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RESEARCH ARTICLE

Displaying to females may lower male foraging time and vigilance in a lekking bird

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ABSTRACT

Males of many species use courtship behavior to attract mates. However, by doing so males may face the associated costs of increased energetic expenditure, reduced foraging time, and elevated predation risk. We investigated the costs of display in lekking male Sharp-tailed Grouse (*Tympanuchus phasianellus*). We used lek-wide scan sampling to study how males allocated time among courtship display ("dancing"), agonism, foraging, and inactivity in relation to female numbers both within and across days. We also addressed the limited attention hypothesis and estimated visual attentiveness by videotaping 13 males and scoring head turns during these different activities. We found that the proportion of males engaged in display increased significantly with female numbers both within and across days. Additionally, foraging decreased with increasing female numbers both within and across days. Our results also suggested that agonism increased on days of high female attendance after females had left the lek. Males turned their heads only half as frequently during display as during other activities. These correlative data suggest two mechanisms by which display costs are potentially incurred: 1) a reduction in on-lek foraging time, and 2) reduced visual attention to the surroundings. It is possible that reduced foraging time and reduced vigilance during display may also be costs of increased courtship display in other nonlekking species.

Keywords: lek, courtship display, foraging, visual attention, Sharp-tailed Grouse

Los despliegues de cortejo frente a las hembras pueden disminuir el tiempo de forrajeo y de vigilancia de los machos en un ave que forma asambleas de cortejo

RESUMEN

Los machos de muchas especies muestran comportamientos de cortejo para atraer a sus parejas. Sin embargo, al hacer esto, los machos pueden enfrentar los costos asociados a un aumento del gasto energético, reducción del tiempo de forrajeo y aumento del riesgo de depredación. Investigamos los costos de las asambleas de cortejo de los machos de *Tympanuchus phasianellus*. Realizamos observaciones de las asambleas de cortejo para estudiar como los machos asignan su tiempo entre los despliegues de cortejo ("baile"), comportamientos agonísticos, forrajeo e inactividad en relación al número de hembras presentes tanto en un mismo día como entre días. También evaluamos la hipótesis de atención limitada y estimamos la atención visual mediante la grabación de videos de 13 machos y contabilizamos las vueltas de cabeza durante estas diferentes actividades. Encontramos que la proporción de machos comprometidos en los despliegues aumentó significativamente con el número de hembras presentes tanto en un mismo día como entre días. Adicionalmente, el forrajeo disminuyó con un aumento en el número de hembras presentes tanto en un mismo día como entre días. Nuestros resultados también sugieren que los despliegues agonísticos aumentan en los días de alta presencia de hembras luego de que las hembras han dejado la asamblea de cortejo. Durante el despliegue, los machos giraron sus cabezas la mitad de veces que durante otras actividades. Estos datos correlativos sugieren dos mecanismos por los cuales potencialmente se incurre en costos de despliegue: 1) una reducción en el tiempo de forrajeo en la asamblea de cortejo, y 2) una reducción en la atención visual de los alrededores. Es posible que una reducción en el tiempo de forrajeo y una menor vigilancia durante el despliegue puedan también ser costos de una mayor exhibición de cortejo en otras especies que no forman asambleas de cortejo.

Palabras clave: asamblea de cortejo, atención visual, despliegue de cortejo, forrajeo, *Tympanuchus phasianellus*

INTRODUCTION

Courting males face tradeoffs between the benefit of attracting mates and the associated costs of display. Male courtship behavior is constrained by a wide variety of costs, which can include increased energy expenditure from physiologically demanding displays, reduced time allotted to foraging, and increased predation risk (reviewed in Magnhagen 1991, M. Andersson 1994). However, in lekking bird species the proximate mechanisms by which these costs arise are still not well understood.

In avian lek-mating systems, males contribute no parental care and therefore primarily incur the reproductive costs of courtship display that are associated with competing for and attracting mates (Wiley 1974, Emlen and Oring 1977, Höglund and Alatalo 1995). Males compete through differential lek attendance (endurance rivalry), aggressive interactions that determine territory ownership, and variation in display effort that influences female mate choice (Gibson and Bradbury 1985, Höglund and Lundberg 1987, McDonald 1989, Pruett-Jones and Pruett-Jones 1990, Alatalo et al. 1991, Gibson et al. 1991, Gratson 1993, Fiske et al. 1998, Rintamäki et al. 2001, Alonso et al. 2010). In addition, females assess males based upon variation in traits that remain relatively stable over the breeding season, including differences in acoustic display quality (Gibson et al. 1991), the size and color of sexual ornaments (Alatalo et al. 1996, Stein and Uy 2006, Siitari et al. 2007, Dakin and Montgomerie 2011, 2013), and territorial characteristics (Gibson et al. 1991, Gratson et al. 1991, Hovi et al. 1994, Kokko et al. 1999).

