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2 TITLE: Successfully-mating male sage-grouse show greater laterality in courtship and
3 aggressive interactions

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23 Word Count: 6698

Lateral biases in behaviours are common across animals. Greater laterality may be beneficial if it allows for more efficient neural processing, yet few studies have considered the possible importance of individual variation in lateral biases in wild animals, particularly for social behaviours. We examined lateral biases in lekking greater sage-grouse *Centrocercus urophasianus*, a species in which males show lateral orientations during aggressive encounters and courtship interactions. For aggression, we found no significant lateral bias in fights, but when examining another agonistic behavior, the side-to-side facing past encounter, we found a left-eye bias but only in males that successfully mated with females. For courtship behaviour, we found that successfully-mating males were more strongly lateralized than non-mating males but the direction of laterality depended on whether males were using their binocular frontal field (left-eye bias) or monocular lateral hemifield (right-eye bias). Bias depended on social context as well; non-mating males showed a bias in courtship orientation only when far from the female. Our results reveal a complex pattern of laterality depending on the mating success of the male, his behaviour, and the social environment in which he is acting. We found support for the hypothesis that greater laterality may be beneficial, although the mechanism for this relationship in this species remains unknown.

Key Words: Laterality, aggression, mating success, courtship, *Centrocercus urophasianus*, sage-grouse, visual field, lek

48 Laterality, the propensity to show side biases during behaviours, is widespread among
49 animals (Vallortigara & Rogers, 2005). Many examples of laterality are the result of
50 hemispherical specialization, when specific sensory information, motor control, or other
51 cognitive functions are processed on one side of the brain more than the other. One of the
52 most general adaptive hypotheses states this specialization may allow animals (including
53 humans) to process information more efficiently by avoiding ‘hemispheric indecision’
54 caused by conflicting signals from different regions of the brain, and may also allow
55 multi-tasking by segregating processing in each hemisphere (Crow, Crow, Done, &
56 Leask, 1998; Rogers, Zucca, & Vallortigara, 2004). This functional hypothesis predicts
57 more strongly lateralized individuals or populations will have better performance on
58 relevant tasks. In animals, support for a relationship between the degree of laterality and
59 better performance primarily come from ecological tasks, such as foraging, navigation,
60 and predator detection (e.g., Magat & Brown, 2009; Rogers et al., 2004).

61 Many social behaviours, including courtship and agonistic interactions, also show
62 laterality across a wide range of animals (George, Hara, & Hessler, 2006; Hews,
63 Castellano, & Hara, 2004; Templeton, Mountjoy, Pryke, & Griffith, 2012; Ventolini et
64 al., 2005). There has been some attention to understanding population-level biases in
65 interactions (Arnott, Ashton, & Elwood, 2011). However, few investigations have
66 assessed inter-individual variation in laterality during social interactions and its
67 relationship to performance in these tasks or to other measures of fitness, particularly in
68 the wild. Instead, most studies examining inter-individual variation in laterality of social
69 interactions have focused on short-term tactical biases that are not directly related to
70 known asymmetries in brain function. For example, lateral biases can be plastic and
71 contingent upon phenotypic asymmetries, such as in male fish preferentially presenting
72 the more attractive side of their body to females (Amcoff, Arnqvist, & Kolm, 2009;
73 Gross, Suk, & Robertson, 2007), or birds turning to optimize their signal efficacy in an
74 asymmetric signaling environment (Dakin & Montgomerie, 2009; Yorzinski & Patricelli,
75 2010). Regardless of whether lateral biases are related to asymmetries in brain function,
76 in sensory capabilities, or in signal production, the importance of variation in laterality
77 among individuals in social behaviours generally remains an open question.

