



# Drawn into the vortex: The facing-past encounter and combat in lekking male greater sage-grouse (*Centrocercus urophasianus*)

Sergio M. Pellis<sup>a,\*</sup>, Melissa A. Blundell<sup>b</sup>, Heather C. Bell<sup>a</sup>, Vivien C. Pellis<sup>a</sup>,  
Alan H. Krakauer<sup>b</sup> and Gail L. Patricelli<sup>b</sup>

<sup>a</sup> Department of Neuroscience, University of Lethbridge, Lethbridge, AB, Canada T1K 3M4

<sup>b</sup> Department of Evolution and Ecology, University of California at Davis,  
Davis, CA 95616, USA

\*Corresponding author's e-mail address: pellis@uleth.ca

Accepted 22 June 2013

---

## Abstract

Lekking male greater sage-grouse (*Centrocercus urophasianus*) compete with neighbours not only by strutting to attract females but also by directly challenging other males. These challenges include approaching another male and adopting an anti-parallel orientation at close quarters ('facing past encounter') and fighting, in which the birds strike one another with their wings. Facing past encounters and facing past encounters that led to fights in free-living sage-grouse were videotaped and analysed to test predictions arising from two sets of hypotheses to account for the features of such encounters. They could be used to assess or threaten opponents (index signal or threat signal hypotheses) or they may be the result of a stalemate in which one bird's attempts to gain an vantage point for attack are neutralised by counter moves by the other bird (combat hypothesis). Frame-by-frame analyses of both facing past encounters and fights were used to extract data to test specific predictions arising from the three hypotheses. The results, overall, support the hypothesis that the facing past orientation arises from combat. However, the results also suggest that, once in the anti-parallel orientation, opportunities emerge for communication to take place.

## Keywords

index signal, threat signal, fight, territoriality, attack, defense, game theory, movement analysis, high-speed video.

## 1. Introduction

Red deer (*Cervus elephus*) provide a classic study in the escalation of aggression (Clutton-Brock et al., 1979, 1982). During the rutting season, the males

roar at long distances from one another. Roaring appears to be energetically costly and the rate of roaring may function as a condition-dependent handicap signal (Zahavi, 1977; Clutton-Brock & Albon, 1979; Grafen, 1990; McComb, 1991), providing information about fighting potential. Moreover, the formant frequencies of the roar are determined by the size of the vocal tract and may, thus, function as an index signal — that is, a signal where the information is inextricably linked to the form of the signal (Reby & McComb, 2003; Enquist & Hurd, 2005; Reby et al., 2005; Bradbury & Vehrencamp, 2011). Females also assess roaring vocalisations, preferring roars that indicate a larger body size (Charlton et al., 2007). If a male is deemed likely to be beatable based on roaring, the rival may approach, but as a further test of fighting potential, the opponents approach and walk parallel to one another at close quarters, presumably using the coordination of movement and close inspection of antler size and underlying body musculature as further clues to fighting strength. Finally, if neither animal backs away, the encounter can escalate into a fight with the clashing of antlers (Archer & Huntingford, 1994). The parallel walk, like the roaring, may, thus, function as an index signal, revealing body and antler size, or as a threat signal with honesty maintained through the increased vulnerability of the rivals being in close proximity through the parallel walk position (Jennings et al., 2003; Hurd & Enquist, 2005; Bradbury & Vehrencamp, 2011).

A similar picture emerges from the territorial behaviour of greater sage-grouse (*Centrocercus urophasianus*), a large galliform bird species native to arid regions of the interior west of North America (Schroeder et al., 1999). Male sage-grouse defend small display areas on a communal breeding ground, called a lek, and females visit the lek in order to choose a mate. Neighboring males perform a complex strut display involving both vigorous bodily movements and low frequency vocalisations (Wiley, 1973a). Males rarely perform these in close proximity to another male, and when they do, the display sometimes appears to provoke an escalation in agonistic behaviour. These strut displays may be followed by a male intruding into a neighbouring territory and initiating a facing past encounter (FPE), in which the opponents, at close quarters, stand side-by-side, facing opposite directions (i.e., an anti-parallel orientation), and often involving coordinated back and forth stepping, circling, harsh, staccato vocalisations and shaking of the tail feathers. Finally, the intrusion into a neighbour's territory may lead to fighting, usually following an FPE (Wiley, 1973b). As in the case of red deer,

the rate and the acoustic features of the strut displays are related to male mating success with females (Gibson & Bradbury, 1985; Gibson, 1996; Patricelli & Krakauer, 2010), suggesting that these behaviours function in both inter- and intra-sexual selection. In contrast, FPEs and the associated manoeuvring appear to be used exclusively for competition among males. Also, similar to red deer, sage-grouse perform the vocal displays (strutting) more frequently than they do the close-quarter FPEs. In turn, FPEs are more frequent than actual fighting (Wiley, 1973a, b) — a pattern consistent with theoretical frameworks predicting how aggressive encounters progress in their escalation (Maynard Smith, 1974).