Several studies indicate that lekking male birds lose mass throughout the breeding season and are therefore not in energy balance (Beck and Braun 1978, Höglund et al. 1992, S. Andersson 1994, Lebigre et al. 2013). It is uncertain whether this loss is due to increased energy expenditure (see Vehrencamp et al. 1989, Höglund et al. 1992), a reduction in food intake, or a combination of the two. If food intake decreases, it could be attributed to a reduction in available foraging time off the lek (due to increased time spent on the lek). Additionally, in species that forage on-lek as well as off-lek, male foraging time might further be reduced by participation in display or male competition while on the lek.

Lekking birds may also face increased predation risk while on vs. off the lek (e.g., Hartzler 1974, Trail 1987, Gibson and Bachman 1992). Males may reduce time on the lek in response to increased predation risk (Käläs et al. 1995, Boyko et al. 2004), choose lek sites that reduce visibility to aerial predators (Aspbury and Gibson 2004), and form mixed-species leks to reduce individual predation risk (Gibson et al. 2002). Collectively, these observations implicate predation as an additional cost of lek display. However, the mechanisms by which lek display increases exposure to predators are not well studied. Several possible processes could be involved: 1) displaying males could be more conspicuous to predators, 2) males could have increased exposure to predation risk due to increased time on the lek when females visit, and 3) males could pay decreased visual attention to their surroundings during courtship, as suggested by the limited attention hypothesis (Dukas and Kamil 2000a, 2000b). The limited attention hypothesis posits that animals have limited cognitive attention, and that therefore when engaged in demanding visual tasks individuals are less likely to notice peripheral targets such as an approaching predator (Dukas and Kamil 2000a, 2000b, Dukas 2002, 2004, 2009, Kaby and Lind 2003, Fernández-Juricic et al. 2004).

Evaluating changes in male behavior on the lek when females are present could help to identify some of the cost-incurring mechanisms mentioned previously. When females are present, males shift their behavior toward courtship display (Wiley 1973, Höglund and Lundberg 1987, McDonald 1989, Pruett-Jones and Pruett-Jones 1990, Gratson 1993, Rintamäki et al. 2001, Nooker and Sandercock 2008), and may stay longer on the lek (e.g., Boyko et al. 2004). Examining compensatory shifts in other behaviors (such as foraging) could reveal temporal tradeoffs by which the costs of display arise.

In addition, if male activities change with female presence, and if visual attention levels change during different activities, then overall visual attention levels could vary with female presence. Although visual attention during different behaviors is difficult to measure in a nonlaboratory setting, a possible way to evaluate the limited attention hypothesis in the field would be to use head movements as a proxy measure of visual attention (Fernández-Juricic 2012), as birds rotate their heads either to track objects detected in the peripheral visual field on foveal areas of high receptor density or to scan their surroundings (Andrew and Dharmaretnam 1993, Land 1999, Dawkins 2002, Jones et al. 2007, Gall and Fernández-Juricic 2010).

We were interested in addressing the costs of display both through tradeoffs with other behavioral activities and by evaluating the limited attention hypothesis using Sharp-tailed Grouse (*Tympanuchus phasianellus*) males. Sharp-tailed Grouse are lekking galliforms found throughout prairie grassland, steppe, and mixed-shrub habitats in the central and northern regions of North America (Connelly et al. 1998). On the lek, Sharp-tailed Grouse males are vulnerable to both aerial (raptor) and ground (coyote) predators (S. A. Cowles personal observation), which birds detect visually (e.g., Evans et al. 1993). Lek size averages 9–10 males (Gibson et al. 2002). Males defend territories, and most territorial males are faithful to a single lek site for the spring breeding season (Kermott 1982). The spring (northern hemisphere) lekking season lasts from late

FIGURE 1. Sharp-tailed Grouse male in display posture. Photo credit: Robert M. Gibson

March to mid-May (Kermott 1982, Landel 1989). Each day, males arrive ~45 min before sunrise and stay on the lek up to 3 hr after sunrise (Kermott 1982), which is the morning lekking period. Throughout this period, male Sharp-tailed Grouse transition among various activities, including fighting with other males, sitting or standing, and courtship display "dancing." Dancing includes an active dance phase with both visual (rapid movement of tail retrices and exposure of white undertail covert feathers) and acoustic (vocalization and tail clicking) components, followed by an inactive pause phase in which the bird holds the display posture but remains still (Figure 1). In contrast with many lekking species in which males do not obtain any benefit other than matings on the lek, Sharp-tailed Grouse allocate some time to foraging on forbs while on the lek arena (Gibson et al. 2002, S. A. Cowles personal observation). The average mass of Sharp-tailed Grouse males declines throughout the spring breeding season (R. M. Gibson personal observation), which suggests that Sharp-tailed Grouse males are in negative energy balance during this time.