78 We studied lateral biases in inter- and intrasexual behaviour in a lekking bird, the greater
79 sage-grouse (*Centrocercus urophasianus*). Sage-grouse have been the subject of decades
80 of research on female mate choice and sexual selection (Gibson, 1996; Gibson &
81 Bradbury, 1985; Gibson, Bradbury, & Vehrencamp, 1991; Johnson & Boyce, 1991;
82 Patricelli & Krakauer, 2010; Wiley, 1973b). Male sage-grouse compete to defend small
83 display territories on the lek; females visit leks and are relatively free to assess the
84 displays of different males and choose a mate. Copulations are generally easy to observe,
85 allowing researchers to relate variation in male behaviour with female mating decisions
86 (Gibson, 1996; Patricelli & Krakauer, 2010). This species is particularly amenable to
87 questions of lateral biases in behaviour since most intra- and intersexual behaviours occur
88 in lateral orientations to their (male or female) social partner (Figure 1). This allows one
89 to determine which eye is being used, and, assuming contra-lateral processing of visual
90 inputs, which hemisphere may be involved initially in processing information during a
91 given interaction.

On sage-grouse leks, agonistic interactions are common, and typically involve males approaching each other at a territory boundary, moving into a “facing-past encounter” (FPE), and often culminating in physical fighting (Pellis et al., 2013; Wiley, 1973b). FPEs occur when males are side-to-side and facing opposite directions (e.g., the left side of one male is facing the left side of the opponent). Although fighting behaviour is undoubtedly critical for maintaining territories and avoiding interruptions during courtship, the rates and intensity of agonistic interactions have yet to be assessed with respect to mating success in this species despite their importance in other lekking grouse (Alatalo, Hoglund, & Lundberg, 1991; Nooker & Sandercock, 2008).

Female greater sage-grouse are thought to base their mating decisions on variation in male sexual displays and males frequently adopt lateral orientations towards females during these displays (Gibson, 1996; Gibson & Bradbury, 1985; Patricelli & Krakauer, 2010). The courtship display of male sage-grouse involves a single stereotyped behaviour (the “strut”) lasting approximately two seconds consisting of movements of the wings and vocal sac, mechanically generated feather sounds and vocalizations (Krakauer et al., 2009; Wiley, 1973a). Males may produce several strut displays per minute, typically moving and re-orienting themselves in between struts. Some early naturalists thought males were ignoring females due to their apparent lack of frontal focus directed towards nearby females (see Bent, 1932), but recent studies on acoustic radiation patterns suggest males may in fact be beaming the loudest sides of their highly-directional vocalizations at females (Dantzker, Deane, & Bradbury, 1999).

Given that sage-grouse engage in a number of laterally oriented social behaviors, and those behaviors are used in circumstances critical to fitness, this species provides an excellent opportunity to examine the adaptive context of behavioral laterality. Our study uses behavioural observations of lekking males to ask two questions: first, do male sage-grouse show a lateral bias in their inter- and intrasexual behaviours, and secondly, does the degree of bias relate to male mating success? We address these questions by examining multiple aggressive behaviors as well as a range of courtship conditions, and therefore consider whether laterality varies across these contexts as well. Our results broaden the taxonomic and behavioural scope of existing studies of lateral biases in free-living animals, and more importantly, link individual variation in these behaviours to a measure of fitness.

METHODS

Study species and study site

Our field observations were collected at a sage-grouse lek (“Monument Lek”), approximately 30km from Lander, WY, USA. Leks were watched daily from early March until the end of April in 2007. Males ($n = 42$) were individually identified using idiosyncrasies in undertail coverts (Krakauer et al., 2009; Wiley, 1973b), and their positions mapped relative to a 10x10m grid of stakes. Lek attendance varied among males, with males detected on as few as two to as many as 46 days. All agonistic and courtship behaviours were filmed continuously using 3 HD camcorders (Sony HDR-HC1

or –HC3) starting as soon as it was bright enough to film and until the last male departed the main lek area, typically 1h - 3h per day. All methods were approved under Wyoming Department of Game and Fish permit #405 and University of California Davis Institutional Animal Care and Use Committee protocol #11662.