The close relatives of the greater sage-grouse typically fight from a face-to-face position, rather than the side-by-side position of the FPE (Johnsgard, 1983; Connelly et al., 1998). This leads to the question of how this FPE behaviour functions in sage-grouse. Did this anti-parallel position evolve to facilitate signalling and assessment or has this posture been adopted primarily for its role in combat? Given the similarity of these encounters to those of the male red deer, the FPEs of the grouse may be interpreted as an index signal, a display that reveals body size, not unlike the red deer's parallel walking (Archer & Huntingford, 1994; Jennings et al., 2003; Bradbury & Vehrencamp, 2011). However, there is an important difference between the parallel walking of the red deer and the facing past encounter of the grouse. In the red deer, an escalation to fighting requires the opponents to reorient from a parallel orientation, in which they are facing in the same direction, to an anti-parallel orientation, facing one another. From this position, they clash antlers (Clutton-Brock et al., 1982).

In contrast, it is usually from the anti-parallel, facing past orientation that the grouse physically attack one another by vigorously beating each other with their wings (Wiley, 1973b). Therefore, unlike the case of the red deer, in the sage-grouse, the anti-parallel orientation brings the wings, the primary combat weapon, into the position ready for deployment. That is, rather than the FPE being an assessment display, it could simply be an attempt to gain an advantageous position from which to launch an attack. If this is so, the higher frequency of facing past encounters compared to fighting may not be evidence of an escalating assessment process, but instead, evidence of the opponent positioning itself for a counterattack, leading only to a few encounters in which the intruder has an opportunity to launch a low-risk attack (see Geist, 1978).

There is an alternative in which the anti-parallel orientation may serve as a signal. The ready-to-use presentation of weapons is used as a threat signal among various animals, indicating a willingness to fight (Számádó, 2003; Bradbury & Vehrencamp, 2011). The honesty of the signal is maintained through the risk of being in close proximity to a rival, since part of that readiness for use of weapons is to approach the opponent within striking distance (Számádó, 2008). These signals are also called 'positive handicaps', since the animals assume a position that will give them an advantage in a fight (Bradbury & Vehrencamp, 2011). Therefore, in this communicatory hypothesis, the FPE is not a condition-dependent handicap or index signal, but a threat signal directed at the opponent. However, once animals are engaged in an aggressive contest at close quarters, it becomes difficult to judge which of the actions present are used for signalling and which are used for combat (e.g., Geist, 1978; Blanchard & Blanchard, 1994; Pellis, 1997). Nonetheless, the tendency in the literature is to assume that many actions are performed for communicatory purposes (e.g., Enquist & Jakobson, 1986; Bruski & Dunham, 1987; Waas, 1991, 2006).

The FPE of sage-grouse, therefore, may be explained by three competing functional hypotheses: (1) the index signal hypothesis, which proposes that the FPE is an honest indicator of fighting ability, used to deter the rivals from attempting to fight, (2) the threat signal hypothesis, which proposes that the FPE is a tactical proximity threat signal performed to demonstrate a willingness of the performer to escalate the interaction into a fight, or (3) the combat hypothesis, which proposes that the FPE arises from the combat tactics used. These alternative hypotheses make different predictions about the movements performed during the facing past encounters and their sequelae. Prediction (i): If the FPE is performed as an index signal, then, when a bird begins to withdraw, the withdrawal should be uncontested, as the role of such signalling is to assess opponents and so avoid escalation to serious fighting (Maynard Smith, 1974, 1982; Bradbury & Vehrencamp, 2011). Similarly, a threat should act to intimidate the opponent and so reduce the risk of a fight emerging. The opposite is predicted by the combat hypothesis in which the relaxation of defence that is needed to disengage (Geist, 1978) affords the opponent a low risk opportunity to attack. Difficulty in disengaging from the FPE configuration would count against the communication hypotheses and lend support to the combat hypothesis.