In this study, we investigated how male Sharp-tailed Grouse allocated time to display and other behavioral activities on the lek with changing female numbers both within and across days using time budget analysis. We predicted that as female numbers increased both within each day and across the lekking season, males would allocate more time to displaying at the expense of other lek-based activities. In addition, using head movements as a proxy measure of visual attentiveness, we explored the limited attention hypothesis in the field to see whether Sharp-tailed Grouse males were potentially distracted during display. We predicted that male Sharp-tailed Grouse would turn their heads less during courtship display than during other activities performed on the lek.

METHODS

Study Site

We studied male Sharp-tailed Grouse lek behavior on and adjacent to the Valentine National Wildlife Refuge, in the Sandhills region of north-central Nebraska, USA. The 72,000-acre refuge and surrounding area consists of alternating sand dune ridges and valleys covered by a mixture of prairie grassland and wetland habitats. We observed two different Sharp-tailed Grouse lek sites: the Nelson lek for 29 days between April 5, 2011, and May 5, 2011, and the West Twin Lake lek for 23 days between April 10, 2012, and May 5, 2012, as the Nelson lek had only four males in 2012. All observations were made from first light to the end of the morning lekking period, up to 3 hr after sunrise, from an observation blind placed on the edge of the lek. We entered the blind in darkness before the birds arrived and stayed until they departed.

In each year, males were captured with walk-in funnel traps (Schroeder and Braun 1991) and were given a unique combination of three color bands and one metal band. In addition, to aid individual identification during courtship display, we marked each captured bird's white under-tail covert feathers with a unique black pattern using a permanent marker. Seven of 9 males captured in 2011 and 4 of 6 males captured in 2012 attended the study leks on a daily basis. During periods of data collection, maximum male daily counts were (mean ± SE) 8.72 ± 0.18 on the Nelson lek and 15.09 ± 0.61 on the West Twin Lake lek.

Daily and Seasonal Activity Budgets

To determine how male activity allocation varied with changes in female lek attendance and to test the prediction that males would increase display at the expense of other activities with increased female numbers, we conducted lek-wide scan samples on 20 days at the Nelson lek in 2011. Sampling started as soon as all males were clearly visible and continued until the last male left the lek. However, for analyses we focused on a standard period from 10 min before to 2 hr after sunrise for which complete data were available on all 20 sample days. We recorded the total number of males and females present on the lek and the activity of each male present on the lek at 10-min intervals, and later classified male activities into five separate categories: courtship display, foraging, agonistic behavior or agonism (fighting and faceoffs—a form of agonistic behavior in which males sit and face each other, also called confronted crouching; Hjorth 1970), inactivity (sitting and standing), and "other" behaviors (preening, walking, and running). For each 10-min interval, we then calculated the proportion of males in each behavioral category, which allowed us to assess changes in lek-wide activity over time. The category of courtship display broadly consisted of males in dancing and pause phases, doing flutter jumps, and cooing (display vocalizations); however, courtship display mainly consisted of males in dancing and pause phases, as there was a high positive correlation between the proportion of males in the broad category of courtship display (mean ± $\mathrm{SE} = 0.16 \pm 0.01$) and the proportion of males only in dancing and pause phases (mean ± $\mathrm{SE} = 0.12 \pm 0.01$; Pearson correlation: $r = 0.93$, $n = 280$, $P < 0.001$).

Head Turning Rates

To examine differences in head turning rates among different behavioral categories in order to test the prediction that Sharp-tailed Grouse males are less visually attentive during courtship display, videos of focal Sharp-tailed Grouse males in each of the four most common behaviors—courtship display (dancing and pause phases only), foraging, faceoffs (a form of agonistic behavior), and inactivity (sitting and standing)—were collected opportunistically throughout the morning lekking period. We videotaped seven color-banded males at the Nelson lek in 2011 and six males at the West Twin Lake lek in 2012. Two of the six males recorded in 2012 were unbanded, but they were stable territory holders and were bordered by banded territory neighbors. We videotaped males at 30 frames sec^{-1} in AVCHD format using a Panasonic Lumix DMC-GH2 camera and a 100–300 mm Panasonic zoom lens (Panasonic Corporation, Kadoma, Osaka, Japan).

