Behavioral Flexibility in a Variable World: The Influence of Social Environment and Habitat Structure on Greater Sage-Grouse Courtship and Communication

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# Behavioral Flexibility in a Variable World: The Influence of Social Environment and Habitat Structure on Greater Sage-Grouse Courtship and Communication

By

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DISSERTATION

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# DISSERTATION ABSTRACT

Animal courtship—a set of behaviors with critical fitness consequences—is, at its core, a dyadic interaction between two individuals. However, the environment in which courtship occurs can be complex. In addition to the physical structure of the environment, which can influence courtship signaling and signaling behaviors, there is often a complex social environment as well. Individuals may have to contend with multiple competitors and potential mating partners simultaneously. Additionally, this complexity is rarely static; the habitat or social structure may be spatially or temporally variable. The ability for animals to flexibility adjust their courtship behaviors in response to the surrounding context can help animals successfully find a mate; individual differences in behavioral plasticity have far-reaching fitness consequences.

In this dissertation, we investigate how some of this natural complexity influences courtship behaviors. Using greater sage-grouse (*Centrocercus urophasianus*), a species of lekking bird, as a model species, we conducted a series of experiments in wild populations to better understand sage-grouse courtship behavior in response to changes in the social environment and to variable habitat structures. In Chapter 1, using robotic female stimuli, we experimentally induced a courtship encounter and then introduced a potential second courtship partner to compare the relationship between male display effort and partner number. In Chapter 2, we investigated the role of social information in sage-grouse display behavior and tested whether the transmission pathways of this social information varied with environmental context. In Chapter 3, we tested whether the visibility of locations in sage-grouse courtship environments was predictive of male strutting behavior. Chapters are described in more detail below.

**Chapter 1** details the results of a field experiment conducted to investigate the relationship between male sage-grouse display effort and female number. Considering a lek as a

mating marketplace has served as a useful framework to understand courtship dynamics. This chapter develops this framework by investigating the economic idea of outside options—the investment decisions made during an ongoing negotiation when a second potential partner approaches. To test the hypothesis that male sage-grouse will adjust their courtship display effort in response to outside options in ways that influence their mating success, we first introduced a single biomimetic robotic female onto our two study leks to allow males to initiate a courtship display. Then, we either maintained the same social context for the entire experimental trial or introduced a second robot and scored male display behavior. By simultaneously modeling display rate and display persistence, we were able to evaluate multiple aspects of sage-grouse's bout-structured display behaviors. While our results supported prior findings—that sage-grouse males adjust their display effort in response to female behavior—we found no evidence that sage-grouse males adjusted their display behavior when a second female is introduced, contrary to our prediction. Our results highlight the usefulness of using the mating marketplace as a framework in which to investigate complex courtship dynamics.

**Chapter 2** highlights the role of social information use and transmission in male sage-grouse courtship displays. Female sage-grouse partake in mate-choice copying, a type of social learning, and it has long been theorized that males use social information to inform their display behavior. In this chapter, we experimentally introduced a cue of female presence (through either a robot or a playback) to a sage-grouse lek that was either visually open or experimentally manipulated (with a barrier) to be visually occluded. We then tracked the male behavioral response to our cue and used network-based analyses to quantify the use of social information about female presence on sage-grouse leks. We found evidence that, across all contexts and modalities, male sage-grouse use social information to inform their strutting behavior.

Additionally, by comparing multiple potential transmission pathways, we demonstrate that sage-grouse flexibly use social information through different pathways depending on the surrounding context. We also provide evidence that, in some transmission pathways, adding a visual obstruction changes the degree of social information use. Lastly, we found a bias in social information flow depending on male mating success in some networks. In addition to quantifying social information use in sage-grouse males, our work shows that animals may exhibit plasticity in gathering social information across complex natural habitats. Understanding the role of social information use and pathways of transmission, especially in fitness-critical behaviors such as courtship, can inform better conservation methods and habitat management strategies.

**Chapter 3** demonstrates how fine-scale mapping technologies can be used alongside behavioral experiments to test the influence of habitat structure on animal behavior. Sensory drive predicts that the characteristics of an animal's environment will shape its signals and signaling behavior. The effects of habitat structure on signal structure are well demonstrated but the impacts on habitat choice at the individual scale is less understood. We experimentally induced courtship behavior in sage-grouse by presenting males in sage-dense, visually occluded areas with a female stimulus (either a robot or a playback) and recorded male display behavior. We combined this behavioral data with fine-scale habitat renderings of our study sites. In doing so, we were able to test the hypothesis that visibility (both horizontally and directly between the male and female) predicts locations where sage-grouse strutted (as opposed to random, nearby locations). We found that lower horizontal visibility indicated a higher chance that a location was a strut location and, counter to our prediction, that direct line-of-sight visibility did not predict strut location.

## DISSERTATION ACKNOWLEDGEMENTS

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We returned each year from Wyoming with hundreds of hours of video recordings of sage-grouse leks. Going through these videos to score male mating success required the assistance of many UC Davis undergraduates, whom I would like to acknowledge, in no particular order, for their efforts: Mitchell Petures, Quynh Tran, Jack Quinn, Bilawal Mahmood, Angel Fong, Martha Campos, Kate Kimura, Maritza Gonzalez, Kaitlyn Yapjoco, Ruihan Zhang, Stephanie Hernandez, Anna Jiang, Wahib Ead, Danielle Hammond, Elyna Tran, Marwa Harig, Mounika Bhaskara, Brian Valera, Vivian Tran, Vinh Do, Ning-Kit Tang, Gregg Cohen, Floriana Masia, Elyna Tran, Emily Yang, Sarah Heimbach, Joann Mendoza, Jasmine Fu, Krista Schmidt, Rachel Jackson, Selin Louie, Madonna Abdelnour, Haruka Endo, Hannah Horowitz, Joshua Gates, Ethan McCullough, Jasmine Rosario, Adelaide Llewellyn, Katrina Shi, Konshau Duman, Janice Juarez, Jordyn Williams, Lauren Watson, Sarah Netland, Mario Rodriguez, and Genevieve F Hernandez. I would like to extend a special thanks to the undergraduates that worked on special projects and/or helped me collect experimental data: Christina DiBernardo, Alexandria Patrick, Kimberly Mitchell, Britt Dryer, Anne Hylback, and Rosie Frolich.

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# **CHAPTER 1:** Two's company, three's no different: lekking males adjust courtship displays to female behavior, but not number

Ryane M. Logsdon, Anna C. Perry, Alan H. Krakauer, David J. Harris, Christine DiBernardo, Alexandria Patrick, Jennifer S. Forbey, Gail. L. Patricelli

## ABSTRACT

In many species, male courtship displays are energetically costly. By tactically adjusting courtship behaviors in response to the social context (i.e., displaying at a high effort only when a female is nearby), some individuals can alleviate some of the energetic demands of displaying. These behavioral tactics have been studied using economic models as a framework—the courtship dynamic is represented as a negotiation between a pair. In this work, we expand the dyadic courtship negotiation to include the introduction of a second potential mating partner—an outside option—into the mating marketplace. By experimentally introducing one or two robotic female models onto Greater sage-grouse leks, we tested alternative hypotheses about how males adjust their display effort in response to female number. Additionally, as individual differences in social skill can have impacts on reproductive success, we investigated the relationship between individual males' response to female number and their male mating success. Using advanced modeling techniques that account for the bout structure of sage-grouse displays, we found no evidence that male sage-grouse adjust their courtship displays in response to female number. Consistent with prior findings, we did find an important influence of female behavior on male display effort that was predictive of mating success.

## INTRODUCTION

Animal courtship has been described using the analogy of an economic negotiation between two parties—a buyer and a seller; this provides a framework to investigate the dynamic behavioral changes occurring within a courtship interaction (Smith 1982, Binmore 2010). The primary focus of courtship research has been the dyadic interaction at the core of this negotiation but, by extending the study of courtship negotiations to include the broader mating marketplace, we can more fully consider the social context in which these interactions occur (Noë and Hammerstein 1994, Noë and Hammerstein 1995, Patricelli, Krakauer et al. 2011).

One important reason to understand the social context of courtship is the possibility of audience effects—the impact that an observing bystander can have on an individual's behaviors. Audience effects have been found to influence both mate-choice decisions (Baltz and Clark 1997, Plath, Blum et al. 2008) and courtship displays (Desjardins, Hofmann et al. 2012), as well as a variety of other behaviors such as vigilance behaviors (le Roux, Cherry et al. 2008), parental care decisions (Hector, Seyfarth et al. 1989, Semple, Gerald et al. 2009), and aggressive interactions (Matos and McGregor 2002). Audience effects have also been found to influence physiology, causing changes in hormones (Hirschenhauser, Wittek et al. 2008) and brain activity (Desjardins, Becker et al. 2015).

Audience effects may be an important feature of the mating marketplace. In courtship negotiations, this may include what economists call "outside options," alternative partners for one or both parties engaged in the negotiation (Fudenberg, Levine et al. 1987, De Fraja and Muthoo 2000). Outside options may be particularly important in species with mating systems such as leks, where males and females aggregate for courtship and outside options are abundant (Cherry, Frykblom et al. 2004). During courtship on a lek, there is regularly more than one male being assessed by females or more than one female interested in courtship by a given male (Patricelli, Krakauer et al. 2011). Further, an individual may transition from the role of an audience member to that of a participant, or the reverse, in an ongoing negotiation. However, little research has been done into how an individual changes their courtship behavior when an outside option arrives during courtship.

Adjusting courtship behaviors in response to outside options may be favored because courtship displays can be costly. These costs may include the metabolic expenditure physically required to perform the display (Bennett and Houck 1983, Vehrencamp, Bradbury et al. 1989, Chappell, Zuk et al. 1995, Mowles 2014), muscle fatigue from displaying repeatedly or over long periods of time (e.g. lactic acid buildup or depleted glycogen stores; Payne and Pagel 1997, Mitchell, Poland et al. 2008, Mowles and Jepson 2015), or opportunity costs of time allocation—time spent displaying takes time away from other fitness-related behaviors such as foraging or vigilance (Payne and Pagel 1996, Rivers and Morin 2012, Cowles and Gibson 2014). Males may lessen these costs by tactically adjusting their courtship displays in response to female feedback (Patricelli, Krakauer et al. 2016). Such tactical behavioral adjustments have been found in a broad range of taxa including veiled chameleons (Kelso and Verrell 2002), hummingbirds (Simpson and McGraw 2018), and gobies (Wong and Svensson 2009). During courtship, the degree of male responsiveness to female behaviors—such as directing courtship behaviors only towards receptive females or only producing high-quality displays when a female is nearby—can be positively associated with mating success (Patricelli, Uy et al. 2002, Patricelli and Krakauer 2010, Sih, Chang et al. 2014, Sullivan-Beckers and Hebets 2014).

When outside options are introduced to an ongoing courtship negotiation—like the arrival of a second potential mating partner—males have an opportunity to adjust their negotiation tactics in multiple ways. First, adding a female may increase the value of mating. The new female may be of higher value or have more interest in mating. In species with mate-copying, mating in the presence of other potential partners could also have non-additive, positive impacts on a male's mating success. In either of these situations, males may show an **increased investment response**; they may increase their display effort with additional partners as the value of mating increases (Figure 1.1A, B, C). Alternatively, the presence of a second partner may alleviate some of the costs of displaying, as either female may accept a lower-effort display. Just as a seller has more bargaining power (i.e., leverage) after a second buyer arrives and may be less inclined to haggle down a price, males may have more leverage when a second female approaches if the presence of the second female increases the overall probability of mating. Males in this case may show a **leverage response**, decreasing their display effort in response to the presence of a second female (Figure 1.1D, E, F). Lastly, males may not adjust their display effort in response to female number (Figure 1.1G), as would be the case if males are unable to detect changes in female number or if there is no advantage to making display adjustments in this context.

Not all males may benefit from responding the same way to multiple potential courtship partners. As is often the case in bargaining games, the optimal tactic of an individual is dependent on the broader context, such as the social environment, past experience, male quality, and female assessment behavior (Dugatkin and Reeve 2000, Muthoo 2000, McElreath and Boyd 2008, McNamara, Fromhage et al. 2009, Colman 2013). When displays are metabolically expensive, males may differ in optimal tactic depending on the constraints they face. These constraints—aspects of their physiology and experience that limit their behaviors—may include available energy stores, anaerobic metabolic capacity, relative accumulation of lactic acid, hormone levels, diet, parasite load, genes, and past experiences (Crews and Moore 1986, Folstad and Karter 1992, Briffa and Sneddon 2007, Koch and Hill 2018).

Another factor that might cause differences among male responses to the presence of one versus multiple females is differences in social skills. Social skills are here defined as an individual's ability to perceive and respond in an optimal way to a conspecific's behavior (Sih, Sinn et al. 2019). Social skills may be important whenever an individual is interacting with conspecifics and, as almost all sexually reproducing species interact with conspecifics at least during breeding, these skills can have broad-reaching fitness consequences (Taborsky and Oliveira 2012, West-Eberhard 2014, Bshary and Oliveira 2015, Sih, Sinn et al. 2019). Variation in social skills may impact variation in courtship behaviors and mating success; these skills are likely to increase in importance in species with higher aggregation, such as those with colonial or lekking breeding systems. ***The goal of this research is to investigate if and how males of a lekking species, greater sage-grouse, respond to the presence of multiple potential courtship partners and how this response relates to mating success.***

Here, we propose four alternative hypotheses which relate tactical, behavioral adjustments in males to mating success and to the number of potential partners present. Our first hypothesis, the **social skills hypothesis**, builds upon the idea that males vary in their ability to detect and respond to changes in the social environment during courtship and that males with greater ability to respond appropriately to these changes—those with better social skills—will have greater reproductive success (e.g., Patricelli, Uy et al. 2002, Gersick, Snyder-Mackler et al. 2012). The social skills hypothesis thus predicts that successful males will show a greater response to female number than unsuccessful males (either increasing or decreasing his effort via the increased investment or leverage responses, respectively; Figure 1.1A, D).

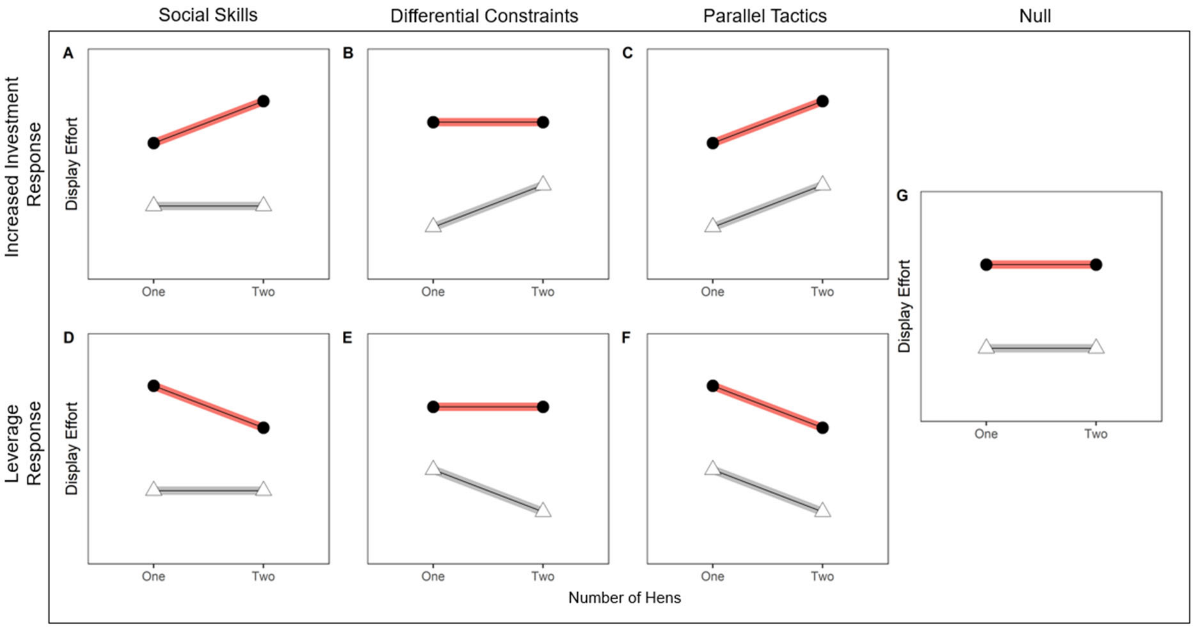

**Figure 1.1**. Predictions of alternative hypotheses for male display effort in response to the presence of one or two hens. The red lines are the predictions for successful males (those who mated at least once); grey lines represent unsuccessful males. Males may show the increased investment response (A, B, C) or the leverage response (D, E, F) in response to an additional female. The predictions of our four hypotheses are depicted: the social skills hypothesis (A, D), the differential constraint hypothesis (B, E), the parallel tactics hypothesis (C, F), and the null hypothesis (G).

Alternatively, if overall display effort is the primary driver of mating success among males, this would support the **differential constraint hypothesis**. Males with fewer constraints are thus expected to maximize their display effort whenever they are displaying to assessing females while males with more constraints adjust their display efforts in response to the social context as a way to efficiently spend their limited metabolic stores. This hypothesis predicts that unsuccessful males will respond to a higher degree (either increasing or decreasing display effort) in response to female number, while successful males will not adjust their display effort (Figure 1.1.1B, D).

