collared males. Collared males in Idaho produced primary whistles with a narrower bandwidth and produced shorter whistles than non-collared males, which may be due to a lower whistle amplitude (i.e. the end of the whistle drops below detectible amplitude sooner, thus appearing shorter). Similarly, the shorter duration of the coo notes in collared males from Idaho may be due to a lower amplitude of these notes. Further studies of vocalizations using recordings calibrated for amplitude are needed to test this possibility.

Previous studies on sage-grouse also found positive correlations between male mating success and the maximum frequency of the primary whistle as well as the difference between the maximum and minimum frequency of the primary whistle (i.e. the whistle bandwidth) in some, but not all, years and leks (Gibson and Bradbury 1985, Gibson et al. 1991, Gibson 1996). In our study, collared males produced primary whistles with a lower maximum frequency and a narrower bandwidth than non-collared males (Fig. 4). If these display characteristics are important to females in either the Nevada or Idaho population, then collared males may be less attractive to females and therefore less likely to reproduce. The average maximum primary whistle frequency among collared males in Idaho was 2163 Hz compared to 2605 Hz in non-collared males. Among the six collared males in Idaho, one male produced a primary whistle with a maximum primary whistle frequency within the range produced by non-collared males (2545 Hz), but the other five males produced primary whistles with maximum frequencies more than 200 Hz below the range found in the non-collared males (the range of these five collared males was 1967–2279 Hz and the range of all seven non-collared males we measured in Idaho was 2507–2756 Hz). Similarly,

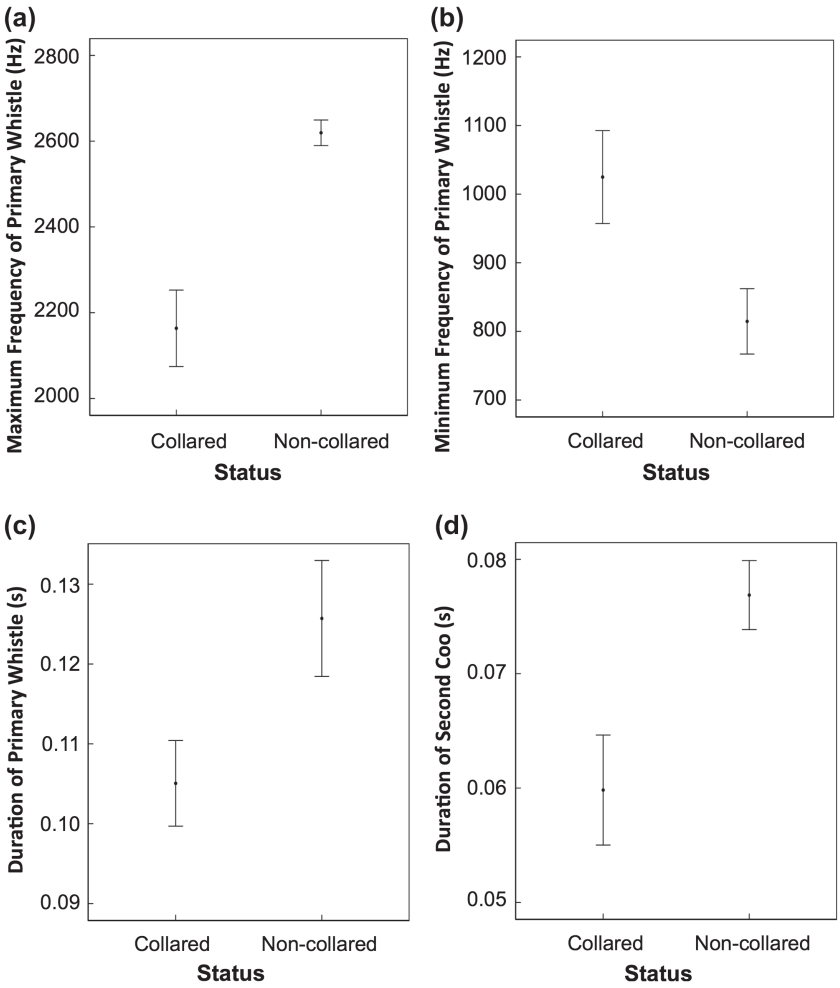

Figure 4. Significant differences in vocal characteristics between collared and non-collared male greater sage-grouse *Centrocercus urophasianus* in Idaho during spring 2014 included (a) maximum frequency of primary whistle (Hz), (b) minimum frequency of primary whistle (Hz), (c) whistle duration (s), and (d) duration of second coo (s). All graphs show mean ± SEM comparing the average value for each vocalization characteristic for six collared and seven non-collared birds (except (d), where there were five collared and seven non-collared because the secondary coo was not visible for one collared male).

the two collared males in Nevada produced primary whistles with maximum frequencies of 2132–2183 Hz, which were about 400 Hz lower than the four non-collared males (ranging from 2542–2718 Hz). The maximum frequencies of primary whistles produced by collared males were highly unusual not only for these Idaho and Nevada populations, but also compared to populations throughout the range of the sage-grouse. Four of the six collared males from Idaho produced maximum primary whistle frequencies that fell below the range of calls from non-collared males (n = 350 birds) measured across seven populations of sage-grouse (range = 2053–2837 Hz, mean = 2413 Hz; Krakauer et al. 2009). Interestingly, the two males that produced vocalizations within the range of non-collared sage-grouse measured by Krakauer et al. (2009) were collared by the same trapper, suggesting that techniques employed by individual trappers may influence the severity of impacts on individual birds. Because the present study had a small sample size, the average maximum primary whistle frequency found here may not accurately represent the vocalizations of a larger sample of collared males. However, this study suggests that collaring can have a large effect on vocalizations of some males, causing their fitness-relevant acoustic signals to be outside the normal range of variation in this species and outside of the range of non-collared males within the same population.