Video was collated by activity using the video software program Adobe Premiere Elements 9 (Adobe Systems, San Jose, California, USA). The mean video times recorded for the seven males in 2011 were (reported as mean ± SE): display, 2.2 ± 0.4 min; foraging, 4.2 ± 0.7 min; agonism, 8.0 ± 1.5 min; and inactivity, 7.3 ±1.2 min. In 2012, the mean video times for the six males were: display, 3.0 ± 0.3 min; foraging, 3.7 ± 0.5 min; agonism, 6.0 ± 0.6 min; and inactivity, 5.5 ± 0.8 min. S. A. Cowles scored head turns for males in each behavioral category. Only right–left rotational head turns in the horizontal plane were scored. These turns were discarded if the head rotation was followed by a body turn (i.e. birds were turning their heads when changing direction). This method also discounted the normal forward head-bobbing motion of walking birds (compensatory head movements; Dunlap and Mowrer 1930), but included rotations in the vertical plane (i.e. looking at the sky) that always involved a rotational component in the horizontal plane. We also discarded any up-and-down head movements during foraging, as these were assumed to be associated with food-searching. This makes our estimate of head turns during foraging a conservative estimate of visual attention. In preliminary analyses, we found no difference in head turning rates between the dancing and pause phases of courtship display (paired t-test: $t_{12} = 1.13$, $P = 0.28$) and therefore combined dancing and pause phases when calculating the head turning rate for display.

Data Analyses

We analyzed the relationship between female numbers and male activity allocation at two temporal scales. First, we examined variation between scans within days from 10 min before to 2 hr after sunrise using repeated measures models (SAS Proc mixed, version 8.0; SAS Institute, Cary, North Carolina, USA). In these models, we used Julian day as the repeated measure and the number of females present on the lek and time of day as explanatory variables to investigate relationships with the proportion of males in display, foraging, agonism, and inactivity on a daily time scale. Analyses using female numbers omit five days with no females. Because numbers and identities of males on the lek remained relatively stable over the sampling period, female- and time-related variation in male activities is unlikely to be due to changes in lek composition.

We also analyzed covariation between female numbers and male time allocation across days. We first averaged the proportion of males in each behavioral category across 10-min intervals within days to give a single proportion per day for each behavioral category. We then used generalized linear models (GLMs) in R version 2.11.1 (R Development Core Team 2010) to examine relationships between the maximum female daily count and the proportion of males in display, foraging, agonistic behavior, and inactivity on a seasonal time scale. In addition, we also examined models with both the maximum female count and date as explanatory variables to examine seasonal changes in behavior. The fluctuation in daily mean number of males per scan (mean male number) did not change with day in season (mean ± $\mathrm{SE} = 0.02 \pm 0.02$, $t_{18} = 0.84$, $P = 0.41$). We also included daily mean male number as a covariate with female numbers in the models to check that variation in male numbers across days did not confound the patterns already identified with female numbers.

Further analysis suggested that the discrepancy between the effects of female numbers on male agonism within and across days was explained by variation in the temporal distribution of male activity throughout the morning. A reduction in agonism when females were on the lek (within days), but no reduction on days when more females attended, suggested that in the latter context agonism might have increased later in the morning after females had left. To investigate this possibility, we split days into "low" (0–1 females, 9 days) and "high" (2–7 females, 12 days) female attendance categories and tested for an interaction between time of day and attendance category. To test for this interaction, we used a linear mixed effects model (LME) in the lme4 package in R version 2.11.1 (R

TABLE 1. Repeated measures analyses of the effects of female numbers and time (minutes after sunrise) on the proportions of male Sharp-tailed Grouse engaged in each of four behavioral categories within days. Panel A (upper) shows bivariate relationships, and Panel B (lower) shows partial effects in models including both female numbers and time. Analyses using female numbers omit five days with no females.