Prediction (ii): If, as posited by the combat hypothesis, the FPE is gained and maintained by the birds jockeying for an advantageous position from which to launch an attack, then FPE encounters should contain many offensive and defensive movements. The threat signal hypothesis, as characterised by Számadó (2003, 2008), predicts that the bird should put itself in harm's way. However, threat signals are typically derived from the movements performed during agonistic attack, such as lunging forward and raising the wings, which emphasise preparing the weapons for deployment (Bradbury & Verhencamp, 2011), and these signals are usually held for prolonged periods to ensure the clarity of the message to the opponent (Walther, 1984). Similarly, as the point of the FPE in the index signal hypothesis is to display potential fighting ability, not fighting per se, the presence of offensive and defensive manoeuvres would be inconsistent. To be useful as index signals, any added movements should be stylised to emphasise stamina and speed. Therefore, the communicatory hypotheses would predict that no additional offensive or defensive movements would be incorporated into such encounters unless there is an escalation to fighting.

Prediction (iii): Similarly, the combat hypothesis predicts that the FPE is a compromise between the functional demands of attack and defence, and as a consequence, the bird's movements during encounters reflect its attempt to gain the optimal position from which to launch attacks. Thus, it is likely that the position attained in the typical FPE configuration is not the most advantageous position from which to launch attacks. In contrast, the threat signal hypothesis would predict that the most common position, the typical FPE, would be the principle attack posture. The index signal hypothesis might also predict the FPE configuration as useful for displaying size and, possibly, strength, but moving out of the FPE to gain an advantageous combat position from which to strike would not be predicted.

Prediction (iv): If the FPE is a combat related position, then the combat hypothesis would predict more postural adjustments attuned to the movements of the opponent during encounters when the birds are in the FPE configuration compared to other relational configurations. That is, as one bird moves away from the FPE position to gain a vantage point from which to strike, the partner should compensate, re-establishing the FPE configuration. In contrast, since in the communication hypotheses the object is to establish an FPE position to display threat or prowess to the opponent, movement away from the FPE should be less likely to evoke a compensatory movement

by the other bird. That is, the opponent should be just as likely to establish or re-establish the FPE position irrespective of the movements and position of the other bird.

Prediction (v): Vocalisations and movements, particularly of body parts not directly related to combat, such as the raising and fanning of the tail (Wiley, 1973b), would be consistent with the index and threat signal hypotheses, as these would add information or amplify the attention getting qualities of the display (Hasson, 1989).

Videotaped sequences of FPEs without fights (i.e., FPE only) and FPEs leading to fights (i.e., FPE with fights) from free living, lekking male sage-grouse were subjected to both qualitative and quantitative analyses. The qualitative analyses focused on evaluating the correlated movements of the opponents. Patterns derived from these analyses were used to quantify aspects of the encounters so as to test the predictions.

## **2. Methods**

The behaviour of free-living male greater sage-grouse during the lekking period was observed on 8 April 2005, and daily between 14 March and 30 April in 2007, 17 March and 11 April in 2008, and 23 March and 1 May in 2011 at Monument Lek (Fremont County, WY, USA, 42°49'44.42"N, 108°30'24.08"W) from first light until all birds left the lek, typically 1–3 h total per day. Males were individually identified by plumage patterns (Wiley, 1973b), using a combination of video identification or real-time identification by observers in blinds on a hill, approximately 200 m from the lek. Real-time lek observers used Eagle Optics Raven 20–60 × 78 or Alpen 20–60 × 80 spotting scopes and noted male locations to the nearest 1 m relative to a grid of survey stakes placed at 10 m intervals on the main area of lek (approx. 100 × 130 m).

In each year, lekking activity was filmed continuously using 3 HD camcorders (Sony HDR-HC1 or -HC3) overlooking the lek from a nearby hill. Using data from 2007, we analysed all the agonistic behaviours for visible males on the lek during an hour-long sample (one video tape) on a subset of days that season (5, 12, 13, 16 and 17 April). These data were used to calculate descriptive statistics for major events during agonistic interactions (see details below).