Collection of behavioural data from video

Agonistic interactions were recorded from approximately 1h all-occurrence samples from five days during the 2007 lekking season. Only FPEs (side-to-side “facing past encounters”) and the starting orientation of physical combat (hereafter fights) are considered given that they were the most commonly observed behaviors and more often performed in lateral orientations compared to other behaviours (e.g. approaches, chases). A single interaction between two males could involve multiple events—FPEs, fights—separated by different behaviours, and males could change orientation within an interaction when changing behaviours. Male orientation for each event during an interaction was scored as (L)eft eye towards opponent, (R)ight eye towards opponent, or undetermined orientation. Only Left and Right data are used in analyses.

Courtship interactions were observed from videos taken on 9 days during the 2007 field season. Our data come from a combination of courtships of live females (N = 2052 struts) and courtships of a biomimetic robotic female (N = 1242 struts) deployed during experiments on male courtship plasticity (Patricelli & Krakauer, 2010). For each strut event during a courtship interaction, male orientation to the nearest female or robot (hereafter “strut angle”) was estimated to the nearest 15° with the aid of a transparent overlay marked in 15° increments that was held up to the video monitor. The head is held rigidly forward during the strut itself, although males may swivel their head somewhat before and after strutting. Male location at the conclusion of each strut was recorded, and distance to the nearest female at the time of each display was estimated by interpolating female position from locations recorded approximately every 15sec.

To measure mating success, we watched all lek videotapes for copulations starting 4 days before the first copulation in the field was observed until the end of the season. The identity of the male in approximately 90% of copulations could be determined using this method (AHK unpub. data). Female sage-grouse could not be identified individually in our study; therefore mating success represents the sum of all mating events rather than the number of individual females with which a male mated. Molecular paternity analyses suggest mating success is likely a good, although not perfect, estimate of male reproductive success (Bird et al., 2013; Semple, Wayne, & Gibson, 2001). Given the extreme skew in mating success in this species, no appropriate statistical transformation for the raw number of copulations was available. Instead we treat mating success as a binary variable with males being either observed to copulate or not (i.e. “successfully-mating” or “non-mating” males respectively).

Statistical analysis

Fights, and in particular, FPEs, typically occur in orientations such that both animals are viewing each other with the same eye (i.e. left eye or right eye for both animals, Pellis et al., 2013). Given that agonistic interactions necessarily involved two males, we randomly

assigned each event within an interaction to one of the two males to prevent double-counting of the same behaviour. In the rare cases where males were viewing each other with different visual fields during a given event, for consistency we also randomly selected only one male of the pair for inclusion in our analysis. Therefore, our data for each male consist of approximately half of the events from each interaction, and the proportion left and right-eye orientation is tallied across multiple interactions if the male engaged in multiple agonistic encounters during our sampling period. Additionally, we only utilized data from identified males with known mating histories. We tested for differences in bias related to male mating success in three sets of agonistic behaviours: all fights, all FPEs, and only the initial FPEs in an interaction sequence. Unlike the courtship analysis (see below), the numbers of events for each male in these analyses were insufficient to use a generalized linear mixed model with male ID as a random effect to account for non-independence of male data across behavioural category. Instead we ran separate generalised linear models with binomial error distributions—pooling all events for each male to a single pair of [left, right] values—using the *glm* function in R (R Development Core Team, 2010). We weighted each male according to the number of events belonging to that male in the sample, thereby allowing us to favor males with more certain laterality estimates (note that no weight exceeded three times uniform weighting). The response variables for all three agonistic models were the proportion of events in which the left eye was directed towards the opponent, and models also included male mating success as a binary variable.