	Females			Time		
Behavior	Slope (SE)	t (df = 14)	P	Slope (SE)	t (df = 19)	P
Panel A						
Display	0.163 (0.032)	5.01	<0.001	−0.003 (0.000)	−8.47	<0.001
Foraging	−0.052 (0.012)	−4.21	<0.001	0.002 (0.001)	4.38	<0.001
Agonism	−0.068 (0.018)	−3.74	<0.01	0.001 (0.001)	2.41	0.03
Inactivity	0.013 (0.023)	0.56	0.58	−0.001 (0.000)	−1.48	0.16
Panel B						
Display	0.128 (0.030)	4.19	<0.001	−0.002 (0.000)	−6.48	<0.001
Foraging	−0.031 (0.010)	−3.02	<0.01	0.002 (0.001)	3.73	0.001
Agonism	−0.050 (0.016)	−3.14	<0.01	0.001 (0.001)	1.52	0.14

Development Core Team 2010) to examine changes in agonistic behavior, with date as a random effect and three fixed effects: time of day, female attendance category, and the interaction between time of day and female attendance category. Additionally, to obtain separate estimates of changes in agonistic behavior throughout the morning for the high and low female attendance categories, we used two LME models (one for high female attendance days and one for low female attendance days) with date as a random effect and time of day as a fixed effect.

To analyze differences in head turning rates, we used random effect generalized linear mixed models (GLMMs) in the nlme package in R version 2.11.1 (R Development Core Team 2010). All values reported in the Results are means ± SE.

RESULTS

The Effect of Females on Male Activity

Across days, the total time that males spent on the lek during the morning lekking period (186.6 ± 5.8 min) did not increase significantly with maximum female numbers (1.2 ± 2.8, $t_{21} = 0.44$, $P = 0.66$). Subsequent analyses therefore focused on male time allocation.

Within the morning display period, the mean proportions of males engaged in the four main activities were: display, 0.165 ± 0.016; foraging, 0.173 ± 0.026; agonism, 0.336 ± 0.025; and inactivity, 0.290 ± 0.020. The proportion of males engaged in display, foraging, and agonism, but not inactivity, varied with numbers of females on the lek (Table 1). Male display significantly increased with female numbers, whereas both agonism and foraging decreased (Table 1). However, the proportion of males displaying also declined throughout the morning, whereas agonism and foraging increased, coincident with decreasing female numbers (Figure 2, Table 1). To separate the effects of female numbers and time of day on male activity, we ran GLMs with both time and female numbers as predictors of each activity. After controlling for time of day, display increased with female numbers while agonism and foraging decreased with female numbers as before (Table 1). Additionally, after controlling for female numbers, display decreased whereas foraging increased with time of day.

Across days, the mean proportion of males engaged in display increased significantly with increasing female numbers (all model estimates reported as slope ± SE: 0.022 ± 0.006, $t_{18} = 3.57$, $P = 0.002$), whereas the proportion of males engaged in foraging behavior significantly decreased (–0.027 ± 0.011, $t_{18} = -2.44$, $P = 0.03$) and the proportion of males engaged in inactivity showed a nonsignificant negative relationship (–0.011 ± 0.010, $t_{18} = -1.13$, $P = 0.27$) with female numbers. Unlike the within-day pattern, however, across days the proportion of males engaged in agonism did not decrease with increasing female numbers (0.019 ± 0.011, $t_{18} = 1.68$, $P = 0.11$; Figure 3). With date added to the models, the proportion of males engaged in display showed a nonsignificant negative trend with date (–0.003 ± 0.001, $t_{17} = -1.84$, $P = 0.08$), the proportion of males engaged in foraging significantly decreased with date (–0.007 ± 0.002, $t_{17} = -3.20$, $P = 0.005$), and the proportion of inactive males did not change with date (0.003 ± 0.002, $t_{17} = 1.52$, $P = 0.15$). In these three previous models, the patterns with female numbers did not change. However, with date in the model, the proportion of males in agonism increased significantly with female numbers (0.022 ± 0.009, $t_{17} = 2.42$, $P = 0.03$) and increased significantly throughout the season with date (0.007 ± 0.002, $t_{17} = 3.35$, $P = 0.004$).

There was a significant interaction between the effects of female attendance category (high and low) and time of day on the proportion of males engaged in agonism (0.0021 ± 0.0007, $t_{252} = 3.10$, $P = 0.002$). In the two separate high and low female attendance LME models, agonistic behavior increased throughout the morning on