However, if all males are able to adjust their display effort in response to the social environment, this would support the **parallel tactics hypothesis**. The parallel tactics hypothesis predicts that mating success will not be limited by a male's ability to assess the social context, but by their physiological limits. Thus, we expect to see a relationship between overall display effort and mating success, with a similar pattern of courtship adjustment (either increasing or decreasing) by all males (Figure 1.1 C, E).

Alternatively, males may not respond to female number by adjusting their display, regardless of their mating status. The **null hypothesis** thus predicts only a positive relationship between display effort and mating success, with no pattern of adjustment in behavior in response to the number of females (Figure 1.1G).

### Study species

We use the greater sage-grouse (*Centrocercus urophasianus*; Figure 1.2) as a model species to test our hypotheses about courtship investment tactics. The greater sage-grouse is a well-studied, lekking species with stereotyped, metabolically-expensive courtship displays called "struts" (Scott 1942, Wiley 1973b, Vehrencamp, Bradbury et al. 1989). Mate choice in this species is thought to be primarily driven by male courtship behaviors; only one morphological trait—visible ectoparasite load—correlates (negatively) with mating success (Gibson and Bradbury 1985, Gibson, Bradbury et al. 1991, Johnson and Boyce 1991, Gibson 1996). The frequency of displays—the strut rate—is related to male mating success, with successful males strutting at an overall higher rate than unsuccessful males (Gibson and Bradbury 1985, Gibson, Bradbury et al. 1991, Gibson 1996). Strut rate is also positively correlated with daily energy expenditure, indicative of a physiological cost on males to perform this courtship behavior (Vehrencamp, Bradbury et al. 1989). Additionally, while these performance costs impact all displaying males, they do so differentially; there is a negative relationship between daily energy expenditure and weight loss in sage-grouse such that males that are able to strut at higher rate (who are likely more successful in mating) lose less weight throughout the season (Vehrencamp, Bradbury et al. 1989). Greater sage-grouse are an excellent candidate species to study tactical behavioral adjustments in response to multiple courtship partners because males tactically alter their courtship behavior in response to female presence, proximity, and interested versus uninterested female behavior (Gibson 1996, Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019).

**Figure 1.2**. Male sage-grouse (left) in an erect posture next to two hens (right).

In this study, we tested predictions of our hypotheses by experimentally manipulating the number and behavior of females on the lek using robotic female models (fembots). We first presented the target males with a single fembot, allowing them to begin a courtship interaction. During the second phase of our experiments, we either maintained the same, single-fembot interaction or introduced a second fembot. The first fembot always maintained a behavior associated with uninterested females (a bent-forward posture with pecking movements to indicate foraging); the second fembot performed either the uninterested or an interested behavior (remaining upright and looking toward the target male; Perry 2017). We then examined male courtship effort in response to these social contexts and how it relates to mating success with real females.

## METHODS

### Lek observations

Two leks were monitored daily in Fremont County, Wyoming (42 49' 44.42"N, 108 30' 24.08" W) from 11 March to 4 May 2015 (except for 4 days when poor weather hindered lek access). Field assistants, who were positioned in blinds 50-200m from the lek, recorded daily observations using spotting scopes. These observations began at first light and continued until no birds remained on the lek. Males were individually identified using color bands or unique plumage patterns of the under-tail coverts (Wiley 1973a, Patricelli and Krakauer 2010). The breeding behavior and positions (±1m) of 48 regularly-identified males were recorded periodically relative to an on-lek grid of stakes placed at 10m intervals (Krakauer, Tyrrell et al. 2009, Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019). Daily activity, as well as experimental trials, were recorded using 1-2 high-definition video cameras (Sony HDR-PJ430V and HDR-FX1, Tokyo, Japan). This footage, combined with data collected in the field on male position, male ID, and time, was used by trained UC Davis undergraduate interns to identify and track individual males post-season to record copulation and strut events. This research was approved by the Wyoming Game and Fish Department (Permit ID 405) and the UC Davis Animal Care and Use Committee (protocol 18080).

### Robotic female model

Two biomimetic robotic female models ("fembots") were used as controlled stimuli to elicit male courtship behaviors (e.g., Patricelli and Krakauer 2010). The electronic components of the fembot are concealed inside a taxidermy body form dressed with real skins gathered from multiple female sage-grouse (collected by Wyoming wildlife managers after mortality events and donated to the project; for additional information on fembot construction see Perry, Krakauer et al. 2019). These fembots have three axes of body movement: (1) head rotation side to side, (2) head and neck movement up and down, and (3) body tilting forward towards the ground and back upright. In combination, these movements allow the fembot to present two ecologically relevant behaviors: (1) an upright posture with side-to-side head movements, simulating a grouse looking around—a behavior with high likelihood of preceding solicitation from females and our "interested" behavioral treatment and (2) a bent forward posture with pecking head movements simulating foraging behaviors—a behavior with lower likelihood of preceding solicitation and our "uninterested" behavioral treatment (Wiley 1973a, Perry 2017) . Additionally, the fembots have four independently rotating wheels, which allows fairly free movement across the lek. Prior work has validated that males respond similarly to the fembots as they do real females (Forbey, Patricelli et al. 2017, Perry, Krakauer et al. 2019). Each robot was operated by the same researcher in all trials (GLP or AHK) and the robot-driver was randomly assigned to each trial. Operators attempted to keep the robot's behavior consistent in all trials. However, it was not possible for the robot operator to be blind to which experimental treatment was being conducted. Robot/driver ID is controlled for in all analyses.

## Experimental methods

Experimental trials were conducted between 16 March and 30 April 2015. Most experimental trials were conducted after the peak of breeding (78.5% of total copulations had occurred prior to the experimental trials), though two trials occurred before any breeding had occurred. Trials were conducted between 0635 and 0820, when males were regularly strutting; this time frame is before the average time of male departure from leks (0840) and encompasses maximum male (0740) and female (0707) lek attendance. Female lek attendance is incredibly variable throughout this timeframe (0 – 104 hens present with a mean = 5.97 and SD = 13.66); all trials were conducted when no live hens were present or visible within 50m of the lek.

We presented male sage-grouse with either one or two fembots; for a given trial 4-13 males were present (mean = 7.53, SD = 2.44), including 3-9 (mean = 6.9) individually identifiable males with known mating success as well as 0-7 (mean = 2.15) unidentified males. All robot trials (N = 13) consisted of a three-minute pre-trial and three-minute post-trial to determine baseline strut rates for all males present on the lek both before and after the experimental presentation of fembots. The trials also contained two three-minute treatment phases (Phase 1 and Phase 2). In Phase 1, the first fembot was driven from an on-lek observer blind along a pre-planned trajectory to the edge of 3-5 male's territories, where she stayed for the duration of Phase 1 (three-minutes); an audio recording of female grouse landing was played immediately before the presentation of the fembot. In phase 2, a second fembot was (or was not) introduced according to the treatment type (Control, Treatment 1, or Treatment 2); phase 2 also lasted for three-minutes (in two trials, this phase was extended to four minutes to allow more time for male response; this addition is considered in the statistical models). During the Control trials (N = 8 trials), the single fembot remained in place for both Phase 1 and Phase 2 (for a total of six minutes) engaged in the uninterested, foraging behavior. During Treatment 1 trials (N = 2 trials), we introduced a second fembot performing the uninterested behavior on onto the lek after Phase 1 was compete. Treatment 2 trials (N = 3 trials) were the same as Treatment 1 except the second fembot performed interested behaviors (remaining upright). At the end of Phase 2, all fembots were driven back to the blind and the three-minute post-trial began (Table 1.1). Throughout both Phase 1 and 2, the fembots moved every 30 seconds within a 1m radius of a central target flag to better mimic the behavior of real hens.

**Table 1.1**. Overview of experimental design. Phase 1 serves as the introduction of the first fembot, Phase 2 either maintains the Phase 1 condition (Control) or introduces a second fembot (Treatment).

| | **Pre-Trial (3 minutes)** | **Phase 1 (3 minutes)** | **Phase 2 (3 minutes)** | **Post-Trial (3 minutes)** |
|---|---|---|---|---|
| **Control** | No fembot | 1 uninterested fembot | No change | No fembot |
| **Treatment 1** | No fembot | 1 uninterested fembot | + 1 uninterested fembot | No fembot |
| **Treatment 2** | No fembot | 1 uninterested fembot | + 1 interested fembot | No fembot |

### Mating success

Mating success was determined by scoring the total number of copulations observed on-lek for each male throughout the breeding season (e.g., Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019). This data was recorded both in-field and through video observations by trained UC Davis undergraduates. This is not a comprehensive measure of reproductive success, as copulations occurring off-lek or at night are likely to be unmarked, so we cannot correct for multiple mating by the same female. However, mating success is a good proxy for reproductive success in this species (Semple, Wayne et al. 2001, Bird, Aldridge et al. 2013). Males during the

2015 breeding season were observed mating between 0 and 112 times. The distribution of this mating success is highly skewed, as is typical in this species (Figure 1.3).

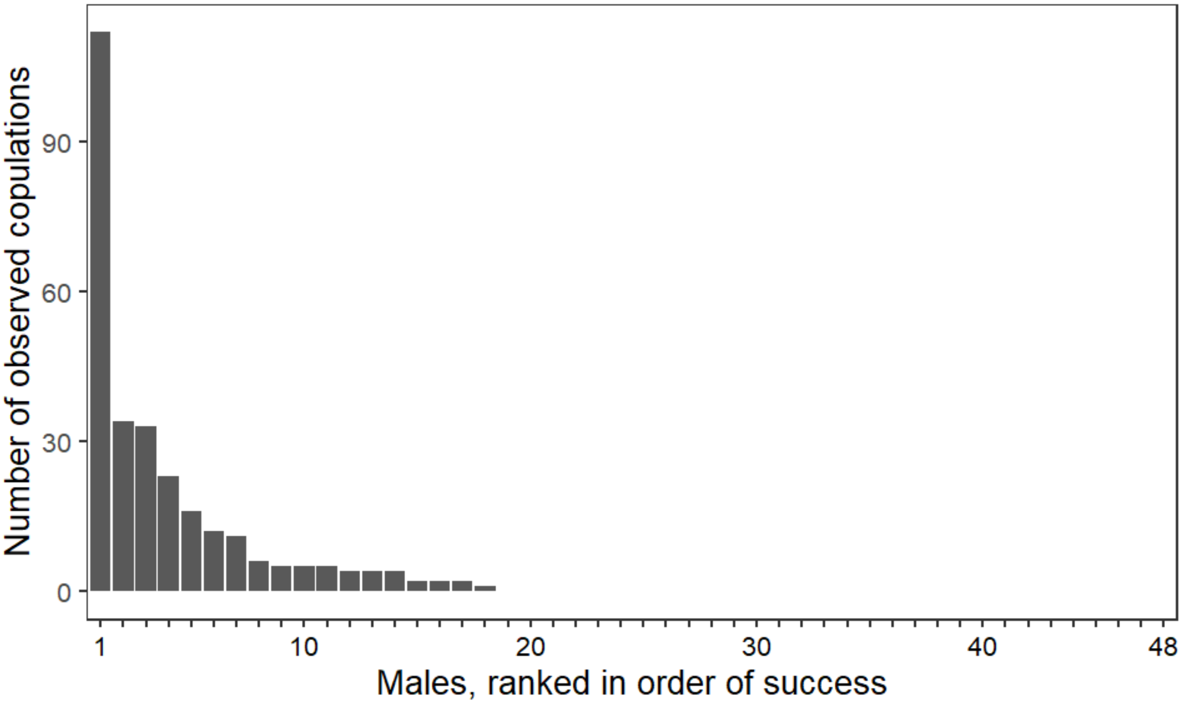

**Figure 1.3**. Mating skew pooled across our two study leks in 2015 (48 males total).

Statistical analysis of male display effort

Sage-grouse have a bout-structured display system; males often perform multiple struts in short succession (a bout) interspersed by longer breaks between bouts (Wiley 1973b; Figure 1.4). Due to this bout-structure, the interval lengths between strut displays (i.e., inter-strut intervals) fall into two categories: shorter, within-bout intervals (typically <10 seconds), and longer, between-bout intervals. To investigate males' display effort, we built a mixed model based on the methods described in more detail in Perry et al (2019). These models predict the distribution of interval lengths that occur between strut displays under different social or environmental conditions (see Model Parameters below); these interval lengths are our unit of replication for this model (N = 2686 intervals). Specifically, we modeled the distribution of interval lengths as a mixture of short intervals (drawn from a Weibull distribution with a small mean) and long intervals (drawn from a Weibull distribution with a large mean). The means of both distributions could also be affected by several predictor variables, including both fixed and random effects (described below), via a log link function. The relative weight given to the two mixture components (i.e., the estimated probability of a short vs. a long interval) was modeled using a similar set of predictor variables, via a logit link. In this model, male sage-grouse can separately adjust two aspects of their courtship: the rate at which they produce strut displays (via the mean of their Weibull distributions; Figure 1.4A & B), and the average number of struts per bout (via the mixture weights; Figure 1.4A & C). We implemented our multi-level, mixed model using the brms package in R (Bürkner 2017).

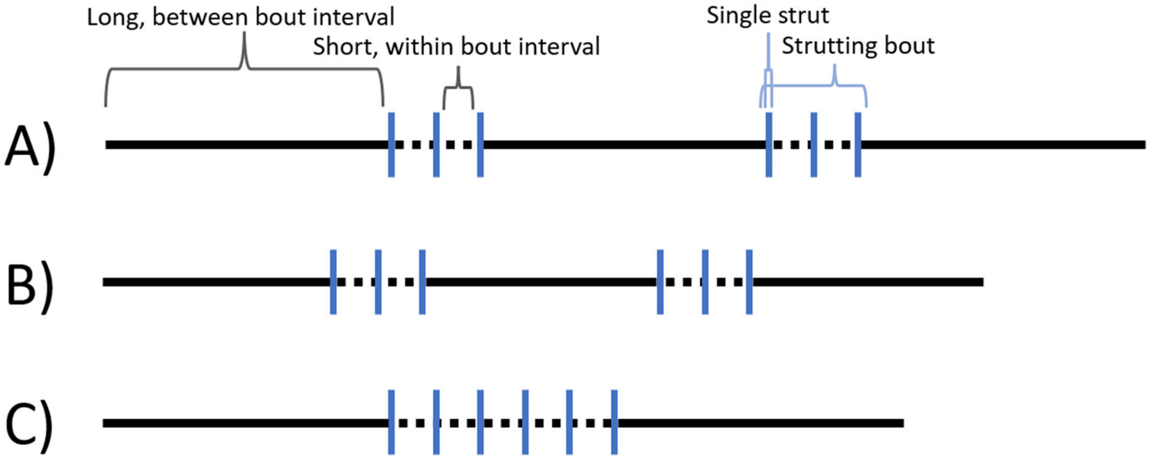

**Figure 1.4**. Examples of sage-grouse courtship structure. Struts are represented as vertical blue lines. Intervals between struts are horizontal black lines; between bout intervals are solid, within bout intervals are dashed. A, B, and C all contain 6 struts and 7 intervals. A and B contain the same probability of a long interval, but the mean long interval length is greater in A than in B; A produces strut displays at a higher rate than B. A and C contain the same mean long interval length, but the probability of a given interval being long is higher in A than in C; A has a lower number of struts per bout than C.

*Censored Intervals:* Our sampling periods were initiated and concluded without regard to male behaviors—males were often between struts at these times. We do not know the full duration of these partially-observed intervals, because they did not fall entirely within our observation window, but do have a lower limit of this value; these are called right-censored observations (Type I; Lagakos 1979). Using the brms package in R, we included these censored intervals in our model (R Development Core Team 2010, Bürkner 2017, Bürkner 2018). By including these intervals as censored values, we avoid the possibility of underestimating average interval lengths (as would happen if we included the observed interval length without censoring) and avoid biasing towards males with higher display effort (as would happen if we discarded incomplete intervals; Perry 2017).

*Model Parameters*

***Fixed Effects***: The following variables were included as fixed effects in our reported model. For all candidate models and model comparison, see Supplementary Info.

*Lek:* We collected observations of male behavior on either Chugwater (CHG) or Cottontail (COT) lek. To account for possible inter-lek variation in the data, we included focal lek ID as a predictor variable.

*Day in season:* Prior work has shown that male sage-grouse display effort varies throughout the season; interval lengths tend to increase as the season progresses (Perry, Krakauer et al. 2019). To account for this variation, we included the date of each experiment in our model, defined as the number of days from the start of the season on 11 March 2015 (which we defined as day zero). These values were z-transformed for ease of interpretation.

*Time of day:* Sage-grouse display intervals also tend to lengthen throughout the morning (Wiley 1973a). To account for variation in experiments conducted at different times in the morning, we calculated the number of minutes that elapsed between the start of each experiment and nautical dawn. We used nautical dawn as it better approximates when males arrive on the lek in the morning (Wiley 1973a, Perry, Krakauer et al. 2019). These values were also z-transformed.

*Robot presence*: We included two model parameters to determine how males responded to the presence of zero, one, or two robots. The intercept of each candidate model describes social conditions where zero female stimuli were present. We then used one binary parameter to indicate if the first fembot was present on the lek (1 = first fembot present). We used a second binary parameter to do the same for the second fembot (1 = second fembot present). Prior work shows that male sage-grouse will adjust their display effort when a female stimulus arrives on the lek following a ≥3-minute period with no female present (Perry, Krakauer et al. 2019). Our experimental design will allow us to test whether males also increase their display effort in response to the addition of a second female stimulus.