Our results suggest that collared males may have difficulty producing normal breeding vocalizations. Displaying males inflate their esophageal air sac by exhaling air from their lungs and directing it into their esophagus (Clarke et al. 1942). The strut display is produced by the rapid distension and contraction of the inflated esophagus behind a pair of pliable apterygia on the breast (i.e. the vocal sacs). This produces a visual display and increases the amplitude of the acoustic signal by resonating sound energy and coupling the sounds to the surrounding air (Dantzker et al. 1999, Krakauer et al. 2009). We propose that collars that encircle the esophagus may interfere with inflation or movement of the vocal sac during display. This interference may increase the costs of an already costly behavior (Vehrencamp et al. 1989), and potentially decrease male reproductive success by decreasing the effectiveness of these vocalizations for attracting females and competing with other males for

breeding territories. Several species of grouse have esophageal air sacs used in their display, including both greater and Gunnison sage-grouse *Centrocercus minimus*, greater prairie-chicken *Tympanuchus cupido*, lesser prairie-chicken *T. pallidicinctus*, sharp-tailed grouse *T. phasianellus*, dusky grouse *Dendragapus obscurus*, sooty grouse *D. fuliginosus*, Caucasian grouse *Lyrurus mlokosiewiczi* and black grouse *Lyrurus tetrix*. These species may experience similar difficulty producing normal display vocalizations when collared, although the body position during display for some species (*Tympanuchus* and *Dendrogapus*) may allow the transmitter to hang below the air sacs and could reduce interference with the display. Further research is required to determine the extent of collar impacts on species with less prominent esophageal air sacs or different postures during displays.

Male mating success is also strongly correlated with the rate of strut displays by males and with male lek attendance (Wiley 1973, Gibson and Bradbury 1985, Gibson et al. 1991, Gibson 1996, Patricelli and Krakauer 2010). Strut rate did not differ between collared (mean ± standard deviation: 0.068 ± 0.019 1 s^{-1}) and non-collared males (0.079 ± 0.02 1 s^{-1}), suggesting that collared males capable of holding territories are not decreasing their strut effort on the lek. We did not compare lek attendance between collared and non-collared males in the Idaho population used in this study. However, the two collared and four non-collared males from Nevada leks were monitored as part of a larger study addressing radio-collar effects on male sage-grouse (Gibson et al. 2013). That study found a 3–5 fold decrease in detection of collared males on leks compared to non-collared males, indicating a dramatic decrease in lek attendance related to collaring. In the Idaho population, six of the 19 (31.6%) collared males were observed strutting on leks, suggesting that the impact of collars on attendance may have been less for this population, as some males may have been displaying on leks not visited by observers, some males (n = 3, 15.8%) were present on leks but too far from the observer to record, and two (10.5%) died within the year between collaring and observation. However, the lek attendance rates for collared birds in Idaho were not compared to those of non-collared birds. This limitation is also true for previous studies on male sage-grouse and sharp-tail grouse where collared males have been observed on leks (Baumgardt 2011, Drummer et al. 2011). These previous studies also did not identify whether males at leks were actively displaying or only present but not displaying. The distinction between attending and displaying is important, but it is costly and difficult to measure differences in attendance and behaviors between collared and non-collared birds effectively, as it requires intensive monitoring efforts to compare birds marked with color bands only versus those birds with radio-transmitters or among birds outfitted with alternative harness designs. In the later case, it would be ideal to use identical transmitters – we note that the transmitters used in Nevada were 30% heavier than those used in Idaho, although still well under the recommended guidelines of 4% body weight (Theuerkauf et al. 2007) for a >2 kg adult male greater sage-grouse.

The decrease in lek attendance by some sage-grouse observed by Gibson et al. (2013) also highlights the difficulty of recording vocalizations on a large sample of collared males for a study such as this. Given this decrease in attendance, it is also important to consider that the males who we were able to record for this study may have been among those suffering less of an impact from collaring, which may lead us to under estimate the impacts of collars on vocalizations and strut rate. Additionally, it is possible that birds learned to compensate for or adjust to their collar for the year between fitting and recording, and that impacts may be more acute immediately after collars were fitted. In some cases, the effects of transmitters on demographics (e.g. mortality) or behavior are more pronounced within several weeks of fitting, but effects decrease over time (Perry et al. 1981, Suedkamp Wells et al 2003, Woolnough et al. 2004, Casas et al. 2015). Therefore, our results are specific to long-term collar impacts, and immediate impacts of collars on vocalization characteristics may be more severe. It is possible that differences in transmitter weight, or harsher environmental conditions (making it more difficult for males to compensate for the weight of the collar in their energy budgets), contributed to the lower observed lek attendance by collared males in Nevada.

Taken together with previous studies showing a dramatic decrease in lek attendance by collared males (Gibson et al. 2013), these results suggest necklace collars may negatively impact males' fitness by reducing male lek attendance and, for males that do attend leks, impacting the quality of their vocalizations. Therefore, the use of collars is not recommended for behavioral studies of male sage-grouse, including lekking behavior, reproduction, and attendance. Future studies should evaluate alternative transmitter-attachment methods (e.g. rump mounted transmitters, backpack-style transmitters) for impacts on lekking behavior. In studies where it is critical to track male behavior, we recommend the use of other attachment methods to mitigate potentially negative impacts.

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