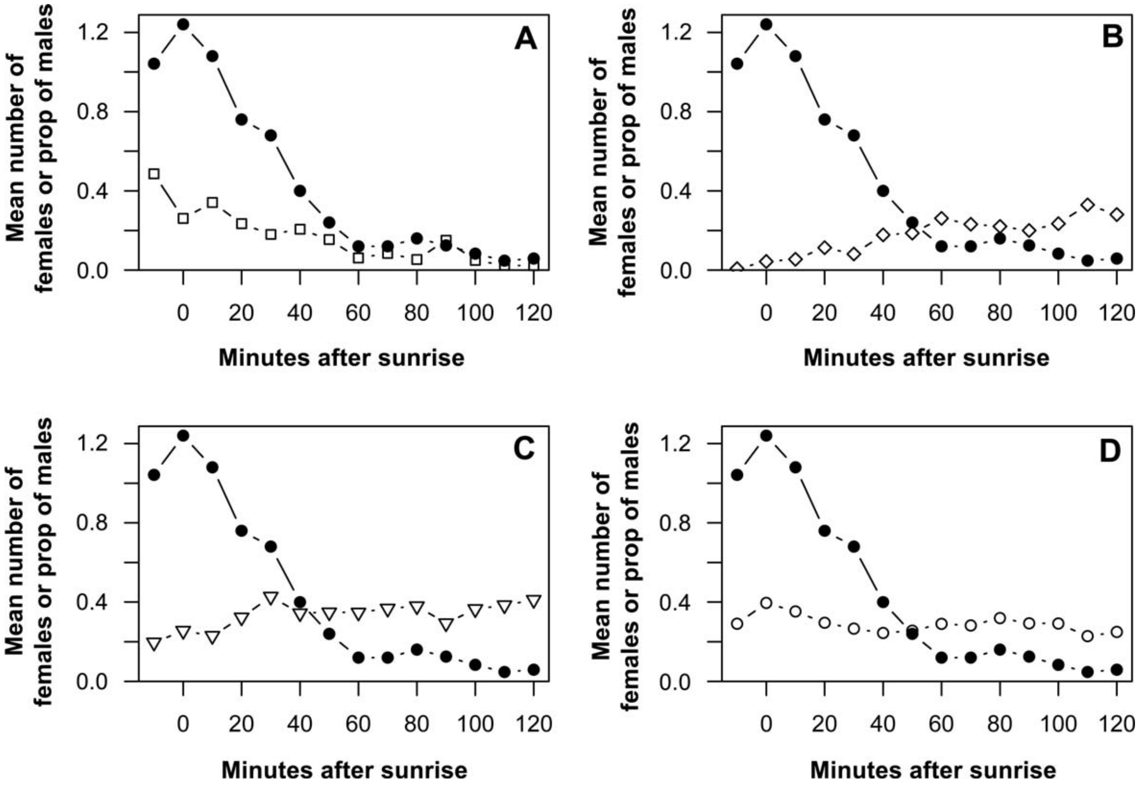

FIGURE 2. Within-day temporal profiles of mean female attendance (closed circles) and mean proportions of male Sharp-tailed Grouse engaged in each of four major behavioral categories: (**A**) display (open squares), (**B**) foraging (diamonds), (**C**) agonism (triangles), and (**D**) inactivity (open circles). See Table 1 and text for statistical analysis.

high female attendance days (0.0021 ± 0.0005, $t_{138} = 4.32$, $P < 0.001$), but not on low female attendance days (–0.0001 ± 0.0005, $t_{114} = -0.10$, $P = 0.92$). None of the other behaviors showed a significant interaction between female attendance category and time of day.

Head Turning Rates

Head turning rates (Figure 4) differed significantly among the four behavioral categories of display, foraging, agonism, and inactivity ($F_{3,36} = 18.43$, $P < 0.001$) using a random-intercept GLMM with behavioral category as a fixed effect and bird nested within year as a random effect. This model was a better fit than a model with the same fixed effect but a random effect of bird only (likelihood ratio test: $G_1 = 10.24$, $P = 0.001$). Since the model including year in the random effect was a better fit to the data, there was a difference in head turning rates between the two years, with higher head turning rates across all behaviors in 2012 (24.8 ± 2.0 turns min^{-1}) than in 2011 (15.8 ± 1.2 turns min^{-1}). Using post hoc Tukey HSD (honestly significantly difference) tests, the rate of head turning during display was significantly lower than during the other three activities ($Z > 5.17$, $SE = 2.12$, $P < 0.001$), which did not differ from each other (see Figure 4).

DISCUSSION

Courting males must trade off the benefit of increased display with its associated costs. We found that male Sharp-tailed Grouse allocated more time to display with increasing female numbers at the expense of foraging both within and across days. In addition, we examined head movement rates during different activities and found that males turned their heads only half as much during display than during other behaviors. This suggests two mechanisms by which display costs may be incurred: 1) a reduction in foraging time, and 2) reduced visual attention to the surroundings.