*Robot behavior*: Our two experimental treatments differed by the secondary fembot's posture (the upright "interested" posture or the forage-mimicking "uninterested" posture); a behavior which male sage-grouse respond to differently during courtship (Perry, Krakauer et al. 2019). As male sage-grouse displays are influenced by female distance (Wiley 1973a), the influence of the closest hen is often used in analysis (Gibson and Bradbury 1985, Gibson, Bradbury et al. 1991, Gibson 1996). Thus, we included a parameter defining the posture of the closest fembot to each male to determine the impact of female behavior on male display effort.

*Distance to closest robot*: Prior studies show that male sage-grouse display response is influenced by the distance to hens (Wiley 1973a). To account for this effect, we have included a parameter indicating the distance from each male to the closest robot (Gibson and Bradbury 1985, Gibson, Bradbury et al. 1991, Gibson 1996, Patricelli and Krakauer 2010). The raw distance calculations were inversed, z-scaled, and square-root transformed for ease of interpretation and to account for skew in the data. These distances were calculated at the beginning of each sampling period, to avoid including treatment impacts on distance (as males could adjust their position by moving closer or further to a robot). For phases where there was no robot on the lek (i.e., pre-trials) or when there was no second fembot present, we set the distance to the respective fembot as infinity. Calculating the inverse distances sets these infinite values to zero within the model.

*Closest robot ID:* We included the ID of the closest robot to account for any variation in male response to the different robots or—as each robot was operated by the same researcher in all trials—any apparent behavioral differences caused by the robot operator.

*Experimental design effects:* We included a set of binary parameters to account for variation in male display caused by the experimental design. We included a parameter to indicate the periods between sampling phases when the fembot(s) were moving across the lek, a parameter to indicate the second phase (either control with one fembot or the treatments with two) of the experiment, and a parameter to indicate the post-trial (the period after the fembots have been pulled off the lek).

***Varying Effects*:** The following variables were included as varying effects in our model to account for the variance occurring from repeated measures in our data.

*Male ID:* To account for variation in interval length and probability of continuing a bout driven by repeated sampling of individuals, we included a varying intercept for each male (N = 25 regularly identified males and 26 males whose identities were unable to be confirmed). We also allowed individual male slopes to vary in response to robot presence and the behavior of the closest robot to further determine how individuals adjusted their display responses to changes in the surrounding social context.

*Sampling Period*: Our experiments were broken into discrete sampling periods: pre-trial, phase 1, phase 2, and post-trial. To account for variation in interval length caused by differences in sampling period that may impact display conditions (i.e., wind speed, a potential predator passing overhead, etc.), we included a varying intercept for each sampling period for both display rate and the average number of struts per bout.

### Statistical analysis of mating success

To assess which aspects of male's displays best predicted their mating success, we needed to determine if the male-specific estimates from our display model correlate with the male's mating success. Only regularly identified males that were present in at least one experiment (N = 25) were used in our mating success analysis, as we do not know the mating success of the unidentified males present for our experiments. Our mating success dataset contained a heavy skew (Figure 1.3). This skew, plus the small sample size, led us to use a rank correlation to determine the relationship between male-specific behaviors in response to our treatments and their mating success; rank correlations reduce the impact of outliers in correlation analyses. Thus, for each posterior sample (N = 20,000) of our top-ranking model, we calculated the Spearman rank correlation between a male's mating success and the estimated, male-specific parameter values (i.e., the varying effects) predicting the probability of a long interval, the mean interval length for short intervals, and the mean interval length of long intervals for the relevant experimental parameters (the intercept, robot presences, and robot behavior). We then determined which of the parameter correlations had 95% of their samples either above zero, indicating a strong positive correlation with mating success, or below zero, indicating a strong negative correlation with mating success.

## RESULTS

### Male display effort

The display model output is summarized below (Tables 1.2, 1.3, 1.4); the mean posterior values and error, 95% credible intervals are included for all parameters. Our potential scale reduction factor ($\hat{R}$; Gelman and Rubin 1992) did not detect any convergence problems with any parameter ($\hat{R}$ = 1.00 for all parameters).

By looking at the 95% confidence intervals of our fixed effects that do not overlap zero, our model indicated that the probability of a given interval being long (i.e., being a between-bout interval) increased throughout the season and decreased as the nearest robot got closer. We also found that, for the average male, the closest fembot showing an uninterested behavior decreased the probability that the interval was long, meaning that these males were more likely to be actively strutting. Our model indicated that the short interval lengths increased in duration as the nearest robot got closer. While seeing an increase in short interval length—indicative of a less rapid display rate within a bout—in response to a closer robot is contradictory to prior results (Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019), males are less likely to be within a strutting bout as distance increases (Perry, Krakauer et al. 2019); we do not expect the high rate strutting at more distant females to be ecologically relevant. We found that, on average, long intervals (between-bout breaks) increased in length as the season progressed but decreased in length in response to the arrival of the first robot.

**Table 1.2.** Mean posterior values from output summary for parameters determining the probability of a long interval in the full model. A higher probability of a long interval—the between-bout interval—indicates a lower display effort. Fixed effects that do not overlap zero are shown in bold. The estimates of the varying effects and slopes represent the estimate of the variation (SD) around the intercept or slope.

| | *Variables* | *Estimate* | *Estimate Error* | *lower 95%* | *upper 95%* |
|---|---|---|---|---|---|
| *Fixed Effects* | Intercept | 1.26 | 0.44 | 0.4 | 2.14 |
| | Cottontail Lek | 0.17 | 0.33 | -0.49 | 0.82 |
| | Time from Dawn[a] | -0.01 | 0.14 | -0.28 | 0.26 |
| | **Days from Start[a]** | 0.46 | 0.14 | 0.19 | 0.74 |
| | **1/Distance to closest robot[a,b]** | -0.48 | 0.13 | -0.75 | -0.22 |
| | First robot present | -0.05 | 0.33 | -0.71 | 0.61 |
| | Second robot present | -0.25 | 0.45 | -1.12 | 0.64 |
| | **Closest robot behavior - uninterested** | -0.82 | 0.34 | -1.49 | -0.16 |
| | Phase 2 | -0.09 | 0.34 | -0.76 | 0.57 |
| | Post-Trial | 0.04 | 0.32 | -0.59 | 0.67 |
| | Robot movement | -0.04 | 0.30 | -0.65 | 0.53 |
| | Robot/Driver ID – Robot 2 | -0.33 | 0.17 | -0.68 | 0.01 |
| *Varying Intercepts* | Male ID | 0.57 | 0.21 | 0.08 | 0.93 |
| | Sampling Period | 0.64 | 0.11 | 0.44 | 0.88 |
| *Varying Slopes (on male ID)* | Male response to first robot presence | 0.22 | 0.17 | 0.01 | 0.61 |
| | Male response to second robot presence | 0.2 | 0.18 | 0.01 | 0.67 |
| | Male response to behavior of closest robot | 0.54 | 0.24 | 0.04 | 0.97 |

Intercept: Chugwater lek, pre-trial, no robot present. The default Robot was labeled Robot 1. The default robot behavior was interested.

[a] Z-transformed variable

[b] Square root transformed variable

**Table 1.3.** Mean posterior values from output summary for parameters determining the short interval length in the full model. A longer duration short (within-bout) interval corresponds with a decrease in display effort. Fixed effects that do not overlap zero are shown in bold. The estimates of the varying effects and slopes represent the estimate of the variation (SD) around the intercept or slope.

| | *Variables* | *Estimate* | *Estimate Error* | *lower 95%* | *upper 95%* |
|---|---|---|---|---|---|
| *Fixed Effects* | Intercept | 1.80 | 0.09 | 1.62 | 1.99 |
| | Cottontail Lek | 0.14 | 0.08 | -0.01 | 0.29 |
| | Time from Dawn[a] | -0.03 | 0.03 | -0.08 | 0.02 |
| | Days from Start[a] | -0.05 | 0.02 | -0.09 | 0 |
| | **1/Distance to closest robot[a,b]** | 0.08 | 0.03 | 0.02 | 0.13 |
| | First robot present | -0.13 | 0.06 | -0.24 | 0 |
| | Second robot present | 0.14 | 0.08 | -0.01 | 0.29 |
| | Closest robot behavior - uninterested | -0.01 | 0.08 | -0.16 | 0.14 |
| | Phase 2 | 0.02 | 0.05 | -0.08 | 0.12 |
| | Post-Trial | 0.02 | 0.05 | -0.09 | 0.13 |
| | Robot movement | -0.07 | 0.05 | -0.17 | 0.03 |
| | Robot/Driver ID – Robot 2 | 0.06 | 0.03 | -0.01 | 0.12 |
| *Varying Intercepts* | Male ID | 0.18 | 0.04 | 0.08 | 0.26 |
| | Sampling Period | 0.07 | 0.02 | 0.04 | 0.11 |
| *Varying Slopes (on male ID)* | Male response to first robot presence | 0.09 | 0.04 | 0.02 | 0.16 |
| | Male response to second robot presence | 0.07 | 0.05 | 0 | 0.19 |
| | Male response to behavior of closest robot | 0.06 | 0.05 | 0 | 0.18 |

Intercept: Chugwater lek, pre-trial, no robot present. The default Robot was labeled Robot 1. The default robot behavior was interested.

[a] Z-transformed variable

[b] Square root transformed variable

**Table 1.4.** Mean posterior values from output summary for parameters determining the long interval length in the full model. A longer duration long (between-bout) interval corresponds with a decrease in display effort. Fixed effects that do not overlap zero are shown in bold. The estimates of the varying effects and slopes represent the estimate of the variation (SD) around the intercept or slope.

| | *Variables* | *Estimate* | *Estimate Error* | *lower 95%* | *upper 95%* |
|---|---|---|---|---|---|
| *Fixed Effects* | Intercept | 6.22 | 0.31 | 5.63 | 6.83 |
| | Cottontail Lek | 0.39 | 0.22 | -0.05 | 0.82 |
| | Time from Dawn[a] | 0.03 | 0.09 | -0.15 | 0.20 |
| | **Days from Start[a]** | 0.39 | 0.10 | 0.20 | 0.58 |
| | 1/Distance to closest robot[a,b] | 0.09 | 0.11 | -0.12 | 0.30 |
| | **First robot present** | -0.54 | 0.22 | -0.97 | -0.10 |
| | Second robot present | 0.12 | 0.29 | -0.44 | 0.69 |
| | Closest robot behavior - uninterested | -0.43 | 0.25 | -0.92 | 0.04 |
| | Phase 2 | 0.24 | 0.22 | -0.20 | 0.68 |
| | Post-Trial | 0.25 | 0.20 | -0.13 | 0.64 |
| | Robot movement | -0.13 | 0.18 | -0.47 | 0.22 |
| | Robot/Driver ID – Robot 2 | -0.19 | 0.13 | -0.45 | 0.06 |
| *Varying Intercept* | Male ID | 0.07 | 0.10 | 0 | 0.39 |
| | Sampling Period | 0.29 | 0.08 | 0.12 | 0.45 |
| *Varying Slopes (on male ID)* | Male response to first robot presence | 0.05 | 0.05 | 0 | 0.19 |
| | Male response to second robot presence | 0.05 | 0.05 | 0 | 0.19 |
| | Male response to behavior of closest robot | 0.59 | 0.11 | 0.32 | 0.76 |

Intercept: Chugwater lek, pre-trial, no robot present. The default Robot was labeled Robot 1. The default robot behavior was interested.

[a] Z-transformed variable

[b] Square root transformed variable

Mating success

We ran a Spearman's rank correlation between male mating-success and the male-specific parameter values predicting our three display metrics (short interval length, long interval length, long interval probability). The results are summarized in Table 1.5. Using the criterion that 95% of the samples had a correlation either above or below zero, indicating a positive or negative correlation, respectively, we found a positive relationship between mating success and male adjustment of the long interval duration in response to the behavior of the closest robot.

**Table 1.5**. Percentage of parameter samples with Spearman rank correlations that fall above zero. Values above 95%, indicating a positive correlation between the individual male behavior and mating success, or below 5%, indicating a negative correlation, are in bold.

| | | |
|---|---|---|
| Length of short interval | Intercept | 92.6% |
| | First Robot Presence | 79.7% |
| | Second Robot Presence | 64.8% |
| | Closest Robot Behavior | 60.7% |
| Length of long interval | Intercept | 64.0% |
| | First Robot Presence | 53.5% |
| | Second Robot Presence | 45.7% |
| | **Closest Robot Behavior** | **99.5%** |
| Probability of continuing long interval | Intercept | 86.6% |
| | First Robot Presence | 45.8% |
| | Second Robot Presence | 38.6% |
| | Closest Robot Behavior | 44.3% |

The average male in our model posterior—a group that includes mated, unmated, and unknown males—has a long interval length that is 176.22 seconds shorter when the closest fembot is displaying the uninterested behavior than the interested behavior. However, when looking at how males of different mating success respond to the behavior of the closest fembot, we find that the long interval lengths of mated (mating success > 0) males are, on average, 121.72 seconds longer when the closest fembot is uninterested than when it is interested, while the long intervals of unmated (mating success = 0) males are, on average, 151.34 seconds shorter. In Figure 1.5, we have shown the difference in parameter estimates predicting long-interval length for successfully and unsuccessfully mated males as compared to the average male. Consistent with the null hypothesis (Figure 1.1G), we found little evidence that males adjust their display rates (via long-interval length) or the average number of struts per bout (via probability of long-interval) in response to female number; Figure 1.6 again shows the predicted response of mated and unmated males to robot number as compared to the average male.

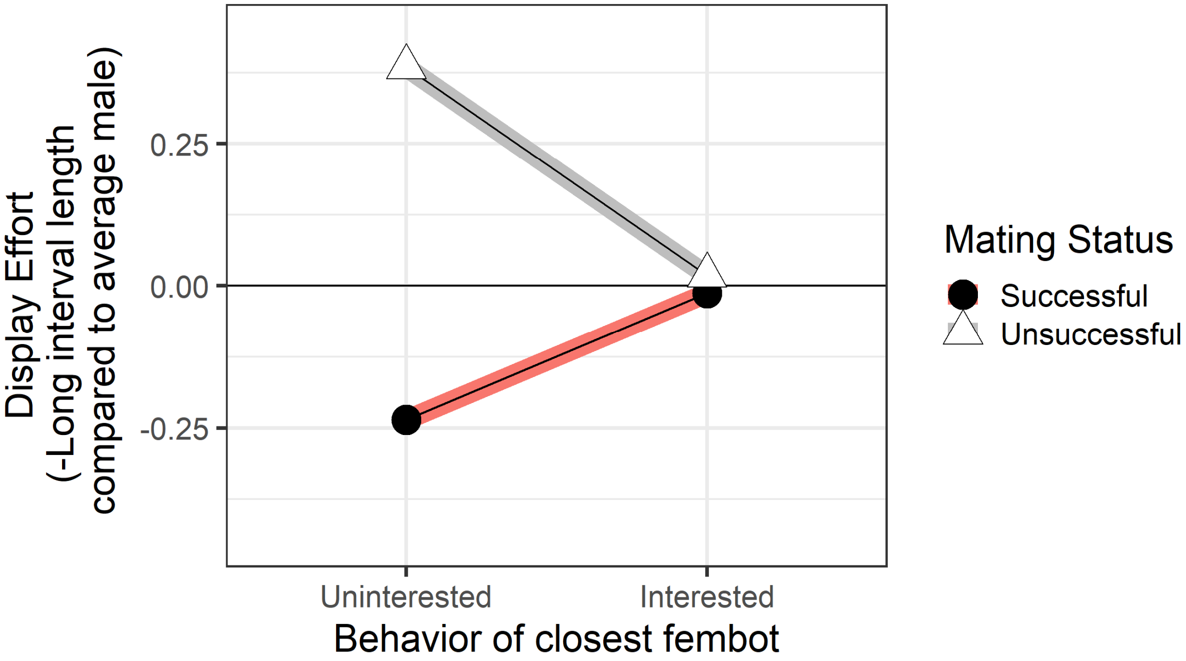

**Figure 1.5**. The negative difference in long interval lengths of successful and unsuccessful males from the average male in response to the behavior of the closest fembot. We took the negative difference for ease of interpretation: in this figure, a positive value depicts a higher display effort than average and a negative value depicts a lower display effort than average.