For more detailed analyses of interactions involving FPEs with and without fighting, close-up footage was collected opportunistically by an observer

(G.L.P.) in a blind placed in the main portion of the lek. The behaviour was filmed in standard (30 fps, Sony HDR-FX1, Tokyo, Japan) and high-speed video (500 fps, video acquired through a Motion Corder Analyzer, Model SR-500; Kodak, Rochester, NY, USA, and recorded on a Sony GV-D1000 mini-DV Video Walkman). Opportunistic video footage was collected on the following dates: 8 April 2005, 21 March–11 April 2008 and 28 March–3 April 2011. In the final season of data collecting (2011), we focused on filming fights with high-speed video; the birds' more vigorous and rapid movements during fights make high speed footage especially useful for measuring the wing strikes. From the high speed and regular videotapes, 33 individually identified males were used to extract male–male interactions. To contrast the movements of the birds during FPEs that did and did not involve fighting, 40 FPEs only and 38 FPEs with fights were identified and used for analysis. Twenty-one of the 33 birds contributed to FPEs only (mean = 3.8 FPE per bird, range = 1–17) and 20 contributed to the FPEs with fights (mean = 3 fights per bird, range = 1–13). Two additional FPEs only and five FPEs with fights in which the identity of one or both of the opponents were unknown were also videotaped. For six of the birds filmed in 2005 and 2008, their engagement in both types of FPEs was recorded.

### *2.1. Data analysis*

To ensure that the sage-grouse interactions in this study conformed to the pattern previously reported (Wiley, 1973b), hour-long videotapes from the hill overlooking the lek in 2007 were used. All agonistic interactions that occurred within a 1-h sample period every day for 5 days (see above) were scored. A total of 671 interactions involving 43 birds were recorded. For each interaction, the series of events that occurred, and the beginning and end times for each event, were scored. Data were recorded for three types of events: 'approaches' were scored when one bird walked or ran toward another bird; 'facing past encounters' were scored when males entered the anti-parallel position described above; and 'fights' were scored when one or both opponents struck or attempted to strike the other (beginning at the first wing strike and ending after active strikes or attempted strikes ceased). Many interactions involved combinations of all three types of events. Only events from interactions that were completed by the end of the 1-h sample were included. From these data, the occurrence and duration of these events within each interaction were calculated.

For detailed frame-by-frame analyses, close-up footage of interactions (2005, 2008, 2011) was used. Videotaped sequences were downloaded in digital format using iMovie '09 (version 8.0.6, Apple, Cupertino, CA, USA). This was the format used for real-time, slow motion and frame-by-frame inspection on a computer screen. The high-speed camera provided a time code for the sequences recorded at 500 fps, allowing each frame to be individually identified. For the standard speed filming (30 fps), a time code with 30 per second intervals was added to facilitate frame-by-frame analysis.

To determine the organisational structure of the interactions, in terms of the relative contributions of each participant, videotaped sequences were analysed using the Eshkol Wachman Movement Notation (EWMN) (Eshkol & Wachman, 1958), a qualitative technique suitable for detecting and describing the correlated movements among body parts and between animals (e.g., Golani, 1976; Pellis, 1982, 2011; Eilam & Golani, 1988). For the relational changes between the birds, three measures were used: (i) the relative horizontal distance between the birds, measured in bird lengths (from the tip of bill to the base of the tail when the bird is standing upright in a relaxed posture), (ii) the relative orientation of the longitudinal axis of one bird to the other, and (iii) the parts of the body most closely opposing one another (e.g., Moran et al., 1981; Pellis, 1982, 1989). For more details, see the Appendix.

For the EWMN analyses, encounters were selected on the basis that the birds were clearly visible from the start to the end of the interaction, that they occupied at least 25% of the computer screen (i.e., they were close up), that the individual participants were identifiable and, for fights, that they were filmed with the high speed camera (a sub-sample was filmed at both low and high speed). To avoid sampling bias, the first 12 of each type of encounter viewed that met the above criteria were used (FPEs with fights from 2011, FPEs only from 2005 and 2008), with 13 individuals contributing to the FPEs with fights and 10 to the FPEs only. To minimise the impact of particular individuals on the patterns observed, encounters between different partners were used before using encounters between the same pair mates (two and three cases, respectively).

The FPEs with and without fights not used for the EWMN analyses were the pool of interactions from which the quantitative scores to test the predictions were derived. Common to all of the quantitative assessments, only birds that were individually identified were used. Similarly, when the quality of the video permitted, the six birds for which both FPEs only and FPEs with

fight were available were quantitatively compared so as to ensure that the patterns identified were general for the type of interaction, rather than being distinctive for individual animals. Some methods of quantification require an understanding of the findings from the qualitative analyses (e.g., Prediction (i)) and these will be described in the Results section, the remainder are described below.