For courtship data, we initially pooled data for all identified males and calculated a mean strut angle using a Rayleigh test for unimodal circular distributions using the *CircStat* package in R (R Development Core Team, 2010). Given that our data were unlikely to come from a unimodal distribution, we also compared numbers of displays in the left and right field of vision. Using the strut angle we further subdivided the numbers of displays in which the target of courtship was in the lateral and frontal hemifields; prior research on domestic chicks indicated that laterality in some social tasks may differ depending on whether the frontal or lateral hemifield is being used, and that some input to the frontal field may be processed by the ipsilateral hemisphere (Vallortigara, Cozzutti, Tommasi, & Rogers, 2001). No measurement of the visual field exists for sage-grouse; instead, we based our categorization of lateral and frontal visual fields using values published for other species (see Fig. 2; Dawkins, 1995; Fernández-Juricic, Erichsen, & Kacelnik, 2004). We defined the frontal field as containing struts up to 30° from center, and the lateral hemifields as extending from 45° to 135° and 225° to 315° degrees. We were unable to surround males with multiple cameras as in previous directionality studies (Patricelli, Dantzker, & Bradbury, 2007; Yorzinski & Patricelli, 2010), meaning some strut angles near the border between frontal and lateral hemifields could be incorrectly assigned. While the limits of the frontal field may be closer to 15°, we felt that the 30° threshold for the frontal field would be conservative since the potential inclusion of some lateral hemifield orientations in the frontal hemifield category would make it more difficult to detect differences in bias between the frontal and lateral visual fields. Male-female distance was assigned to one of three bins (< 9 m, 9-25m, or > 25m); these categories relate approximately to close courtship, having an intervening territory between the male and female, and having multiple intervening territories, respectively.

Our statistical approach for analyzing courtship data was as follows: we used generalized linear mixed models with a binomial variance structure, proportion of struts on the left as the response variable, male mating success, distance (as a categorical variable) and visual field region (binocular or lateral), male identity as a random effect, and weighted by the number of observations per male. Models were tested using the *lmer* function in the *lme4* package in R. We started with a full model including all interaction terms and iteratively dropped terms until the simpler model was no longer equivalent when compared using the *anova* function. We initially included stimulus type in the glmm to test for differences in laterality of courtship toward real females and robotic females, however the model failed to converge due to poor balance of observations across combinations of males and stimulus type. A binomial glm with the same explanatory variables failed to yield any significant term involving stimulus (all $P > 0.19$). Moreover, mean male strut rate toward the robot was not significantly different than strut rate toward real females ($p > 0.9$) and there was a significant correlation between male strut rate in real versus robotic courtships (Patricelli & Krakauer, 2010). Therefore we pooled data across both natural courtships and courtship of the robot.

To obtain parameter estimates for the proportion of left-eye behaviors in each group, we transformed the model coefficients from the binomial glm or glmm models (for the agonistic and courtship analyses, respectively). Since model coefficients of categorical variables represent contrasts with the baseline category (i.e. intercept), interaction terms were calculated e.g., estimated left-eye proportion for factor X = $e^{(\text{intercept} + \text{factor X})} / [1 + e^{(\text{intercept} + \text{factor X})}]$. We also calculated 95% confidence intervals for these estimates, e.g., upper limit of the 95% CI for estimate of factor X = $e^{(\text{intercept} + \text{factor X} + 1.96 * \text{S.E. of factor X})} / [1 + e^{(\text{intercept} + \text{factor X} + 1.96 * \text{S.E. of factor X})}]$.

RESULTS

Agonistic behaviours

We recorded agonistic behaviours ($N = 63$ fights and $N = 310$ facing past encounters) from a total of $N = 9$ successfully-mating and $N = 25$ non-mating males (Fig 3, Table 1). Individual sample sizes ranged from 1-5 fights per male (mean = 2.3) and 1-25 FPEs per male (mean = 9.1). Our first model indicated that for fights, there was a non-significant trend for successfully-mating males to be more right-eye biased compared with non-mating males ($P = 0.11$). The 95% confidence intervals for both groups overlapped 0.5 left-eye orientation (Table 1). In contrast, the model containing all FPEs revealed that successfully-mating males were significantly more left-eye biased than non-mating males ($P = 0.0002$), and the confidence interval for successfully-mating males did not overlap 0.5 (Table 1). The final model included only the first FPE in a behavioural sequence and returned the same results as the previous model—successfully-mating males were significantly more left-eye biased than non-mating males ($P = 0.002$) and the 95% confidence interval did not overlap 0.5 left-eye orientation (Table 1).