## DISCUSSION

Researchers have recently argued that economic models of negotiation can be used as a framework to help us understand the tactics involved in animal courtship encounters (Noë and Hammerstein 1994, Noë and Hammerstein 1995, Patricelli, Krakauer et al. 2011). In this study,

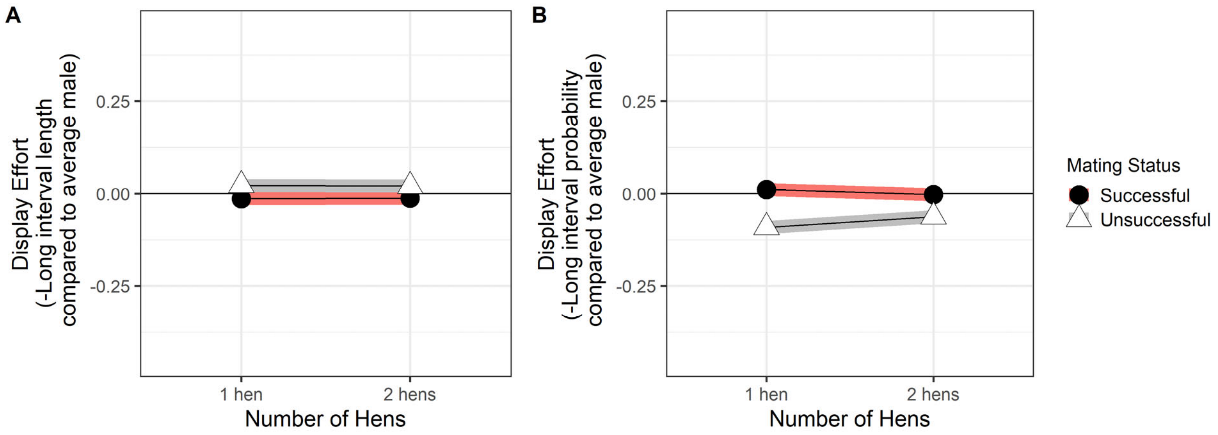

**Figure 1.6.** The negative difference in long interval length (A) and long interval probability (B) of successful and unsuccessful males from the average male in response to one or two hens. We took the negative difference in these figures for ease of interpretation: here, a positive value depicts a higher-than-average mating effort, and a negative value depicts a lower-than-average mating effort.

we tested alternative hypotheses—developed from economic negotiation literature and prior work done on sage-grouse (Fudenberg, Levine et al. 1987, De Fraja and Muthoo 2000, Patricelli, Krakauer et al. 2011)—about how male sage-grouse respond to the arrival of a second potential mate approaching an ongoing courtship encounter and how these responses relate to mating success (Figure 1.1). We did so experimentally, by initiating one courtship interaction with a robotic hen, then introducing (or not) a second robot. As sage-grouse strut displays are bout-structured, we simultaneously modeled characteristics of both the short, within-bout intervals between struts and the long intervals between bouts. By modeling the probability that a given interval was long, as well as the mean length for both short and long intervals, we are able to get a more fine-scale understanding of sage-grouse strut display effort (Perry, Krakauer et al. 2019).

In our system, an increased probability of a long interval indicates a decrease in display effort, as males with increased probabilities of long intervals are less likely to be actively strutting. An increase in the duration of the long intervals also corresponds to a decrease in display effort, as males are waiting longer to initiate a strutting bout. Similarly, an increase in the duration of short, within-bout intervals indicates a slower display rate, a decreased display effort. Results are discussed in detail below. In short, we found that males adjust their display effort in response to time of the season and to robot distance. We also found that males adjust their courtship in response to robot behavior and that these behavioral adjustments were related to mating success. However, we found no evidence that male sage-grouse adjust their display effort in response to the addition of a second hen, which supports our null hypothesis (Figure 1.1G). Additionally, we found that a male's response to the number of hens did not predict mating success.

### Factors related to male display effort

Our display model is consistent with previous results showing that the average male's display effort decreases throughout the mating season (Perry, Krakauer et al. 2019). We found that, on-average, as the season progressed, long intervals were more likely to occur and were longer in duration, indicating that males spent more time in the resting, between-bout state. Males in our study increased their display effort in response to the experimental presentation of the first fembot, showing shorter long intervals compared to an empty lek. This aligns well with the increased probability of continuing a bout in response to a single hen found by Perry et al. (2019) and prior work on other lekking Galliformes (Höglund, Johansson et al. 1997, Nooker and Sandercock 2008). We also found an increase in male display effort as the nearest robot approached, with males showing a decreased probability of long intervals with decreasing distance; this result is consistent with prior work (Hartzler 1972, Wiley 1973a, Gibson 1996, Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019).

Like Perry et al. (2019), we investigated the influence of female behavior on male strut effort. We found that the average male decreased his display effort towards fembots showing the interested behavior, as there was a decreased probability of a long interval when the nearest fembot was displaying the uninterested behavior. Additionally, we found that variation among males in the response to female behavior correlated strongly with mating success; successful and unsuccessful males respond to female behavior differently, as discussed in detail below.

### Change in display effort and mating success

While our display model helped us quantify display effort and understand the behavior of an average sage-grouse male, we were primarily interested in whether males adjusted their display behaviors in a way that predicted their mating success. To examine this, for each of the 20,000 runs of the display model, we ran a Spearman's rank correlation between male mating success and the male-specific parameter estimates from the posterior samples of our model. We did this for all three metrics of male display (long interval probability, long interval length, and short interval length), examining the male-specific response to the addition of the first fembot, the second fembot, and the behavior of the closet robot. If at least 95% of the correlation coefficients fell above zero, this suggests a positive relationship between the male's behavioral response and his mating success; if less than 5% fall above zero, this suggests a negative relationship (Table 1.5).

The only male behavior found to correlate with mating success was the change in long interval duration in response to the closest fembot's behavior. As seen in Figure 1.5, successful and unsuccessful males responded differently to fembot behavior. Prior work conducted by Perry et al. (2019) found that successful males displayed at a high level towards both interested and uninterested fembot, whereas unsuccessful males displayed at a high level only at interested robots. Perry et al. (2019) posit that unsuccessful males invest more display effort courting hens already showing cues of interest in mating due to their energetic constraints and/or lower probability of convincing an uninterested hen to become interested (Vehrencamp, Bradbury et al. 1989, Seymour and Sozou 2009, Byers, Hebets et al. 2010, Clark 2012); successful males displayed at a high level regardless of female behavior. Like these prior results, this study found that both successful and unsuccessful males displayed with a similar effort (relative to the average male) when displaying to interested hens. However, when displaying towards uninterested hens, we found that unsuccessful males showed a higher display effort than the average male (via shorter-than-average long intervals) and that successful males displayed at a lower display effort than the average male (via longer-than-average long intervals; Figure 1.5).

There are a number of possible explanations for the differences in the results of this study and Perry et al. (2019). Both studies were conducted in the same study population, but there were environmental differences between the years the studies were conducted. The year the Perry et al. (2019) experiment was conducted, 2012, was one of the warmest and driest years on record for the state of Wyoming (United States. National Weather 1995), which may have influenced the bird's diets and differential constraints, which could impact choosiness in females (as in wolf spiders; (Hebets, Wesson et al. 2008)) or courtship effort in males (as in *Drosophila*; Droney 1998). Additional research is needed to understand the influence of average precipitation and temperature on sage-grouse diet, female choice, and male display effort. Alternatively, these results may shed additional light on the complexity of sage-grouse display behavior. During Perry et al.'s (2019) trials, a single fembot moved to multiple positions on the lek; in our trials, each fembot only moved to a single location. Further study is needed to determine if the differences in display characteristics in these two studies are nuanced tactical responses to the varying experimental conditions.

As discussed above, we found that male sage grouse do not adjust their display behaviors in response to the addition of a second hen to an ongoing courtship negotiation. Our results support our null hypothesis. We found that both successful and unsuccessful males showed similar display efforts to the presence of either one or two fembots. Our null hypothesis (Figure 1.1G) assumed that successful males would show an overall higher display effort than unsuccessful males based on the results from Perry et al. (2019) and other work on this species (Hartzler 1972, Wiley 1973a, Wiley 1973b, Gibson and Bradbury 1985, Vehrencamp, Bradbury et al. 1989, Gibson, Bradbury et al. 1991, Patricelli and Krakauer 2010). However, once hen behavior was controlled for, we found no difference in the behavior of successful or unsuccessful males towards one versus two hens (Figure 1.6). Interestingly, when we look at male response to the nearest fembot's behavior, our results are similar to Perry et al. (2019) in finding that neither successful nor unsuccessful sage-grouse males differ from the average male's display effort when the hen they are courting appears interested in mating; the differences between successful and unsuccessful males occur during courtship with uninterested hens (Figure 1.5). As male sage-grouse adjust their display behavior as hens approach (Wiley 1973a, Gibson, Bradbury et al. 1991, Patricelli and Krakauer 2010), we posit that they may only respond to the behavior of the nearest hen to them at any given time, regardless of the presence or behavior of another hen.

The degree to which animals adjust their behavior towards audience groups with different compositions varies greatly. For example, tadpoles do not adjust their prey disturbance cues at all, regardless of whether observer groups were familiar or not (Bairos-Novak, Crane et al. 2020), while the number of courtship calls produced by female chimps is directly influenced by the number of other females present (Townsend, Deschner et al. 2008). In sage-grouse, a second hen does not appear to be a sufficient cue to elicit a change in male behavior as compared to a single hen. However, as female sage-grouse traverse the lek in groups ranging from 2 to more than 20 hens (Wiley 1973a) and display mate-choice copying (Gibson, Bradbury et al. 1991), further research is needed to determine whether males respond to the presence of more than two hens. By using models which better capture the intricacies of bout-structured displays, we were able to test multiple hypotheses derived from economic negotiation theory; we believe further investigation of the lek as a mating marketplace will continue to yield insights into the complex process of courtship negotiations (Noë and Hammerstein 1994, Noë and Hammerstein 1995, Patricelli, Krakauer et al. 2011).

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## AUTHOR CONTRIBUTIONS

*RML contributed to study design and execution, field and video data collection, analyses, and drafting the manuscript; ACP contributed to study design, statistical analyses, and manuscript completion; AHK was involved in study design, execution, and field data collection; DJH contributed to statistical analyses and manuscript completion; CD and AP assisted with video data collection; GLP was involved in study design and execution, field data collection, critically revising the manuscript, and, along with JSF, helped coordinate and fund the study. All authors assisted with manuscript revision.*

## SUPPLEMENTARY INFORMATION

### Model comparisons

**Table 1.S1**. Difference in ELPD values and standard errors (SE) from top model for each model tested.

| Model | ELPD difference | SE |
|---|---|---|
| *Full model* | 0.0 | 0.0 |
| *Treatment null* | -10.6 | 4.2 |
| *Female presence null* | -12.5 | 6.7 |
| *Distance null* | -16.8 | 7.8 |

In addition to our full model, described and reported in main text, we created 3 alternative null models to compare: (1) *treatment null* – did not contain fixed effects or varying slopes for the behavior of the closest robot, (2) *female presence null* – did not contain the fixed effects or varying slopes for the behavioral data, the information about female presence, or robot ID, and (3) *distance null* – did not contain the fixed effects or varying slopes for the behavior, presence, or ID of the robot nor the fixed effect of distance of the closest robot. We ran leave one out cross validation (LOO CV) on each model using the *brms* package in R (Bürkner 2017, Bürkner 2018) and found the highest support for our full model. The difference from the top model in expected log predictive density (ELPD) for each model is reported in Table 1.S1.

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# **CHAPTER 2:** Social communication in a manipulated environment: plastic social information use in response to habitat structure

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## ABSTRACT

The degree of social information use in animals varies by context; selection favors those who weigh the costs of gathering information by the reliability of this information. Network-based analyses of social information flow allows researchers to model alternative paths of transmissions between individuals (e.g., through different modalities). However, little work has addressed the potential for plasticity between these transmission paths across contexts. This study investigates how habitat structure influences the use and transmission of social information in a free-living species. We manipulated the habitat structure of greater sage-grouse leks and stimulated male courtship behaviors with a cue of female presence. We then tracked the spread of courtship behaviors through the males and used network-based diffusion analyses to test different hypotheses about information diffusion and to model the degree of social information used in each context. We found strong evidence that male sage-grouse use social information from other males to inform their courtship behavior and that the habitat's occlusion changed the amount of social information used in the system. Additionally, we found that sage-grouse use different transmission networks of social information based on the habitat structure and female cue and, in some pathways, found evidence of a bias towards gathering information from successfully mated males.

# INTRODUCTION

Many animals rely on gathering social information to learn about the environment in ways that shape their behavioral decisions about foraging, movement, courtship and mating, predator avoidance, and aggressive interactions, etc. (Danchin, Giraldeau et al. 2004). Early ethologists often assumed gathering social information was intrinsically adaptive, but more recent theoretical and empirical work suggest that organisms should be selective about gathering information socially versus asocially (i.e., direct sampling) depending on the context and on individual traits (reviewed in Laland 2004, Galef 2009, Jones, Aplin et al. 2017, Barrett, Zepeda et al. 2019). As gathering social information requires connections among individuals for transmission, network-based approaches to social information studies allow researchers to investigate social information use across contexts and the potential paths of transmission between individuals (Franz and Nunn 2009, Hoppitt, Boogert et al. 2010). These networks of individuals are shaped in part by the surrounding habitat, which influences when and how individuals interact (Pinter-Wollman, Fiore et al. 2017, He, Maldonado-Chaparro et al. 2019). However, the influence of habitat structure on social information transmission is still relatively understudied (Jones, Aplin et al. 2017, He, Maldonado-Chaparro et al. 2019) and the potential for plasticity in transmission pathways of social information across contexts has been largely overlooked. In this study, we investigate the flexible use of alternative paths of social information transmission across different structural habitats.

The structure of an animal’s habitat not only influences an organism’s phenotype and fitness-related behaviors (e.g., Sharpe and Van Horne 1998, Ng, Landeen et al. 2013), but the information available to an organism (Hardt and Benedict 2020). As some modalities of information transmission (e.g., acoustic, visual) are more successful in certain environments, habitat structure can influence the paths of information transmission used (e.g., Endler and Thery 1996, Forrest 2015). Additionally, the habitat structure, in conjunction with the limitations of the receiver's sensory physiology and processing abilities, may influence when an animal uses social versus asocial information by altering the costs of gathering reliable social versus asocial information (Endler 1992, Endler and Basolo 1998, Rowe 1999). Lastly, habitat structure can differentially alter the availability of social information originating from certain individuals (e.g., those who are further away or visually obscured), influencing who information is gathered from within a social group (Laland 2004, He, Maldonado-Chaparro et al. 2019).

The process of gathering information is complicated by the fact that an animal's habitat is often spatially and temporally variable; there may be variation in topography, elevation, biodiversity, and physical structure both at the micro- and the macro-scale. Additionally, the environment may change over time. Complex or variable environments reduce the reliability of information—its value may change suddenly or degrade over time—so selection may favor individuals who selectively gather social information, weighing the time spent gathering information by the reliability of that information (Laland 2004). One way that organisms can increase the transmission of social information through a complex or variable environment is by using multiple signals or multimodal displays (Guilford and Dawkins 1991, Johnstone 1996). While the different components of multimodal signals may encode unique information, they may also increase the reliability of information in a signal (via increased redundancy), increase signal efficiency, or allow the signal to persist through variable environments, thus increasing the chance of transmission through a variety of contexts, conditions, and habitats (Bro-Jørgensen 2010, Hebets, Barron et al. 2016, Mitoyen, Quigley et al. 2019).

Another important way that animals may cope with the challenges of a heterogeneous environment is through behavioral plasticity, which allows quick adjustments to changing or variable conditions (Buskirk 2012, Snell-Rood 2013). Behavioral plasticity has limits—it does not allow infinite flexibility and individuals differ in their ability to express plasticity (Stamps 2016). However, it can help animals communicate through variable environments (e.g., Ord, Stamps et al. 2010). As with most behaviors, an animal's use of social information has the potential to be expressed plastically. For example, an organism's reliance on social information can depend on the individual recipient (Rosa, Nguyen et al. 2012), their internal state (Webster and Laland 2010, Templeton, Philp et al. 2017), characteristics of the sender (Kendal, Hopper et al. 2015, Kern, Sumner et al. 2016), the social context (King and Cowlishaw 2007, Riebel, Spierings et al. 2012), and the reliability or recency of the social information (Dunlap, Nielsen et al. 2016, Heinen and Stephens 2016). Additionally, characteristics such as age, sex, and dominance can influence the pattern of information flow through a group of individuals (Aplin, Farine et al. 2015, Canteloup, Hoppitt et al. 2020). The impact of these traits on an individual's plastic use of social information is well researched, however, relatively few studies have examined the impact of the physical and biological environment on social information use. There is growing evidence that environmental impacts may be important in determining social information use—the propensity to use social information may fluctuate in response to changes in light level (Jones, Czaczkes et al. 2019), urbanization (Jones, Aplin et al. 2017, Morand-Ferron, Hermer et al. 2019), and habitat structure (Webster, Atton et al. 2013, Price, Dulex et al. 2019).

Network-based approaches to social information studies have allowed researchers to examine the group-level effects of individual differences in the propensity to use social information. In one of these approaches, network-based diffusion analyses (NBDA), information is not assumed to transmit equally through all individuals in a group (Franz and Nunn 2009, Hoppitt, Boogert et al. 2010). NBDA allow variable weights of connectedness among individuals within a network; these connection weights determine the likelihood of information transmission between individuals. By comparing the underlying network of connections to the timing of observed behaviors, NBDA quantify the strength of social information transmission through a group and allows hypothesis testing to identify the social network which best predicts the transmission pathway (Franz and Nunn 2009, Hoppitt, Boogert et al. 2010, Hoppitt 2017, Hasenjager, Leadbeater et al. 2020). For example, Kulahci et al. (2016) used NBDA to determine that affiliative (as opposed to aggressive) networks best predicted the order in which individual ravens in a group solved a novel task. NBDA allows testing of the hypothesis that different paths of social transmission may be used in distinct environmental contexts within the same group of individuals.