Although our data are correlational, they still provide evidence that reduced foraging and reduced visual attention are possible costs of increased lekking display. Our study used lek-wide activity data. Even though lek-wide activity data provide information about overall tradeoffs faced by displaying males, the data are limited in that they do not provide information about individual variation among males. Nonetheless, our results show that foraging on the lek declines whereas display increases with female numbers, both within and across days. These patterns remained robust when controlling for time both within mornings and across days. As far as we know, this is

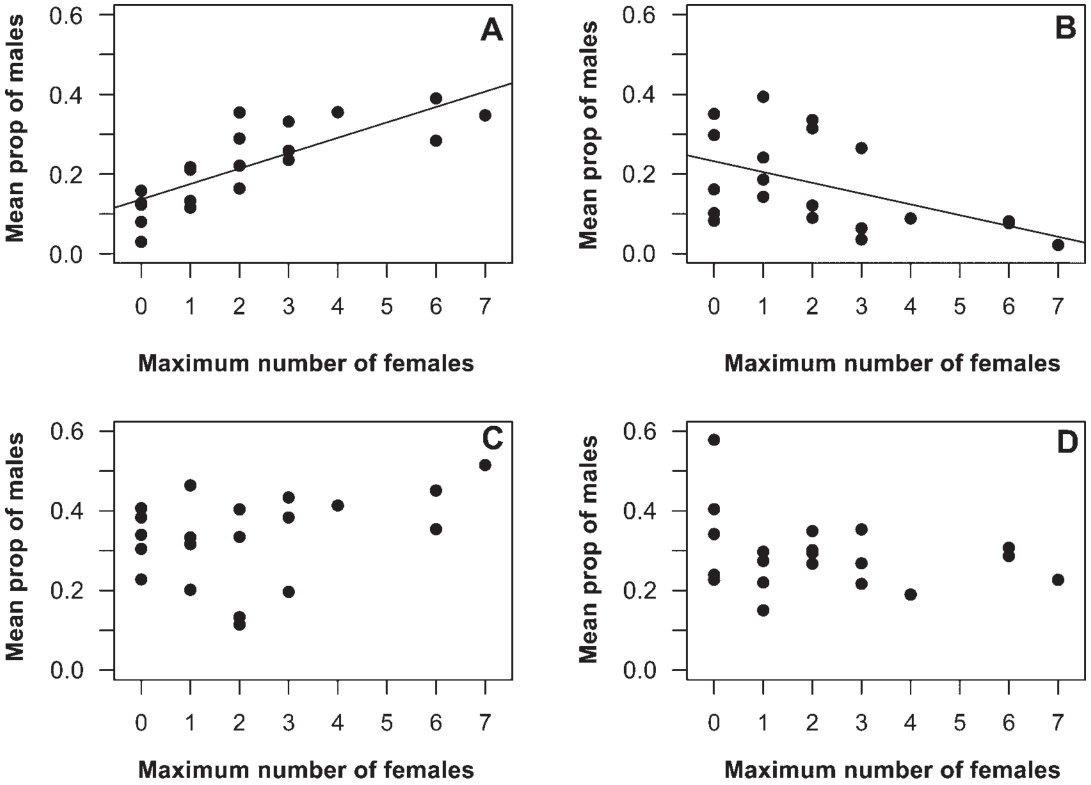

FIGURE 3. Mean proportions of male Sharp-tailed Grouse engaged in (**A**) display, (**B**) foraging, (**C**) agonism, and (**D**) inactivity during the morning lekking period vs. maximum female daily count. See text for statistical analysis. Solid lines indicate statistically significant correlations.

the first demonstration of a possible foraging–display tradeoff in response to female attendance in a lekking bird. This potential tradeoff suggests that time spent foraging likely decreases during peak periods of female attendance and that reduced food intake may be a cost of increased display. However, this inference assumes that males do not engage in compensatory foraging after leaving the lek. While off-lek foraging has not yet been studied, Sharp-tailed Grouse males may return to the lek multiple times each day during the seasonal peak in female lek attendance (R. M. Gibson personal observation), which may mean that time for compensatory foraging may be limited.

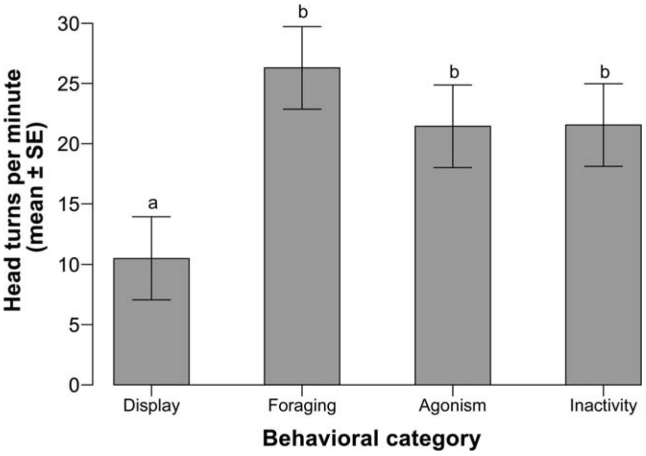

FIGURE 4. Head turning rates during each of four behavioral categories for 13 male Sharp-tailed Grouse. Letters above each bar indicate statistically homogeneous groups (Tukey tests, details in text).