Courtship orientation

Males showed a slight mean right-eye bias of 38° , with a modal angle of 0° (Fig 4; $R = 0.052$, $N = 3294$ struts by 42 males, $P < 0.0001$). We used a generalised linear mixed

model to compare the number of struts in which the left or right eye was aimed at the female. This model included male mating success ($N = 10$ successfully-mating males, $N = 32$ non-mating males), visual field, distance to the female, as well as interactions between mating success and visual field and between distance and visual field (Fig 5; Table 2). Successfully-mating males showed significantly different biases at all distances and with both the frontal and lateral visual fields compared to the baseline group of non-mating males using their frontal field in close courtship. In the frontal field, successfully-mating males were more left-eye biased than the baseline group, while in the lateral field, these males were more right-eye biased than the baseline group. Additionally, non-mating males using their frontal field showed significantly different orientation when far away ($> 25\text{m}$) than when in close courtship ($< 9\text{m}$). There was also a trend ($P < 0.06$) for non-mating males in distant courtships ($> 25\text{m}$) to show different lateral biases when using their lateral versus frontal visual fields. The 95% CI for orientation of successfully-mating males using their frontal visual field did not overlap 0.5; furthermore, this confidence interval did not overlap with that of successfully-mating males using their lateral visual field.

DISCUSSION

Male sage-grouse on a lek face a complex social environment filled with numerous competitors and potential sexual partners. Our results show evidence for lateral biases in two common and laterally-oriented behaviours that males use in navigating these challenges. First, we identified a left-eye bias in the agonistic facing past encounters (FPE), but only in successfully-mating males (Fig 3; Table 1). Successfully-mating males also showed a non-significant trend towards right-eye bias in fights compared with non-mating males. Since many aggressive encounters begin with FPEs then escalate to fighting (Pellis et al., 2013; Wiley, 1973b), this suggests the dominant orientation of at least some males may change as these agonistic interactions proceed.

Several questions arose from these results, including how orientation affects the outcome of fights or FPEs. Interactions between territory-holding males and the typically younger non-territorial males result in clear winners and losers via ejection from the territory or in some cases the lek itself. However, we were not able to identify victors in interactions among the territory-holding males examined in this study using simple behaviours such as who retreats first or second. Thus further investigation into the consequences of laterality will depend on developing a more nuanced ethogram for these behavioural sequences. Similarly, we will need to expand our sample of agonistic events to explore the relationships between laterality, partner choice, social environment, and the manner in which these behavioural interactions play out. In our analysis we treated multiple events within an encounter as independent, as males have the opportunity to re-orient themselves when switching behaviors within an interaction (see *Relationship to other laterality studies* section below). We analyzed only the initial FPE in an encounter and found, just as we did when considering all FPEs, that successfully mating males were more left-eye biased than non-mating males. While this suggests the potential non-independence of behaviours did not effect the findings of this study, a larger dataset would allow us to address more detailed questions related to the interactive nature of

agonistic encounters and the importance of lateral biases in shaping male territoriality and dominance on the lek.

Secondly, we identified a modest overall right-eye bias to the strut display of males in a courtship context. When further partitioning our data using an approximation of the visual field of the sage-grouse, we found patterns of laterality depended on male mating success, whether the female was in the frontal (binocular) field or in one of the lateral (monocular) hemifields, and in some cases, the distance between the male and the target of courtship. Successfully-mating males were significantly left-eye biased in the frontal field; in the lateral field, the direction of bias was significantly more right biased than in the frontal field although the confidence interval for this estimate overlapped 0.5 (1:1 left-eye:right-eye). Distance had a stronger effect on non-mating males; in the frontal field, these males were significantly more left-biased when far from the female (or robotic female) compared with their orientation in close courtship.