In this study, we investigate the use and transmission routes of social information across multiple modalities and through complex environments in a free-living, lekking bird, the greater sage-grouse (*Centrocercus urophasianus*). Sage-grouse are an ideal species to test our objectives as they have long been suspected to use social information (Wiley 1973b, Gibson, Bradbury et al. 1991) and their tendency to plastically adjust their courtship behaviors is related to their mating success (Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019). In addition, the habitat structure of sage-grouse leks is naturally variable, ranging from open, grass-covered fields to occluded display sites covered in sagebrush (Figure 2.1).

To examine whether habitat structure effects the pathways of social information flow, we experimentally increased visual occlusion by introducing a burlap barrier which visually divided

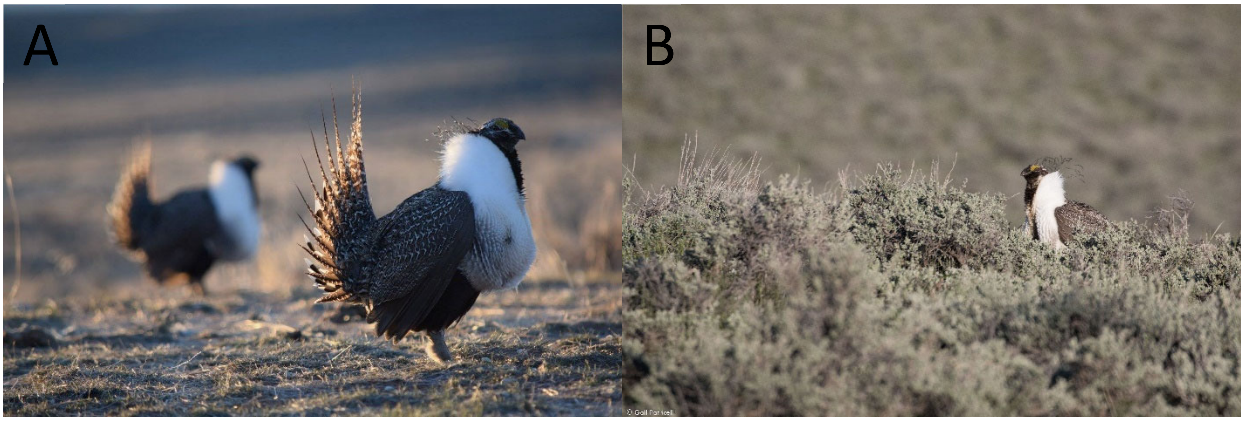

**Figure 2.1**. Male sage-grouse displaying (A) in a visually open area and (B) in a brushy, more occluded area.

the lek (Figure 2.2). In these occlusion (barrier) or unmanipulated (no barrier) treatments, we introduced a cue of female presence to sage-grouse leks either acoustically, via a playback of hen vocalizations, or visually, by means of a biomimetic robotic hen (Figure 2.2). The male's strutting behavior in response to the cues of female presence was video recorded and scored to determine the timing of individual males' responses to the cue. We then built a series of potential social networks connecting males that a) could hear each other (acoustic network), b) could see each other (visual network), c) had overlapping territories (territory networks), and d) were fully connected (homogenous networks, which serve as a null in these analyses) to determine which network best estimated the route of social information flow within each treatment (summarized in Table 2.1, described in detail below). Using this experimental design and network-based diffusion analyses, we tested four non-mutually exclusive hypotheses about the presence, degree, and transmission pathways of social information use in sage-grouse across contexts (Table 2.2).

We first tested the hypothesis that male sage-grouse use social information to inform their strutting behavior (the **social strutting hypothesis**; Table 2.2). We investigated this by scoring the spread of male strutting behavior in response to our female cues within all treatments

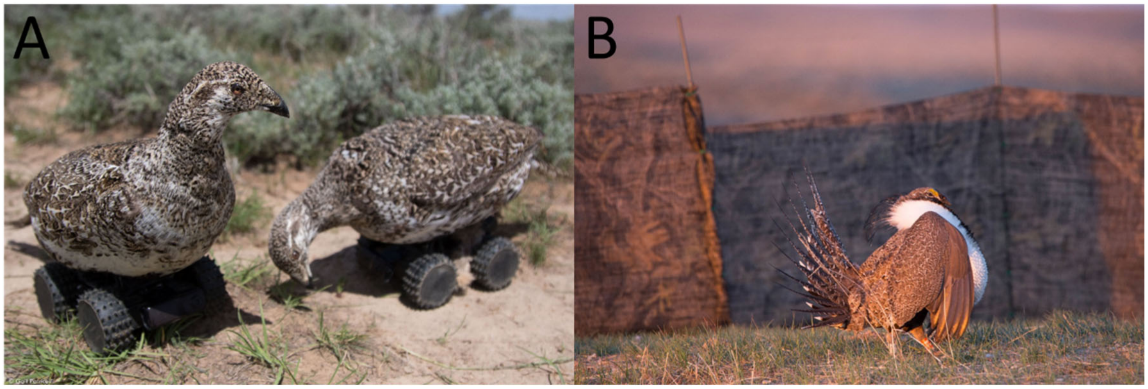

**Figure 2.2.** (A) The two biomimetic robotic hens (fembots). (B) Male sage-grouse in front of constructed barrier. Barrier segments were staggered to allow movement between sides while maintaining visual separation.

**Table 2.1.** Description of networks. The determination of connections within each of the networks is explained (Description); unconnected males are given a connection weight of 0—the model assumes no information can transmit socially between these males. The connection weights—which determine the probability of information transmission along a connection—is also described. In addition, all models contain random effects of site ID and male ID and an individual-level variable describing the distance to female cue as a predictor of asocial learning (i.e., learning directly from the source cue). A complete description of the networks is in the methods section.

| **Network Type** | **Description** | **Weight of connections** |
|---|---|---|
| Acoustic | Connects males who can hear each other | Undirected weight of $\frac{1}{distance^2}$ |
| Visual | Connects males who can see each other | Undirected weight of $\frac{1}{distance}$ |
| Core territory | Connects males with territory overlap from 50% kernel density estimates | Directed weights determined by percent of territory overlap |
| Full territory | Connects males with territory overlap from 95% kernel density estimates | Directed weights determined by percent of territory overlap |
| Homogenous | All males connected, serves as a null network in NBDA | Weights all equal to 1 |
| Asocial | No social connections among males; all males connected directly to stimulus | NA |

and, using NBDA, compared models which include social learning to those with only asocial learning (i.e., learning through direct observation of the robot; Franz and Nunn 2009). There is evidence that social information is used by female sage-grouse during mate choice (Gibson, Bradbury et al. 1991) and descriptive observations suggest that males respond to other males strutting (Wiley 1973b). Therefore, we predict that when information about female presence and location is limited (as in the playback treatments and the robot-barrier treatment), a model including social information will have the strongest support. When all males have access to direct information about female presence and location (as they do in the robot-no barrier treatment), we predict the asocial model will have the strongest support.

Next, we tested the hypothesis that the pathway through which social information transmits between individuals depends on the habitat's occlusion as well as the modality of the female cue (the **contextual transmission hypothesis**; Table 2.2). Using the same comparison as the social strutting hypothesis, we compared models of the putative social networks (acoustic, visual, territory, and null networks; Table 2.1) within treatments. For the treatments in which a social network model has higher support than the asocial model, we predict that the top supported model will vary depending on treatment. Specifically, we predict that when the barrier is present, the acoustic network will best explain the information flow through the group; when the barrier is absent and males are visually connected, we predict the visual network will have the strongest support. Alternatively, males may gather social information only from their neighbors—grouse with whom they encounter the most frequently—and the territory networks may be best supported across treatments.

We then investigated the role of habitat structure on information use, testing the hypothesis that the degree of social information use varies with the visual occlusion of the

**Table 2.2.** A description of our four hypotheses including which comparison was performed to test each hypothesis and what outcomes would be expected if the hypothesis is supported.

| **Hypothesis** | **Comparison** | **Supported outcomes** |
|---|---|---|
| ***Social Strutting*** – male sage-grouse use social information to inform their strutting displays | Within each treatment, the relative support of models that include social information flow was compared with the asocial model | If the best supported model within a given treatment contains a social network, the social strutting hypothesis is supported. |
| ***Contextual Transmission*** – when social information is used, the path of transmission depends on context | Within each treatment, the relative support of social models was determined. These top models were then compared between treatments. | For treatments in which the social strutting hypothesis is supported, if the best supported model is different between treatments, the contextual transmission hypothesis is supported. |
| ***Occlusion*** – the visual occlusion of the habitat changes the degree of social information used | Within each network type, the percent of struts explained by social transmission in the barrier experiments was compared to that in the no-barrier experiments. | If, for a given network type, the barrier experiments have a high probability ($p > 0.95$) of containing more struts explained by social transmission than the no barrier experiments, the occlusion hypothesis is supported. |
| ***Mating Success*** – male mating success influences the spread of information through a group | Within each network type, across all treatments, the percent of struts explained by social transmission in network connections originating from mated individuals was compared to that in network connections originating from unmated individuals. | If, for a given network type, the mated individuals had a high probability ($p > 0.95$) of transmitting more struts explained by social transmission than the unmated individuals, the mating success hypothesis is supported. |

habitat structure (the **occlusion hypothesis**; Table 2.2). To test this, we compared the percent of struts which can best be explained by social transmission (hereafter, “social struts”) in experiments with and without the barrier. In this analysis, each network type was tested separately. When the barrier is present and the visual field of males is limited—eliminating access to direct information about female presence for some males—we predict an increase in social information use (e.g., Webster, Atton et al. 2013) across network types. Alternatively, the increased environmental complexity may cause males to rely more heavily on their own visual field and decrease social information use in the presence of the barrier (e.g., Price, Dulex et al. 2019) within the visual network.

Lastly, we examined whether characteristics of the males in our network affected social information flow. Specifically, we tested the hypothesis that male mating success influences the spread of information throughout the group (the **mating success hypothesis**; Table 2.2). This may occur if male sage-grouse preferentially gather social information about female presence from males that have successfully mated. To test this, we compared the percent of social struts from a network containing connections originating only from mated males to one containing connections originating only from unmated males. We used all experiments in this comparison and repeated this analysis within each network type. Across all network types, we predict to see a higher percentage of struts explained by social information flow in the mated male networks, which represents bias in social information flow originating from mated males.

## METHODS

### Lek observation

Observations were conducted daily on two leks (Chugwater and Cottontail, hereafter CHG and COT) in Fremont County, Wyoming (42 49’ 44.42”N, 108 30’ 24.08” W) from 10 March to 5 May, 2016 (except for 9 days with poor weather). Using blinds located 50-200m from the lek and spotting scopes, we observed and video recorded the leks from before first light—approximately the time that sage-grouse males arrive at the lek—until the last male left the lek each day. Territory-holding males were individually identified (N = 49 males, 16 on CHG, 33 on COT) by unique color bands or plumage patterns of the under-tail coverts (Wiley 1973a). Data on courtship behaviors, time, and male position (± 1m) in reference to a 10m by 10m grid of stakes were recorded throughout each morning (Krakauer, Tyrrell et al. 2009, Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019). Daily activity on each lek and experimental trials were recorded using 1-2 high-definition cameras (Sony HDR-PJ430V and HDR-FX1, Tokyo, Japan). Post-season, all recordings were scored by trained UC Davis undergraduate interns who collected data on copulation and strut events using the notes collected in the field to identify individual males. This research was approved by the Wyoming Game and Fish Department (Permit ID 405) and the UC Davis Animal Care and Use Committee (protocol 18080).

### Experimental methods

We utilize a biomimetic robotic female grouse as a controllable source of visual information (Butail, Ladu et al. 2014) and playback of hen vocalizations as a consistent source of acoustic information about female presence on the lek. All experiments were conducted when no live hens were visible within 50m of the lek—female presence on the lek is often sporadic throughout the morning, so instances when no hens are present are not atypical. The robot and playback serve as sources of direct visual and acoustic information about female presence, respectively. Males may also use the strutting of other males as indirect, social information about female presence. We designed a 2x2 experiment with two habitat treatments (barrier and no barrier) and two sources of direct information (robot and playback); the details of these setups are below. Post-season, we scored the positions and strutting behaviors for all males present in each experimental trial (N = 67 total males, 27 on CHG, 40 on COT) from videos using the software BORIS (Friard and Gamba 2016).

### Barrier construction

The barrier was created in segments using camouflage-print burlap cloth attached to rebar (spaced approximately every 2.5m) and stood ~1m high. While barrier lengths totaled between 30 and 50 meters, no single segment was more than 10 meters in length. Barriers were staggered so that grouse movement across the lek was unimpeded while visibility across the lek was completely obscured (Figure 2.2B). Grouse were observed moving through the barrier's corridors and flying over the barrier (RML, personal observation). We found no difference in the number of copulations or strut rate on days when the barrier was present in comparison to days when the barrier was absent (see supplemental analysis). Barriers were removed from the lek following successful experimental trials, but experiments were sometimes delayed due to weather, the presence of real females, or early departure of the birds from the lek; barriers never remained on a lek for more than five consecutive days. Experiments were staggered such that we never conducted trials on the same lek two days in a row.

### Robot experiments

To determine how male strutting behavior changes in response to direct visual information versus social information about female presence, we conducted experiments using two biomimetic female models ("fembots;" Figure 2.2A). Sage-grouse males respond similarly to the fembots as they do to real hens (Forbey, Patricelli et al. 2017). The electronic components of the robots were concealed within real sage-grouse skins (collected as casualties by local wildlife management; see Perry, Krakauer et al. 2019 for robot design). The robots were used in two experimental treatments: with the visual barrier dividing the lek (N = 2 experiments per lek) and without the barrier (N = 1 experiment on CHG, N = 3 experiments on COT). In each experiment, one fembot was driven to two pre-determined locations on the lek, spent three minutes in each spot, and then was pulled back into the on-lek observer-blind from which it was controlled via radio signals. The target positions were chosen ahead of time such that the fembot would be located at the edge of 3-6 male territories. Female distance impacts male strut behavior (Patricelli and Krakauer 2010), so each male's distance to the robot (in meters) is controlled for during analyses. Each robot was operated by one of two drivers (GLP or AHK) and robot-driver was randomly assigned to each trial. Operators attempted to keep the robots' behavior consistent in all trials; however, it was not possible for the robot operator to be blind to which experimental treatment was being conducted. To maximize the consistency of robot behavior among trials, operators moved robots to new locations every 30 seconds within a 1m radius of the flag marking the target position. Operators manually rotated the fembot's head (which mimics a hen looking around) throughout each trial, mimicking the behavior of a real female in an upright posture.  We ran versions of our statistical models with robot and driver identity included as individual-level variables (i.e., fixed effects) and found that the top weighted model was the same with or without these parameters. However, including the robot and driver variables decreased our model fit so, as the results were unchanged and prior work has shown no significant impact of robot-driver identity on male behavior (Logsdon 2021), we have excluded these variables in the models reported below.

### Playback experiments

To examine the role of acoustic cues on the flow of social information across the lek, we conducted experiments using playbacks of previously recorded vocalizations of hens present on the lek (see supplemental information for playback construction). Males in our study responded at a similar rate to playbacks as to robots (47-100% of individuals responded to the fembot treatments, 66-100% of individuals responded to the playback treatments). We controlled for the distance (in meters) of each male to the speaker in all analyses. Playback experiments were conducted with both the barrier present (N = 1 experiment on CHG, N = 2 experiments on COT) and absent (N = 1 experiment on CHG, N = 2 experiments on COT). In each experiment, the 3-minute playback file was broadcast to the lek through a speaker that resembles a rock (Blickley, Blackwood et al. 2012) which was placed in line with the barrier, equidistant to each side of the lek.

### Networks

For each experiment, we built five networks of connection to compare with NBDA: an acoustic network, a visual network, two territory-based networks, and a homogenous network. These networks are summarized in Table 2.2 and described in more detail here. Our four networks are not mutually exclusive (e.g., males may be using both visual and acoustic cues to learn socially) but are often correlated. While NBDA models can allow for simultaneous fitting of multiple transmission pathways, our networks were often too correlated for good model convergence. Therefore, we analyzed each network type separately.

In NBDA, the weight assigned to the connections between individuals indicate the likelihood of social information to transmit between those individuals. Connections between individuals within a network can be either undirected, indicating that the connection weight is the same in both directions, or directed, indicating different connection weights depending on the direction of the connection. In terms of NBDA, connected pairs in networks with undirected connections are equally likely to transmit social information to each other while those in networks with directed connections have variable transmission likelihoods depending on which individual is the sender and which is the receiver.

### *Acoustic Networks*

Acoustic aspects of the sage-grouse strut occur in low-frequency ranges that propagate well across long distances (Dantzker, Deane et al. 1999), so we assume connectivity between all males in the acoustic network. To account for the degradation of sound intensity over distance (Forrest 2015), we used the squared, inverse distance between two individuals to determine the undirected weight of the edges connecting individuals in our social network. In NBDA, these weights translate to an increased chance of information transmission between individuals that are closer and can better hear each other.

### *Visual Networks*

Individuals within the visual networks were connected based on the ability of individual grouse to see each other on the lek given both topographical constraints and the presence or absence of the barrier. The weight of the network connections is set to the inverse of the distance between the two individuals (Patricelli and Krakauer 2010), such that closer individuals have a higher chance of transmitting social information, and the edges are undirected.