The ability to compensate for reduced foraging and/or increased energy expenditure may depend on territorial or reproductive status, and is possibly species-specific. For example, compensatory foraging is suggested to occur in Greater Sage-Grouse (*Centrocercus urophasianus*), for which Vehrencamp et al. (1989) found that a subset of males that showed high energy expenditure (presumably due to increased display) actually lost less weight per day compared with males that showed lower energy expenditure. However, in lekking Black Grouse (*Lyrurus tetrix*), reproductively successful males lost more mass over the breeding season than less reproductively successful males (Lebigre et al. 2013). This pattern may reflect the energetic costs of increased rates of agonistic interaction experienced by centrally located, reproductively successful males (Rintamäki et al. 2001).

In addition, changes in male foraging behavior or the ability to compensate for increased energy expenditure during the breeding season may be affected by local food availability. For example, Western Capercaillie (*Tetrao urogallus*) males may reduce the quality of their diets during the lekking season by feeding on higher quantities of nutrient-poor pine needles because these take less effort to find near the lek compared with richer nutrient sources (Odden et al. 2003). For three species of lekking manakins, lek sites may have higher food availability than more distant foraging locations (Ryder et al. 2006), which may offer males increased foraging opportunities without traveling far from the lek.

We also found that the reasons why foraging declined with increasing female numbers differed within days vs. across days. Within days, Sharp-tailed Grouse males increased display at the expense of reduced foraging and agonism when female numbers increased. Similarly, males increased display at the expense of foraging with increased female numbers across days. Contrary to the within-day pattern, however, agonism increased with higher numbers of females across days. Our results suggest that males increased agonism later in the morning after females had left the lek on days with higher female numbers. Nooker and Sandercock (2008) found that both display and aggression levels were higher when females were present on the lek in the congeneric Greater Prairie Chicken (*Tympanuchus cupido*). In addition, they found that mating success was higher if males allotted more time to aggressive behavior compared with display behavior when females were not present on the lek.

In the second component of our study, we found that Sharp-tailed Grouse males turned their heads only half as frequently during display (Figure 4) as during foraging, agonism, or inactivity. Assuming that head movements reveal visual attentiveness (see Introduction), this result could indicate that displaying males are less visually attentive to their surroundings (the limited attention hypothesis; Dukas and Kamil 2000a, 2000b). If so, males might be more vulnerable to predation during display. A possible alternative hypothesis is that a static head during display serves some display-specific function, and therefore does not necessarily indicate lowered visual attentiveness. An experimental approach measuring head movements in response to a controllable visual stimulus (as a distractibility measure) in different behavioral contexts would be necessary to critically evaluate the limited attention hypothesis.

We also found higher overall head turning rates in 2012 than in 2011. The lek studied in 2012 was larger than the one studied in 2011, and since individuals may change their head position to monitor other conspecifics (e.g., Fernández-Juricic et al. 2005), a larger lek size in 2012 might account for the higher overall head turning rates that year. Because Sharp-tailed Grouse males consistently defend territory boundaries from neighboring birds, they need to observe conspecifics and may turn their heads to do so.

To summarize, lekking male Sharp-tailed Grouse increased display at the expense of on-lek foraging with increasing female numbers both within and across days. In addition, males turned their heads less frequently during courtship display than during other behaviors, possibly indicating reduced visual attentiveness and therefore potentially increased vulnerability to predation. These two potential costs of courtship display could be further explored by studies that: 1) investigate the effect of increased lek display on overall food intake, and 2) experimentally probe the visual attentiveness of males engaged in display vs. other activities.

Our study suggests that lekking males, in addition to the direct energetic cost of display (Vehrencamp et al. 1989, Höglund et al. 1992), may face additional costs of display through other less-studied mechanisms such as reduced food intake and reduced visual attention to their surroundings. Given that males of many nonlekking species also perform elaborate courtship displays to females (M. Andersson 1994), it is possible that reduced foraging time and reduced vigilance may be costs of courtship for males of many species during the breeding season.

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