In both intrasexual and intersexual interactions, lateral biases tended to be greater in males that successfully mated with females. These represent the first data, to our knowledge, that show a relationship between laterality and an estimate of fitness in a wild system. There are several potential explanations for this relationship. It is possible that there is a causal link between laterality in social behaviours and mating success. Increased laterality could signify better performance in these tasks leading directly to social dominance or increased attractiveness. For example, strut rate is an important correlate of male mating success, and these rates are determined primarily by the repetition rate rather than duration of the display themselves (Gibson et al., 1991; Patricelli & Krakauer, 2010). While strut rates are undoubtedly sensitive to energetic capabilities of males (Vehrencamp, Bradbury, & Gibson, 1989), there might also be cognitive aspects as males assess changes in the positions and behaviours of females and neighboring males and plan the orientation and position of their next display (Patricelli & Krakauer 2010). Additionally, the bias during courtship could be related to asymmetries (i.e. directionality) in males' display signals (Dantzker et al., 1999), with successfully-mating males either more asymmetric or more skillful at courting females at an optimal angle. It is also possible that the relationship between mating success and laterality is indirect. If more lateralized males are also better foragers or are more efficient at recognizing and evading predators, they may be in better condition than less strongly lateralized males, and this ability to maintain condition may be related to mating success (Vehrencamp et al., 1989).

Given the potential benefits to lateralization of behaviours, what could be limiting the expression of side biases in these situations? Why do males fail to use preferred orientations in all conspecific encounters? We can speculate on a number of possible factors that could contribute to the relatively modest levels of laterality observed in our population; discussions of general constraints on laterality can be found elsewhere (Vallortigara & Rogers, 2005). First, there may be trade-offs between achieving an orientation and other aspects of the behaviour. As mentioned above, display rate in sage-grouse is typically the strongest correlate of mating success, and the need to display frequently in a variety of orientations could make precise posturing difficult over an extended bout of courtship. Additionally, males face a complex and dynamic social

landscape, with conspecifics of both sexes moving and altering their behaviour rapidly over time. Therefore males may be balancing many social interactions at once, making it difficult to fully commit to optimizing orientation for any single behaviour or social partner. This complexity highlights the challenges and opportunities of studying behavioral laterality in the field compared with more tightly controlled laboratory environments. Finally, as mentioned above, the possibility exists that the expression of behavioural side bias may be dependent on ontogeny or physiological state, such that not all individuals are expected to show these preferences. This variation would make the detection of population or class-wide biases more difficult.

Relationship to other laterality studies

It can be difficult to generalize about laterality of various behaviours across animals since the direction of side biases is often inconsistent across taxa, (Bisazza, Cantalupo, Capocchiano, & Vallortigara, 2000; Brown & Magat, 2011). That said, our finding of left-eye bias in aggressive interactions is consistent with studies on a range of vertebrates that have similarly found greater aggression on the left side or when using the left eye (Hews et al., 2004; Vallortigara & Rogers, 2005). Studies in domestic chickens suggest the left visual hyperstriatum acts to inhibit aggressive behaviour, leading to the left-sided behavioural bias since the contra-lateral right-eye input is more likely to be suppressed (Deng & Rogers, 1997). This explanation may account for why sage-grouse FPEs tend to be left-eye biased. However, this mechanism may not explain why the most aggressive interactions (i.e., fights), show a tendency toward a right-eye bias. It is possible that assessment of the opponent occurs differently depending on which eye is being utilized, as has been suggested in red deer (Jennings, 2012, 2014). Additionally, because escalation to fighting requires tactical considerations of when an attack can be carried out with minimal risk of a successful counterattack (Pellis et al., 2013), these conditions often take place after sequences of feinted attacks, repositioning, and counter-positioning by both males, which could serve to shuffle male orientation before a fight. Indeed, our data showed that initial FPEs when males commence close interaction were more left-eye biased than were FPEs in general, a larger set of events that included more opportunity for shuffling via counter-positioning. These factors, along with differences in sample size resulting in different statistical power in the various models, could help explain why fighting males appears show weaker and potentially different lateral biases than males in FPEs.