### *Territory- based networks*

Many male sage-grouse maintain an on-lek territory throughout the breeding season. Using the data of male positions collected in the field, we built 50% kernel density estimates for each male, which corresponds to a male's core territory (Gibson and Bradbury 1987). However, as interactions between male sage-grouse regularly occur at territory boundaries, we also included a 95% kernel density estimate, which approximates the full range of a male's territory. Sage-grouse territories may shift slightly throughout the season, so we estimated male's territory boundaries independently for each experiment by aggregating the position data of males from the 20 days prior to the experiment to build our kernel density territory estimates. We chose to use 20 days of data as this was the number of days that occurred before our first experiment and was thus the limiting amount of data available for any of our experimental trials. Once our 50% and 95% kernel density estimates of territories were determined, we calculated the directional percent overlap for each pair of males. We then built a weighted social network that connects males with overlapping territories with a connection weight determined by the percent overlap into each other's territory. Two networks were created for each experiment: once based on the 50% kernel density estimates and one based on the 95% kernel density estimates. Unknown males that were present for experiments (N = 20) are unlikely to hold territories and were thus given 0% territory overlap with all other males. For two territory-holding males in two experiments (one male per experiment), there were not enough data on their positions collected prior to the experiment to successfully run the kernel density calculations. For these two instances, we included position data collected on the day of the experimental trial in the kernel density calculations to establish territory boundaries. All kernel density estimates and percent-overlap calculations were conducted using the package adehabitatHR in R (Calenge 2006, R Development Core Team 2010).

### *Homogenous networks*

In the homogenous networks, all males present within an experiment were connected with a weight equal to 1. In NBDA, if the homogenous network is favored over the tested social networks, it is a good indication that either information is flowing homogenously through the group (i.e., there is no network structure) or that the tested social networks differ significantly than the real transmission pathways (Whalen and Hoppitt 2016).

### Network-based diffusion analyses

To quantify the social information use and test hypotheses about the flow of social information across leks with varying visual occlusion, we used a Bayesian adaptation of network-based diffusion analyses (Franz and Nunn 2009, Hoppitt, Boogert et al. 2010). For all analyses, lek ID and male ID were included as random effects and the measured distance to the playback speaker or robot was controlled as an individual-level variable (i.e., a fixed effect) predictive of learning directly from the female cue (i.e., asocial learning). These NBDA models infer the social transmission of information through a group by comparing the observed timing of each individual's behaviors with a proposed underlying social network (Table 2.1) and estimating the proportion of these behaviors that occurred because of social transmission. To test the **social strutting hypothesis**, we used Watanabe Akaike Information Criteria (WAIC) to compare models created with NBDA that include social learning through each of our networks to those inferring only asocial learning. The asocial models do not contain an underlying social network but do contain the random effects and individual-level variable on asocial learning rate. To evaluate the **contextual transmission hypothesis**, we again compared the model weights of each network type using WAIC to determine which network best explained the spread of response behaviors within each treatment (Whalen and Hoppitt 2016). We then tested the **occlusion hypothesis** by comparing the degree of social information use between the barrier and non-barrier treatments of each network type for all experimental trials combined. Lastly, to test the **mating success hypothesis**, we tested for a bias in social information flow from successful to unsuccessful males (Hasenjager, Leadbeater et al. 2020).

In our NBDA analyses, we used data about either a) the time of each male's first strut in response to the treatment or b) the male's lack of a strut response throughout the entire trial.

Thus, only males that were visible during the start of the treatment phase and either a) strutted at least once during the experimental phase or b) remained in view throughout the phase were included in analyses. Males that did not meet these criteria were excluded, as we do not know if their first strut occurred off-camera (the average number of males per network was 11.13 with SD = 3.86).

## RESULTS

### Social strutting

To test the hypothesis that males rely on social information from other males to inform their strutting behavior, we used WAIC to compare the social and asocial models. Within all our experimental treatments, the best supported NBDA model included a social network (Table 2.2; ΔWAIC values). In all cases, the asocial model had ΔWAIC > 2 from the best supported model. Thus, we have strong support for the hypothesis that, regardless of context, sage-grouse males are using social information to inform their individual strutting behavior.

### Contextual transmission

To test the hypothesis that the networks most important for social information flow would depend on the context (i.e., treatment) we used WAIC to compare models with different underlying social networks for each experimental treatment (Table 2.2; ΔWAIC values). Supporting this hypothesis, we found that the top network(s) for each treatment were different. Table 2.2 also contains information about the percent of struts explained by social transmission (% Social Struts). For the robot-no barrier treatment, the top model contained the core territory network, in which approximately 32% (HPDI: 7%-49.8%) of the struts could be explained by social transmission through the network. In the robot-barrier treatment, the acoustic network

**Table 2.2.** Within each experimental treatment, the percent of struts explained by social transmission through the underlying network (% Social Struts) is presented with 95% highest posterior density intervals (HPDIs). WAIC was used to compare each model. The best fit model for each treatment, as well as any models with ΔWAIC <2 are in bold. NBDA does not calculate % Social Struts for asocial models as there are no network connections present.

| | **Network** | **% Social Struts** | **Lower HPDI** | **Upper HPDI** | **WAIC** | **ΔWAIC** |
|---|---|---|---|---|---|---|
| Robot - No Barrier | Acoustic | 50.665 | 19.4145 | 87.178 | 190.6278 | 4.7596 |
| | Visual | 63.373 | 34.2781 | 87.4582 | 194.7387 | 8.8705 |
| | **Core** | **31.96** | **6.9904** | **49.8235** | **185.8682** | **0** |
| | Full | 38.151 | 6.1312 | 76.3 | 197.2223 | 11.3541 |
| | Homogenous | 63.384 | 27.3786 | 87.4903 | 202.0203 | 16.1521 |
| | Asocial | NA | NA | NA | 212.3274 | 26.4592 |
| Robot - Barrier | **Acoustic** | **61.617** | **42.8483** | **81.8562** | **144.8223** | **0** |
| | Visual | 55.102 | 32.5665 | 72.8307 | 152.0162 | 7.1939 |
| | Core | 40.442 | 29.625 | 50.3116 | 152.4774 | 7.6551 |
| | Full | 56.538 | 40.0303 | 69.6363 | 151.8124 | 6.9901 |
| | Homogenous | 66.934 | 35.8921 | 87.5393 | 163.1856 | 18.3633 |
| | Asocial | NA | NA | NA | 154.6457 | 9.8234 |
| Playback - No barrier | Acoustic | 42.01 | 7.9028 | 64.8999 | 334.1224 | 4.4509 |
| | **Visual** | **70.16** | **50.5542** | **83.1748** | **329.7702** | **0.0987** |
| | Core | 24.63 | 11.2794 | 38.5266 | 331.7959 | 2.1244 |
| | **Full** | **53.92** | **32.141** | **69.0434** | **329.6715** | **0** |
| | Homogenous | 67.96 | 37.086 | 85.2062 | 337.5726 | 7.9011 |
| | Asocial | NA | NA | NA | 332.4803 | 2.8088 |
| Playback - Barrier | Acoustic | 25.23 | 6.5625 | 54.1515 | 221.6419 | 6.0019 |
| | Visual | 42.788 | 10.5553 | 76.9266 | 226.4325 | 10.7925 |
| | **Core** | **36.597** | **24.8727** | **45.9418** | **215.64** | **0** |
| | Full | 43.599 | 19.4359 | 67.8354 | 225.1499 | 9.5099 |
| | Homogenous | 75.89 | 31.7142 | 91.8452 | 234.7931 | 19.1531 |
| | Asocial | NA | NA | NA | 222.1161 | 6.4761 |

model best explained the data (~61.6% [HPDI: 42.8%-81.9%] of struts explained socially). In the playback-no barrier treatment, the full territory network best explained the data (~53.9% [HPDI: 32.1%-69%] struts explained socially), but the visual network was also highly ranked (ΔWAIC = 0.0987; ~70.1% [HPDI: 50.6%-83.1%] struts explained socially). Lastly, for the playback-barrier treatment, the core network had the most support (~36.6% [HPDI: 24.9%-45.9%] struts explained socially).

**Table 2.3.** Across all experimental trails, experiments with and without the barrier were compared. Below, the percent of struts explained by social transmission through the underlying network (% Social Struts) is presented with 95% HPDIs, as well as the probability that the barrier treatment contains more social information than the no barrier treatment; a probability above 0.95 provides support that more social information is being used in the barrier treatments, while a probability below 0.05 indicates more social information use in the no barrier treatments. Both cases in bold.

| **Model network** | **% Social Struts, No Barrier (HPDI)** | **% Social Struts, Barrier (HPDI)** | **Probability of more social information in Barrier than No Barrier experiments** |
|---|---|---|---|
| Acoustic | 28.842 (8.788-51.46) | 32.29 (18.653-48.413) | 0.611 |
| **Visual** | **71.963 (58.531-84.92)** | **54.261 (38.734-70.82)** | **0.049** |
| **Core** | **4.573 (0.007-12.561)** | **35.878 (27.5-42.522)** | **1** |
| Full | 31.588 (5.868-53.697) | 48.816 (37.583-59.824) | 0.905 |
| Homogenous | 73.043 (57.984-85.519) | 74.011 (55.5791-87.770) | 0.55 |

Occlusion

To test the hypothesis that experimental occlusion would affect the degree of social information used, we compared all experimental trials in which the barrier was absent to all those in which the barrier was present for each of the network types. We found no evidence of a difference in the percent of struts explained by social transmission in the acoustic, full territory, or homogenous networks (Table 2.3). Supporting our hypothesis, however, we found that in models built using the visual network, there was a high probability (0.951) of the no barrier experiments containing more social information flow (~72% of struts explained by social transmission) than the barrier experiments (~54.3% of struts). Conversely, for models built with the core territory networks, the barrier experiments contained more social information flow (~35.9% of struts explained by social transmission) than the non-barrier experiments (~4.6% of struts; probability = 1).

**Table 2.4.** The percent of struts explained by social transmission originating from mated and unmated males (% Social Struts with HPDIs) is below, along with the probability that more social information originating from mated males is being used. A probability value above 0.95 provides support that more social information originated from mated males while a value below 0.05 indicates more information originating from unmated males through the respective network type. Both are indicated in bold.

| **Model network** | **% Social Struts from Mated** | **% Social Struts from Unmated** | **Probability of more social information originating from mated than unmated males** |
|---|---|---|---|
| **Acoustic** | **22.66 (13.6-32.06)** | **2.94 (0.02-2.93)** | **1** |
| Visual | 37.22 (25.07-48.45) | 35.06 (18.97-51.48) | 0.57 |
| Core | 4.02 (0.002-9.72) | 8.82 (3.35-13.8) | 0.138 |
| **Full** | **12.12 (1.158-23.70)** | **25.69 (14.34-35.54)** | **0.047** |
| Homogenous | 51.76 (34.75-67.90) | 51.91 (37.90-64.02) | 0.494 |

### Mating success

To test the hypothesis that a male's mating success will influence the probability that he is a source of social information in the network (i.e., that he is influencing the behavior of others in the network, thus transmitting social information), we divided each social network for all experiments into two networks: one containing only connections originating from mated males (N = 31 mated males) and one containing connections originating only from unmated males (N =

10 unmated males). Within the visual, core territory, and homogenous networks, no bias in transmission was found (Table 2.4); information was likely to originate from both mated and unmated males in these networks. We found a strong probability that, in the acoustic network, the social information being used throughout the system was originating more from mated males than unmated males (probability = 1). Conversely, within the full territory network, we found a bias of social information originating more from unmated than mated males (probability = 0.953).

## DISCUSSION

In this study, we observed the courtship behavior of male sage-grouse in response to cues of female presence across different modalities and habitat structures. By constructing a physical barrier across a visually open lek, we were able to examine the role of visual occlusion on the degree of social information diffusing through different transmission networks. Using NBDA, we found that males use social information from other males to inform their strutting behavior and that the paths of transmission of this social information among males depends on context. We also found a bias in information flow across some of our networks relating to male mating success.

### Social strutting hypothesis

Using WAIC, we found that, within each treatment, models that contained a social network explained the spread of strutting behaviors better than asocial models, where males gained information only from the experimental cue (Table 2.2; ΔWAIC values). This supports the hypothesis that male sage-grouse use social information about female presence to inform their strutting behavior. Wiley (1973b) posited that a “stimulus for Strutting might emanate from other Strutting males," but the presence of social information use in males of this species has not previously been demonstrated. Given the evidence of social learning in mate choice by females (Gibson, Bradbury et al. 1991), we predicted that males would use social information when information about female presence was limited; our data support this prediction.

However, when the female's presence and location was available to all males directly, as in the robot-no barrier treatment, we expected to see support for our asocial model but instead found that the best supported model contained the core territory network. This indicates that even when direct information is available, males are still attuning to their nearest neighbors' strutting behaviors. Notably, only ~32% of struts were explained by social transmission in this treatment, the lowest percentage of struts in any of the treatments' top-ranked models (the playback-barrier treatment contained a top rank model that was slightly higher, with ~37% of the struts explained by social transmission; the best fit model in the other treatments were all >50%; Table 2.2). Information about the female's presence was available to all the males on the lek in the robot-no barrier treatment, but not all males may have noticed her emergence and may have instead learned about her presence from their nearest neighbors.

### Contextual transmission hypothesis

Providing support for the contextual transmission hypothesis, we found that different networks best explained social information use in different treatment conditions, suggesting that males are flexible in how they use social information depending on context (Table 2.2). Our networks represent non-exclusive transmission pathways—males are likely gathering information simultaneously across multiple networks—but our analyses allow us to discuss the most prevalent pathway (i.e., the network with the most explanatory support) in each experimental treatment. In both the robot-no barrier and playback-barrier treatments, the models containing the core territory networks had the most support. In both treatments, the female cue matched the visual environment: the robot was visible on a visually open lek during the robot-no barrier treatment, and, in the playback-barrier treatment, a hen was audible (via playback), but not visible on a visually occluded lek. When the female cue matches the environment, it appears sage-grouse males rely primarily on their nearest neighbors as a source of social information. As female distance influences male sage-grouse strutting behaviors (Gibson 1996, Patricelli and Krakauer 2009), attuning to the nearest neighbors may give sage-grouse males information about not only when a female is present, but when she is close.

In the playback-no barrier treatment, where males could hear hens calling on a visually open lek, but could not see her, the models containing the full territory ($\Delta$WAIC = 0) and visual networks ($\Delta$WAIC = 0.0987) garnered the most support. In this treatment, it seems that males are looking beyond just their nearest neighbors—they are looking at males throughout their entire neighborhood and beyond, to all males they can see, and gathering social information about female presence. Considering the low occlusion in this treatment, we are unsurprised that males are relying more on visual transmission and, as they are looking towards the broader lek for social information, may indicate that they are visually scanning the entire lek for information about female presence and location.

As predicted, when the barrier was added to the robot treatment, the model containing the acoustic network had the most support. Information about female presence and location is the most limited in this treatment—only some of the males had access to the information. In this context, when visual occlusion is high, males seem to be attuning to the sounds of strutting of other males across the entire lek.

A potential complication of studying social information flow through a network is that one's position in any given social network dictates the information available and this information may, in turn, influence one's role in the social network (Kulahci, Ghazanfar et al. 2018). The impact of a temporally dynamic social network's influence on the transmission pathways of social information within a system needs additional study.

### Occlusion hypothesis

To test our occlusion hypothesis, which asks whether social information use changes with habitat structure, we examined the percent of social information used within each network type across all experiments where the barrier was either present or absent. When examining the acoustic, full territory, and homogenous networks, we found no evidence of difference between social information use in experiments with and without the barrier (Table 2.3). For the visual network model, we found a high probability that more social information was used in the no-barrier treatments. Considering the barrier's presence visually divides the lek, this result is unsurprising—there are fewer opportunities to learn visually when the barrier is present. However, in the model that contained the full territory network, we found the opposite result: higher levels of social information use when the barrier was present. This network represents males gaining social information from the males that overlap their full territory range but does not indicate *how* they learn—they may be using visual or acoustic cues from these male's struts. So, when the barrier is present, males may still be relying on acoustic information from other male's struts but seem to be learning preferentially from males in their territory's neighborhood. If males were using acoustic information from the entire lek when the barrier was present, we would have seen more social information use in the acoustic network, which includes all males. Our work shows that behavioral flexibility around transmission pathways of social information is likely occurring in response to experimentally manipulated habitats, but further research will determine if these flexible behaviors also occur within environments with naturally variable levels of occlusion.

Mating success hypothesis

For most network types, we found no evidence of a bias of information flow with respect to male mating success. Surprisingly, we found evidence of a bias of information originating from unsuccessful males in the full territory network models. Male sage-grouse that have never mated are more likely to strut than successful males when there are no females on the lek (Perry, Krakauer et al. 2019) or when they are further away (Patricelli and Krakauer 2009); unsuccessful males may be the first to strut in response to a distant hen. As the model containing the full territory network only had the top support in the playback-no barrier treatment, where no hens are visibly nearby, it may be that the unsuccessful males, who likely strut first in these situations, are driving the social information spread in this context.

We also found strong evidence of a bias in social information flow originating from mated males in the model containing the acoustic networks. The acoustic network model had the highest support in the robot-barrier treatment, where information about female presence was most limited. There is high visual occlusion in this treatment, and many males have no direct access to information about the female. In these contexts, where it is difficult for males to see whether a female is nearby or not, it appears that listening to the struts of successful males is the primary way that males gather social information. This finding suggests that males in this species have some knowledge about each other's mating status; however, this information may not be direct knowledge about other's copulation success—they may instead be attuning to the higher distribution of hens near successful males.

## Conclusions

Gathering social information is an important way that animals learn about their environment and behavioral flexibility in gathering and transmitting social information can have fitness consequences (Laland 2004). By using multiple modalities for sharing social information, animals are better able to communicate across complex or changing environments. For example, male wolf spiders increase courtship behaviors in response to female feedback across varying modalities (seismic or visual) and can adjust their courtship behaviors to appropriately match their signaling environment (Sullivan-Beckers and Hebets 2011, Sullivan-Beckers and Hebets 2014). Our work helps to clarify the group-level impacts of these individual behaviors by providing evidence that the underlying pathways of social information transmission through a group are also flexible and depend on the modality of information transmission as well as the broader physical and biological context. Specifically, as the habitat structure influences the social connections between individuals (He, Maldonado-Chaparro et al. 2019), our work demonstrates the ability of animals to gather social information through flexible transmission pathways in response to differences in the habitat's occlusion.

NBDA provide a method to quantify the degree of social information used in a system and to test the predictive ability of multiple underlying social networks on the spread of this information (Franz and Nunn 2009, Hoppitt, Boogert et al. 2010). For example, NBDA has been used to demonstrate that different social networks can transmit different information within the same social group using different signal modalities; Hasenjager et al. (2020) found that honeybee's dance networks predict recruitment to new feeding locations while olfactory-based interactions best predict returns to known food sites. Ours is the first study using NBDA to show that the same information can be flexibly transmitted through different social networks depending on the context. Similar to the spiders that adjust their courtship modalities on different substrates, the degenerate nature of similar information transmitting through multiple pathways of different modalities can help organisms communicate through complex and changing environments (Sullivan-Beckers and Hebets 2014, Hebets, Barron et al. 2016).

In addition to helping us to understand the flexible nature of animal communication, studying how the flow of social information through a group changes in response to variable environmental conditions can impact conservation and management decisions. For example, as sage-grouse are declining in much of their range, understanding which modalities are used to gather information during courtship is important. Prior research has uncovered the impacts of anthropogenic noise on sage-grouse (Blickley, Blackwood et al. 2012, Blickley and Patricelli 2012, Blickley, Word et al. 2012), and this study finds further support that acoustic information is an important source of social information in sage-grouse when visual occlusion is high. Further, these results help us to understand how lekking behaviors may be altered by habitat changes due to human activities. Habitat changes include increased wildfire risk due to invasive grasses and climate change as well as mowing and other sagebrush reduction treatments that are assumed to improve the habitat for sage-grouse; these changes all turn occluded habitats into open habitats. As much of the natural world is rapidly changing—through direct human impact (e.g., development, habitat management), indirect human influence (e.g., climate change), and natural disasters (e.g., fire, flooding; Janetos, Lambin et al. 2005)—understanding the preferred transmission paths of social information through changing and complex environments will be important to further understand the impacts of this behavioral plasticity on animal communication and spatial ecology. Lastly, as the social spread of courtship behavior is comparable to behavioral contagion, our results may have important consequences for the continued understanding of courtship dynamics. Displays that are socially influenced have increased likelihood of being temporally and spatially aggregated; socially transmitted courtship behavior may play an important role in inter-male competition, female assessment behavior, and lek evolution.

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## AUTHOR CONTRIBUTIONS

*RML was involved in study design and execution, data collection, analysis, and drafted the manuscript; WH assisted with statistical feedback and analysis; AHK was involved in study design, execution, and data collection; AH and BD assisted with video data collection; KM* *collected video data and conducted the barrier impact analyses; GLP was involved in study design and execution, field data collection, critically revised the manuscript, and, along with JSF, helped coordinate and fund the study. All authors assisted with manuscript revision. Figure 2.1B and 2.2A were taken by GLP. Figure 2.2B was taken by AHK.*

## SUPPLEMENTARY INFORMATION

### Barrier impacts

To determine the impacts of the barrier on grouse courtship and copulation behaviors, we used Wilcoxon signed-rank tests to compare the average strut rate and the number of copulations that occurred on days with and without the barrier present. To do this, we calculated the raw strut rate and the number of copulations that occurred within a 10-minute sample period during days when the barrier was added to lek. If the barrier was present for more than one day simultaneously, only the first day with the barrier was scored. Each of these samples was paired with a sample taken from the day prior to the barrier's construction. For both sets of data, the 10-minute sample period was scored 30-minutes after sunrise. On days when the barrier was present, only the struts and copulations that occurred within 5 meters of the barrier were counted. For days when the barrier was absent, the same boundaries were used as a control. On average, male had a higher strut rate when the barrier was absent (mean = 1.43 struts/minute) than when the barrier was present (mean = 1.18 struts/minute). However, the Wilcoxon signed-rank test showed no significant difference between the two groups (p = 0.4354). Similarly, the number of copulations recorded was higher on days without the barrier (mean = 1.75 copulations) than with the barrier (mean = 0.789 copulations), but the Wilcoxon signed-rank test indicated no significant difference (p = 0.804). These results indicate that adding the barrier to the lek did not significantly impact the sage-grouse's courtship behaviors.

Creating the playback of hen vocalizations

The playback file starts with sounds of a hen landing on the lek and continues with sporadic vocalizations to mimic natural hen noises. These playbacks were created by sifting through recordings taken over multiple days when hens were present on the lek for distinct female vocalizations that were not masked by other species or male strutting. The hen vocalizations were clipped out of the original recordings and randomized to create a new, 3-minute playback file. The spread of vocalizations (with gaps ranging from 1 to 10 seconds) in the playback was determined by creating a probability distribution of gaps from the original recordings and sampling gap times from this distribution in R (R Development Core Team 2010).

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# **CHAPTER 3:** Testing predictions of sensory drive on habitat choice using fine-scale mapping of sage-grouse leks

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## ABSTRACT

The physical structure of an animal's habitat influences multiple aspects of animal communication. Sensory drive predicts that environmental characteristics will impact the evolution of animal signals and signaling behavior, including microhabitat choice. However, quantifying environmental characteristics, particularly in complex natural environments, is difficult. Using fine-scale, three-dimensional mapping technology, we were able to quantify the habitat structure of wild sage-grouse leks and test predictions of sensory drive. Using experimental presentations of female cues and behavioral responses, we tested the prediction that male sage-grouse males choose display locations that maximize their visibility to females. Contrary to our prediction, we found that male sage-grouse performed courtship displays in locations with a horizontal visibility lower than expected by random chance. Additionally, we found no relationship between visibility and strut location when examining the direct line-of-sight between the male and the female cue.

## INTRODUCTION

An animal's habitat influences all aspects of its ecology. The physical structure of this habitat is especially important; it can provide protection from adverse weather (e.g., Milling, Rachlow et al. 2018), refuge from predators (e.g., Janssen, Sabelis et al. 2007, Ware, Dijkstra et al. 2019, Segura, Jimenez et al. 2020), and can impact signaling and communication (Endler 1992, Menezes and Santos 2020). Mobile animals have a degree of choice about their location within their environment and some of these habitat choices (e.g., where to nest, where to sleep, where to court) can have critical fitness consequences. Many studies have used occupancy modeling to approximate habitat choice in the wild (Beyer, Haydon et al. 2010) and active habitat choice has been extensively tested in the lab (e.g., Nay, Johansen et al. 2020, Sun, Brandt et al. 2021). Historically, quantifying the structural characteristics of natural habitats, especially at small spatial scales, has proved challenging. However, emerging remote sensing technology has made it possible to quantify various characteristics of natural habitat structure and further investigate microhabitat choice for wild animals. In this study, we use fine-scale habitat mapping to investigate the microhabitat choices made during courtship of a free-living species.

The physical structure of an environment can influence many aspects of an individual's behavior (Foster 1999). Differences in habitat structure have been linked to altered foraging behaviors, movement, mating behaviors, social interactions, and communication (e.g., Wiley and Richards 1982, Petren and Case 1998, McIntyre and Wiens 1999, Muir and Colwell 2010, Fewell 2019) across many different taxa (e.g., birds [Jenkins, Thompson III et al. 2017], mammals [Díaz-Ruiz, Caro et al. 2016], fish [Crowder and Cooper 1982], and invertebrates [Krupa and Sih 1993, Downes, Lake et al. 2000]). Animal communication, which involves individuals transmitting and receiving signals, is also affected by habitat structure. The structure of a habitat can influence an organism's visual field, acoustic landscape, and the social dynamics of a group, all of which alter an organism's ability to transmit and perceive social information (Ey and Fischer 2009). Thus, as animals have evolved within a specific environment, habitat structure can have profound evolutionary impacts on animal signals. Sensory drive predicts that a signal's structure, as well as an animal's signaling behaviors, will evolve towards efficacy—propagation and perception with minimal information loss—within the evolutionary environment (Endler 1992, Fuller and Endler 2018, Renoult and Mendelson 2019); evidence of the environment-signal matching predicted by sensory drive is abundant (Cummings and Endler 2018).

However, it may not be beneficial for animals to always maximize their signal efficacy; the biotic context of their environment (e.g., the presence of potential mates vs. predators) should also influence signaling (Endler 1992). For example, in the Trinidadian guppies studied by Edenbrow et al. (2011), an interaction between experience with predators and the structure of the environment influenced courtship behavior; guppies from high-predation areas performed fewer courtship displays in complex environments than guppies from low-predation areas. Additionally, an animal may have conflicting demands—they may need to signal to potential mates while minimizing their visibility to eavesdroppers or predators. In this way, signal efficacy may be differently optimized to balancing with conflicting demands. Lastly, animal's habitats are often spatially and temporally variable, so signals may not be environmentally matched through time or across an animal's entire range. Plasticity in signaling behavior may alleviate some of this mismatch; animals can adjust the timing, intensity, and location of their signaling behaviors to increase (or decrease) signal efficacy. Anoles, for example, increase the speed of their head bob displays and dewlap extensions in noisier environments (Ord, Stamps et al. 2010). We expect to see animals adjusting their signaling behavior in response to the social context and the structure of their microhabitat.

As observed by Endler (1992), there is an evolutionary link between sensory systems, signals, signaling behavior, and habitat choice. Sensory drive predicts that variation in the microhabitat (i.e., lighting conditions, visibility), as well as context, will predict variation in signaling behaviors and habitat choice. Thus, in situations where effective signal propagation has fitness consequences, we expect to see animals signaling in locations that improve signaling efficacy. However, as noted by Cummings and Endler (2018), the habitat choice component of sensory drive is relatively understudied. Extensive research has examined signaling habitat choice at the habitat-type or patch level by looking at animal occupancy (e.g., McKinnon and May 1994, Rosenthal, Hebets et al. 2019), but animals are often making active signaling decisions within these selected environments (i.e., at the microhabitat level). For example, multiple studies have investigated the placement of leks, but relatively few studies have investigated within-lek display locations of individuals (Endler and Thery 1996, Heindl and Winkler 2013). The complexity of natural landscapes is often difficult to quantify, so lab-based studies are often used to investigate active habitat choice on these small scales and to determine which environmental characteristics are important drivers of these choices (e.g., Hebets, Elias et al. 2008, Cole and Endler 2016). However, understanding how animals use their microhabitat in ecologically realistic contexts is necessary to better inform habitat mitigation and restoration and to apply appropriate conservation efforts (e.g., Coates, Brussee et al. 2017). With the emergence of fine-scale habitat mapping tools, we are now able to quantify characteristics of natural habitat structure that are important to signaling behaviors—like sender and receiver visibility—and can better investigate active habitat choice within wild environments.

In this study, we test sensory drive by investigating whether habitat structure predicts the courtship location of a free-living, lekking species, the greater sage-grouse (*Centrocercus* *urophasianus*). Greater sage-grouse are an ideal species to investigate sensory drive as their lekking habitats are quite variable, ranging from open fields to heavily occluded areas of dense sage (Figure 3.1). Sage-grouse also tactically adjust their courtship behaviors in ways that relate to their mating success (Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019). We used TLS (terrestrial laser scanning, a ground-based form of LiDAR) to map the habitat structure of greater sage-grouse lekking grounds. Using the three-dimensional habitat renderings created by these scans, we quantified the visibility at different locations within the landscape. With this design, we tested the sensory drive prediction that the visibility of the environment will influence where male greater sage-grouse will perform their courtship displays ("struts"). To do so, we compared two metrics of visibility—horizontal and line-of-sight—in locations where males were observed strutting and in random locations within 1 meter of the observed strut. The *horizontal visibility* is defined as the percent of unobstructed sight lines emanating from a male on a horizontal plane outward in all directions. The *line-of-sight visibility* is defined as the percent of unobscured sight lines in a path directly between the male and the female. As sage-grouse strut displays are evaluated by prospecting females, we predict that locations with higher horizontal visibility will correspond to actual male strut locations as opposed to randomly chosen locations. Alternatively, as dense sagebrush may reduce a male's ability to detect ground predators, males may strut in areas with lower horizontal visibility while increasing the line of visibility directly between themselves and a female (the "line-of-sight"). We predict that, in the presence of a female cue, locations with higher line-of-sight visibility will correspond with male strut locations as opposed to random points.

## METHODS

### Lek observation

Lek observations were conducted regularly on two leks (Chugwater and Monument, hereafter CHG and MNT) in Fremont County, Wyoming (42 49’ 44.42”N, 108 30’ 24.08” W) from 11 March to 5 May, 2017. On each of our study leks, males strutted in both visually unobstructed, field-like areas as well as in more visually obscured areas dense with sagebrush (Figure 3.1).

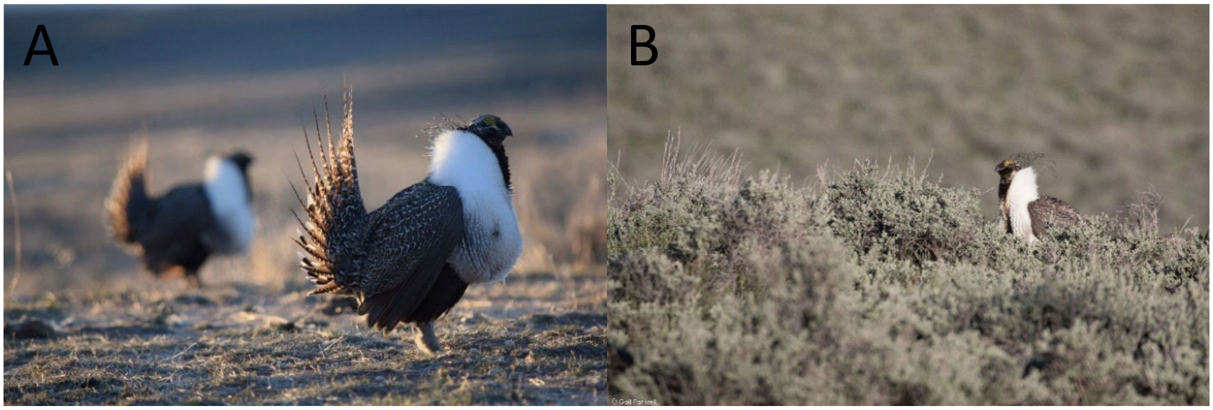

**Figure 3.1.** Sage grouse males strutting in (A) visually open areas and (B) visually occluded areas of the landscape with dense sagebrush.

From blinds placed 50-200m from the lek, we used spotting scopes to observe and video record lek activity from before first light—when male sage-grouse typically arrive—until all grouse had left the lek. Male activity and experimental trials were recorded using 1-2 high-definition cameras (Sony HDR-PJ430V and HDR-FX1) from the blind as well as with 1-2 wide-angle cameras (GoPro CHDHX-401) which were mounted atop telescoping PVC pipes (hereafter, “poles”) and raised ~15m above the ground (Figure 3.2A). These wide-angle cameras provided a top-down view of sage-grouse activity and were necessary for observing and tracking grouse through the occluded, sage-dense areas (Figure 3.2B). As these wide-angle cameras had a limited area of view, we used our in-blind observations to pre-select target areas within the occluded sections to place the wide-angle camera poles. These poles were placed on lek the day prior to an experimental attempt when no grouse were around, were raised into position the morning of the experimental attempt before grouse arrived, and were lowered after the grouse had left for the day. As these extended poles were often the tallest point in the local environment, we discouraged perching by adding perch deterrents to the camera housing; we observed these poles during the entirety of their extension and observed nothing perching on them. Post-season, all experimental video recordings were scored and data on male struts and positions were collected. Sage-grouse males can be individually identified by plumage patterns (Wiley 1973, Patricelli and Krakauer 2010, Perry, Krakauer et al. 2019), but as our target individuals were displaying in occluded areas with dense sage, the identifiable characteristics of their plumage was not visibile to our observation blinds. Therefore, we were unable to collect data about individual traits (i.e., mating success) or identify individuals between days.

**Figure 3.2.** (A) Distant image of the overhead camera setup deployed on a sage-grouse lek. The poles were only raised during active video monitoring and the top of the camera housing was fitted with perch deterrents. (B) The view from one of the overhead cameras. A male sage-grouse is circled in the top right corner of the image.

### Experimental methods

To determine if males adjust their strutting positions in response to female presence, we conducted manipulative experiments within the occluded areas of our study leks. Each experiment (N = 5) began with a 3-minute pre-trial to score baseline male strutting behaviors and positions. We then presented males with a cue indicative of female presence. This cue was either acoustic—a playback of hen noises—or visual—a biomimetic female model ("fembot"; see Perry, Krakauer et al. 2019 for construction details).