The literature on orientation and bias during courtship is both less extensive and more heterogeneous. For example, left-eye biases in male sexual behaviours (e.g. a shorter latency to mate or more frequent mating) have been found in stilts and quail (Gülbetekin, Güntürkün, Dural, & Çetinkaya, 2007; Ventolini et al., 2005). In contrast, male zebra finches sing more complex songs when only their right eye is available compared to their left eye, and male Bengalese Finches show reduced song output and preference for females when their right eye is unavailable (George et al., 2006; Templeton et al., 2012). To complicate matters further, we found male sage-grouse struts were biased in both left-eye and right-eye orientations depending on the region of the visual field they appeared to be using. Without detailed study of the neurobiology of this species, we cannot be certain

whether the dual bias we identified stems from ipsilateral processing of some inputs (Vallortigara et al., 2001), or whether courtship might somehow involve two distinct tasks that are each processed contra-laterally in opposite hemispheres.

Conclusions

Our study reveals the potential intricacies in studying laterality of social behaviours in the complex world of free-living animals. We found variation in bias is often related to the status of the male (in our case, whether they mated successfully or not) along with aspects of the context of the interaction. We also found that bias may depend on the region of the visual field used by the male, suggesting that future researchers may wish to quantify eye-usage with more detail than a simple binary 'left/right' categorization. Although we found general support for the hypothesis that increasing laterality may be beneficial, further research is needed to determine whether such bias could be under sexual selection.

ACKNOWLEDGMENTS

We thank S. Appleby, M. Jones, M. Kong, W. Longo, E. Rose, S. Sells for assistance collecting field data, and the Lander offices of the BLM and Wyoming Game and Fish Dept., especially S. Oberlie, S. Harter and grazing leasees, for logistical support and site access. We are also grateful for the efforts of many UC Davis undergraduates who helped score videos on campus. Members of the Patricelli Lab provided helpful comments on earlier versions of the manuscript; C. Taff and A. Perry also provided assistants with the statistical models. We thank M. Webster as well as two anonymous reviewers for helpful suggestions on a previous version of this manuscript. This research was supported by UC Davis, an NSF Research Starter Grant (IOB-0528563) to G.L.P and NSF grants to G.L.P and A.H.K. (IOS-0925038 and IOS-1258217); M. Blundell was supported by NSF GRF under grant DGE 1148897.

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537

Figure Legends

Figure 1. Examples of sage-grouse social behaviors that typically occur in lateral orientations. Aggressive interactions often progress from (a) facing-past encounters into (b) fights involving wing strikes and feather pulling. Courtship displays (struts) are often performed in lateral orientations (c). All photos by Alan Krakauer.

Figure 2. Scoring of male visual field usage during courtship. Frontal hemifields (F) were defined as $\leq 30^\circ$ from directly in front of the male. Lateral hemifields (L) were defined as 45° - 135° from midline, and rear field (R) was defined as $\leq 30^\circ$ from the rear of the animal.

Figure 3. Male orientation during fights, facing past encounters (FPEs), and first FPEs in a sequence of interactions, with males that successfully mated with females (dark bars) and failed to mate (white bars). Bars show raw data; asterisks denote groups for which the 95% CI for orientation from a generalised linear model do not include 0.5. See Table 1 for model details.

Figure 4. Radial histogram of male orientations relative to female (or robotic female) during strut display. Strut angle data were taken at 15° intervals. Orientations pooled from 42 males (N=3,293 struts); concentric rings indicate intervals of 100 struts.

Figure 5. Mean laterality during courtship depending on distance from the female (or robotic female) and male mating success— successfully mated during the season (dark bars) and failed to mate (white bars). Close refers to $< 9\text{m}$, Mid refers to between 9m and 25m , and Distant refers to $> 25\text{m}$. Bars depict raw data; asterisks denote groups for which the 95% CI for orientation from a generalized linear mixed model do not include 0.5. See Table 2 for model details.