For the playback experiments, a 3-minute playback file consisting of hen vocalizations (see Chapter 2 for playback file information) was played to the target area through a speaker resembling a rock (Blickley, Blackwood et al. 2012).

For the robot experiments, a fembot was driven away from an on-lek blind to three pre-determined target flags, spending 30-seconds at each. The robot then returned via the same path, again spending 30 seconds at each the three target flags, for a total of one minute at each flag. The robot was then returned to the blind and the experiment was concluded. While at each target flag, the fembot maintained an upright posture and exhibits regular head movements to better imitate a live hen.

During one playback experiment, a live female landed in the target area 14 seconds after the playback started and departed 55 seconds later; as males respond similarly to both live hens and robots (Perry 2017), the time when the female was present in this experiment was coded as having a fembot cue. All other experiments were conducted when no live hens were visible within 50m of the target area. Post-season, the timing and location of each strut was scored for every male observed throughout the experimental trials (N = 13 males) using the software BORIS (Friard and Gamba 2016).

### Generating random points

To test our hypotheses, which compare the visibility of locations of male struts to the visibility of random locations, we generated random locations in ArcGIS Pro 2.7.2. We generated five random locations within 1 meter of each strut location; these random locations had to be at least 0.01m apart from each other and at least 0.1m from any strut made by that male during the same day; sage-grouse in our dataset moved at least 0.01m between struts. These random locations represent other areas in the immediate landscape where the male sage-grouse could have chosen to strut. Thus, if the random location was generated where a shrub existed in the landscape, it was moved to the closest location where a sage-grouse could viably strut (a "ground" location).

### Habitat mapping and visibility

Using a Riegl VZ-1000 TLS instrument (Riegl USA, Orlando, Florida), we scanned the target areas on our two study leks from four different positions. The scans were tied together using reflective targets with known GPS locations. TLS, a ground-based LiDAR (light detection and ranging), generates a high density point cloud (~100-1000 points per $m^2$), which was processed in RiSCAN Pro software (Riegl USA, Orlando, Florida).

Horizontal and line-of-sight visibilities were extracted from the point clouds using the viewshed3d package in R (R Development Core Team 2010, Lecigne, Eitel et al. 2020). The horizontal visibility of a male at a strut or random location is defined as the percent of unobscured sightlines (out of total sightlines) emanating 5m from the male in all cardinal directions between the maximum male and minimum female sage-grouse eye heights. This can be visualized as a thick disk within the point cloud centered on the target male with a 5m radius and a height spanning the difference between male and female eye heights (Figure 3.3). Sage-grouse eye heights were measured from photographs (N = 8) using known band widths as a scale in ImageJ (Rasband 1997-2018). Female sage-grouse eye height was set at 20cm, which was below our lowest measured female eye heights, but was reported in (Dantzker, Deane et al. 1999). Male sage-grouse eye height was set at 42cm, the maximum height measurement observed.

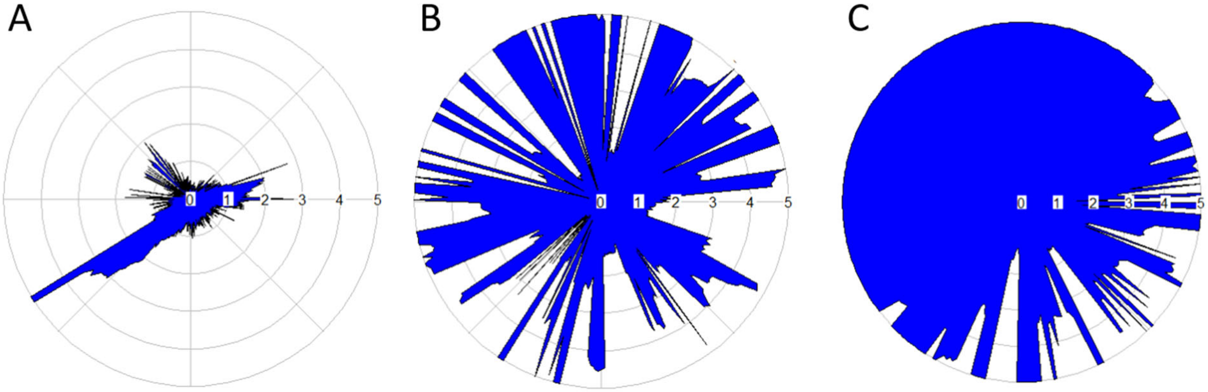

**Figure 3.3.** Radial plots generated by the horizontal visibility analysis. Sight lines, in blue, emanate outward in all directions from the male's location in the center until they hit an obstruction. These data represent views of locations with low (A), mid (B), and high (C) horizontal visibility. These radial plots represent a "top-down" view of the habitat. The numbers indicate the meters from center.

The line-of-sight visibility is calculated as the percent of a sphere (approximately the size of a female sage-grouse; radius = 10cm) visible to a male in each strut or random location. The sphere was located at the source of an experimental female cue, either the robot or playback speaker location. The sphere was centered 11cm off the ground, which allows for a 1cm buffer near the ground and reaches 1cm taller than our female eye height, approximating the top of a female's head height. For this analysis, the viewshed3d package calculates the percent of unobstructed sight lines between the sphere (at the female cue location) and a circle of the same radius at the male location. The male circle was centered at a height of 32cm; its tallest point was at 42cm, our maximum male eye height, and encompasses all measured male eye heights. This can be visualized as a cylinder within the point cloud connecting the female sphere and the male's circle (Figure 3.4). We previously attempted to calculate the line-of-sight in a manner more biologically appropriate to sight—namely, a pyramidal cone emanating from the female's eye towards the male, as opposed to a cylinder connecting the two individuals. However, as the width of conical individual sightlines within the cone increase over distance, and our point cloud has a standard resolution of 1cm, the percent visibility calculated was not biologically realistic.

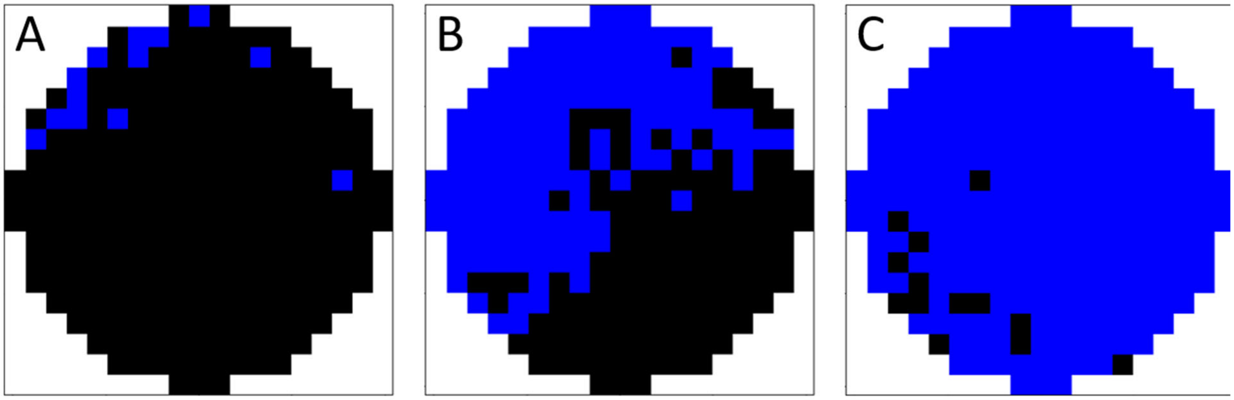

**Figure 3.4**. Cross-section view of the cylinders created by the line-of-sight analysis. Blue points indicate unobstructed sight lines between the male and female; black points represent obstructed sight lines. These data represent line-of-sights with low (A), mid (B), and high (C) visibilities.

<u>Statistics</u>

We tested whether our visibility metrics predicted male location use using two binomial regression models with logit link functions. Both models included location (strut or random) as the response variable; both models included Lek (CHG or MNT), the type of female cue, and either the horizontal or line-of-sight visibility metric as fixed effects. In the horizontal visibility model, which included data from every male strut observed, regardless of whether a female cue was present, female cue was coded as playback, fembot, or no female cue present. In the line-of-sight visibility model, which required a female cue location to calculate, only struts that occurred in the presence of a female cue were included; female cue was coded as either playback or fembot. We ran versions of each model that included male ID as a random effect, but as all male IDs contained the same ratio of strut locations (coded as 1) and random locations (coded as 0s)—a 1:5 ratio of 1s to 0s—Male ID explained no variance in the response variable (variance = 0.00, sd = 0.00) and was thus removed. We tested the overall significance of each fixed effect by comparing the log-likelihood ratio of a model that contained the relevant effect to one that did not. All statistics were run in R v3.6.1. Likelihood ratios and chi-squared tests were conducted using the package lmtest (Zeileis and Hothorn 2002). Plots were created using the ggplot2 and lattice packages (Sarkar 2008, Wickham 2016).

## RESULTS

### Horizontal visibility

We found that as percent visibility—the male's overall visibility in the horizontal plane—increases, the odds that a location is a strut location, as opposed to a random location, significantly decreases (Figure 3.5; Table 1, significant effect of percent visible). Specifically, with every increased percent of visibility, the odds that the location is a strut location decreases by a factor of 0.99. For example, if, at 50% horizontal visibility, the odds of being a strut location is 1:5, then at 75% visibility, the odds of a being a strut location decreases to approximately 3:20. Female cue did not have a significant effect on the odds of the location being a strut location. There was also a significant positive influence of lek (Table 1, significant effect of lek). A location originating on MNT has a higher likelihood of being a strut location; this is likely due to the higher number of struts observed on MNT (N = 237 struts) as compared to CHG (N = 49 struts) in this dataset.

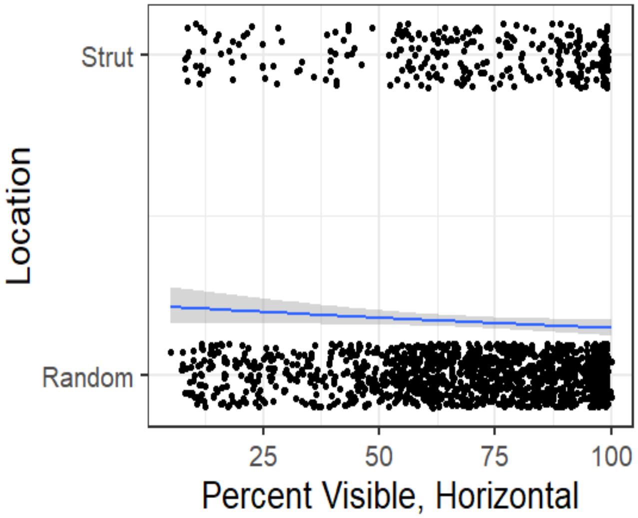

**Figure 3.5**. Percent horizontal visibility by location with the model fit line overlayed. Each point represents a single strut or random location.

**Table 1.** Results of the horizontal visibility model testing the impact of visibility, female cue, and lek on the odds that a location was a strut or random location.

| **Effect** | **Estimate** | **Standard Error** | **Chi Squared** | **P** |
|---|---|---|---|---|
| **Percent Visible** | **-0.011** | **0.004** | **8.131** | **0.004** |
| Female Cue[a] | | | 0.087 | 0.957 |
| No Female Cue | 0.046 | 0.156 | | |
| Playback | 0.019 | 0.171 | | |
| **Lek[a]** | | | **4.41** | **0.036** |
| MNT | 0.541 | 0.26 | | |

Chi Squared values were calculated comparing a model containing the relevant effect to a model without the relevant effect.

[a] Intercept represents experiments on CHG lek with a fembot present.

Line-of-sight visibility

Contrary to our prediction, line-of-sight visibility at a location did not significantly influence the odds that that location was a strut location as compared to a random location (Figure 3.6; Table 2). Similarly, neither female cue nor lek had significant influence on the odds that a location was a strut location.

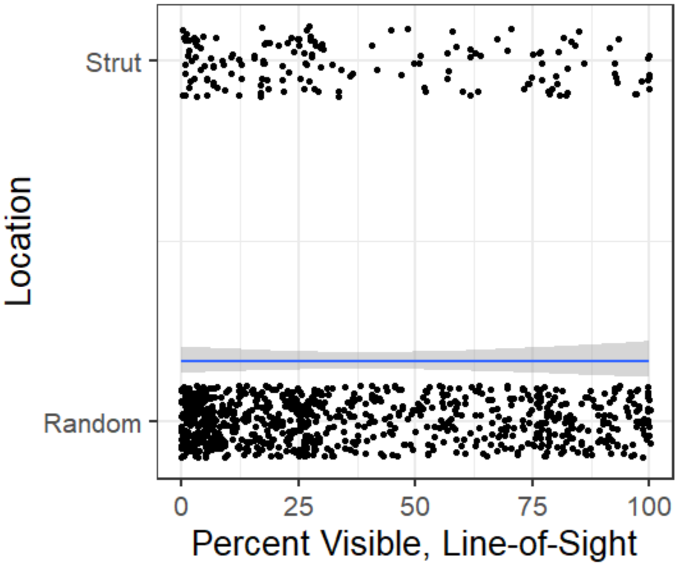

**Figure 3.6**. Percent visibility for line-of-sight metrics by location; the model fit line with standard error is overlayed. Each point represents a single strut or random location.

**Table 2.** Results of the line-of-sight visibility model testing the impact of visibility, female cue, and lek on the odds that a location was a strut or random location.

| Effect | Estimate | Standard Error | Chi Squared | P |
|---|---|---|---|---|
| Percent Visible | -0.0001 | 0.003 | 0.002 | 0.965 |
| Female Cue[a] | | | 0 | 0.999 |
| Playback | 0.0003 | 0.173 | | |
| Lek[a] | | | 0.0004 | 0.985 |
| MNT | 0.0047 | 0.25 | | |

Chi Squared values were calculated comparing a model containing the relevant effect to a model without the relevant effect.

[a] Intercept represents experiments on CHG lek with a fembot present.

## DISCUSSION

While sensory drive is well studied, the prediction that environmental characteristics should influence microhabitat choice for signaling is relatively understudied (Cummings and

Endler 2018), due in part to the difficulty of quantifying habitat characteristics (Théry 2001). In studies conducted on wild populations, the complex nature of habitat structure is often reduced to categorical variables by necessity (e.g., Rosenthal, Hebets et al. 2019). Using fine-scale habitat mapping technology, we quantified the structure of natural sage-grouse strutting habitats to test the predictions that sage-grouse would choose display locations that maximize the signal received by females.

We found that as the overall horizontal visibility of a location increased, it was less likely to be used as a strut location for male greater sage-grouse. This is counter to our prediction that male sage-grouse would choose their strut locations to prioritize their visibility to any female in the area. The decreased visibility of locations where males chose to strut may indicate an increased horizontal concealment in that location, as visibility and concealment are negatively correlated (Olsoy, Forbey et al. 2014). This may suggest that strutting males are minimizing visibility to ground predators. However, we think this is unlikely to be the sole explanation for this behavior, as the majority of observed predation attempts on sage-grouse leks have been aerial predators (Wiley 1973). Further, increased occlusion increases the perceived risk of predation in some species (Ingrum, Nordell et al. 2010, Embar, Kotler et al. 2011). Investigation of sage-grouse vigilance behavior with habitat structure may provide further insight.

To account for this potential risk assessment, we also considered that males may instead choose locations that increase their line-of-sight visibility. Contrary to our prediction, the line-of-sight visibility metric did not predict whether the location was a random or strut location. In our data, the average distance between the male and the female cue was 14m (SD = 8.3m). Our random locations were created within 1m of each strut to represent possible locations that the male could have strut, given his actual position in the microenvironment. However, it is possible that the 1m scale used to determine the random locations was too small compared to the distance to the female cue. Examining this line-of-sight relationship when males and females were in close courtship (i.e., 5m or less) would provide additional insight.

Our results suggest that habitat structure plays an important role in sage-grouse courtship location choice, with males choosing strut locations with higher concealment, but this relationship is the opposite of what would be predicted if males were maximizing overall visibility to females. This suggests that there are other factors important in shaping microhabitat choice. Our study illustrates the need for continued work into the impacts of sensory drive on microhabitat choice. Understanding how sensory drive shapes habitat use is necessary for understanding how selection acts on fitness-critical behaviors, like courtship signaling and antipredator behaviors. By using TLS to generate high-resolution point clouds, we were able to quantify the full complexity of the habitat structure of our study sites and investigate how this structure influences animal microhabitat choice.

Fine-scale mapping technologies are an important tool for developing research in behavioral ecology (Forbey, Patricelli et al. 2017). In addition to quantifying complex environmental characteristics, technologies like TLS can map an environment at a scale that matches an animal's habitat use. Combined with behavioral data, this technology can expand research investigating the influence of microhabitat structure on animal courtship, foraging and nesting behavior, predator-prey dynamics, social interactions, and communication. Additionally, understanding how animals use the microhabitats within their environment can better inform management and conservation practices including habitat mitigation and restoration efforts.

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## AUTHOR CONTRIBUTIONS

*RML contributed to project design and execution, project funding, field and video data collection, statistical analyses, and wrote the manuscript draft. PJO contributed to TLS point* *cloud rendering, visibility data extraction and analysis, and manuscript feedback. AH and RF both assisted in video data cleaning and collection. GLP contributed to project design and execution, field data collection, extensive manuscript revisions, and, along with JSF, coordination and funding of the project.*

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