566

567 Table 1. Fixed effects terms from binomial generalised linear models examining side bias in aggressive interactions.¹

568	Term	Coefficient (S.E.)	Prop. Left-eye (95% CI)	Z-value	P-value
569	Model 1: Fights (N = 28 males, 63 fights)				
570	Intercept (MS = 0)	0.121 (0.220)	0.530 (0.423 – 0.635)	0.548	0.583
571	(MS > 0)	-0.480 (0.307)	0.411 (0.277 – 0.560)	-1.56	0.118
572	Model 2: All Facing Past Events (N = 34 males, 310 FPEs)				
573	Intercept (MS = 0)	0.049 (0.040)	0.512 (0.493 – 0.532)	1.23	0.218
574	(MS > 0)	0.256 (0.070)	0.576 (0.542 – 0.609)*	3.67	0.0002
575	Model 3: Initial FPEs in Sequence (N = 32 males, 101 FPEs)				
576	Intercept (MS = 0)	-0.074 (0.122)	0.481 (0.422 – 0.541)	-0.608	0.543
577	(MS > 0)	0.620 (0.201)	0.633 (0.540 – 0.719)*	3.09	0.002
578					

579 ¹ All models compare the orientation of successfully-mating versus non-mating males. The first model tests for differences during
580 fights, the second model tests for differences during all FPEs, and the third model focuses only on first FPEs within a single encounter
581 between males. In all models, non-mating males represent the baseline group (i.e. intercept), while the other term represents
582 successfully mating males, and is compared with the baseline group. Bold denotes a significant term in the model, while asterisks
583 indicate that the 95% CI for that estimate fails to overlap 0.5 left-eye orientation.

584

585 Table 2. Fixed effects terms from a generalised linear mixed model examining side bias in courtship displays.¹

586	Model Term	Factor Level(s)	Coefficient (S.E.)	Prop. Left-eye (95% CI)	Z-value	P-val
587	Intercept:	MS = 0, Frontal VF, Dist < 9m	-0.123 (0.205)	0.469 (0.372 - 0.569)	-0.600	0.549
588	MS:	MS > 0, Frontal VF, all dist	0.634 (0.250)	0.625 (0.505 - 0.731)*	2.53	0.011
589	Visual Field	MS = 0 Lateral VF, < 9m	-0.192 (0.223)	0.422 (0.320 - 0.531)	-0.859	0.390
590	Dist 9m - 25m	MS = 0, Frontal VF, 9m – 25m	0.124 (0.230)	0.500 (0.389 - 0.611)	0.537	0.591
591	Dist > 25m	MS = 0, Frontal VF, > 25m	0.521 (0.250)	0.598 (0.477 - 0.708)	2.09	0.037
592	MSxVF	MS > 0, Lateral VF, all dist	-0.567 (0.241)	0.438 (0.327 - 0.556)	-2.34	0.019
593	VFXDist 9m – 25m	MS = 0, Lateral VF, 9m – 25m	0.118 (0.264)	0.482 (0.356 - 0.609)	0.446	0.655
594	VFXDist > 25m	MS = 0, Lateral VF, > 25m	-0.542 (0.284)	0.417 (0.291 - 0.555)	-1.92	0.055

595 ¹ MS = Mating Success, VF = Visual Field, Dist categories represent distance between male and female/robot. Intercept term
596 represents the estimate for the baseline group in the model (non-mating males using their frontal field in close courtship); remaining
597 logistic coefficients, Z-values and P-values refer to tests of contrasts against the baseline group. Bold denotes a significant term in the
598 model, while asterisks indicate that the 95% CI for that estimate fails to overlap 0.5 left-eye orientation.

599

Figure 1
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Figure 1

Figure 2

Figure 3

Figure 4

Figure 5