### 2.1.1. Predictions (ii) and (v)

The occurrence of squatting and lateral swerving, as defensive manoeuvres, and raised chest, tail fanning and staccato vocalisations (indicated by the rapid up-and-down shaking of the tail), as behaviours without an apparent combat function, was scored in both FPEs only and FPEs with fights. A squat could be partial, with the ventrum of the bird not touching the ground, or complete, in which its ventrum touched the ground. A swerve was scored if it were of a magnitude of  $10^\circ$  or greater. Smaller magnitude swerves occurred, but these were difficult to see consistently. Similarly, the changes in position of the birds relative to the camera made it difficult to score all occurrences of vocalisations with certainty, so interactions were scored for the presence of at least one vocalisation. Indeed, because squatting, in particular, and most of the signals scored, could be maintained for long durations, for each pair, only the presence or absence of squatting and/or swerving and raised chest/tail fanning/staccato vocalisations was recorded.

Scoring began from the frame in which the birds first attained the anti-parallel configuration to the frame in which the first wing strike occurred. For the FPEs only, the same starting point was used, but then, to make them comparable to the FPEs with fights, a temporal cut-off was used to match the duration of each of the encounters. In this way, the two types of interactions were sampled for a comparable amount of time. Twelve FPEs only and 12 FPEs with fights were scored in which there was at least one minute between attaining the anti-parallel configuration and the cut-off criterion. FPEs with fights that met this temporal criterion were used, provided that that part of the encounter was visible throughout that period and that it involved birds that had been individually identified. To avoid sampling bias, the files were examined sequentially and the first 12 that met the criteria were scored. The FPEs only were scored next, and again, to avoid sampling bias, they were examined sequentially and those that met the two physical criteria were scored and then matched to an FPE with a fight that had the closest comparable duration. Since some of the encounters by the six birds that

engaged in both types of encounters did not meet the duration criterion, they were not included in this analysis; this resulted in two independent samples of 12. Also, for each of the 12 samples, no interactions were included that would have involved the same pair twice.

### *2.1.2. Prediction (iii)*

For the FPEs with fights, the partner-wise orientation, partner opposition and relative distance (see Appendix) were scored on the frame in which a wing strike was launched. Similarly, the location on which the recipient's body was struck was recorded (head, neck, upper torso or lower torso). Since some FPEs with fights contained multiple strikes and some only one, only the first strike in the encounter was compared. The first 20 FPEs with fights in which the location of the hit by the wing could clearly be seen were used.

### *2.1.3. Prediction (iv)*

The first 12 FPEs in which the animals were close and not obscured by brush or other birds, were scored. One other criterion for selection was that there had to be periods in the interaction in which the birds had been in both the anti-parallel orientation ( $\pm 22.5^\circ$ ) and in other configurations. For each encounter, the frame in which the birds achieved the anti-parallel orientation was the starting point, and then the next 60 s were scored. For comparison, a segment was scored in which, for the same duration, the two birds were not in the anti-parallel configuration. In both cases, the opponents had to be within two body lengths of each other. For some of the interactions, 60 consecutive seconds were not available, so sections of the interaction of smaller durations were used until they added up to 60 s. Interactions for which both samples could not be scored were eliminated, and, in all cases, only interactions lasting more than three minutes yielded the requisite data. This provided 12 matched samples. However, six of the encounters qualifying for inclusion involved the same pairs, with one pair contributing four cases. For this pair, a further two cases were found and the six interactions were compared to assess intra-pair consistency.

What was scored was whether movements by one bird (e.g., steps, body rotation) were combined with those of the other bird in order to maintain the current inter-animal configuration — in which the partner-wise angle was kept within  $22.5^\circ$ , distance was maintained to within 1/2 body length of the starting frame and the opposition remained within the head-to-head and shoulder-to-shoulder axis when in the anti-parallel configuration. For

the configurations that were not anti-parallel, the birds were given the same margin of variation for maintaining the configuration present at the starting frame.

## *2.2. Statistical analyses*

As most of the measurements for the movements performed used nominal or ordinal scales for the ratings, non-parametric tests were used for the statistical comparisons (Siegel & Castellan, 1988). Both the qualitative and quantitative scoring methods were reliable and consistent across observers (see Appendix).

## **3. Results**

Data from the sampling of all aggressive events from multiple days in 2007 yielded 671 interactions, 331 of which involved the birds only approaching each other and separating before FPEs arose. Of the other 340 interactions, 3% escalated immediately to a fight without a preceding FPE, 29% involved FPEs with fights and 68% involved a FPE only. Of the 98 interactions that included both periods of fighting and periods in the FPE position, in 78% the FPE position preceded fighting. These data also showed that aggressive interactions were highly variable in duration, with some involving only brief approach and withdrawal and others involving protracted engagement. FPEs with fighting were more than twice as long as interactions with FPEs only (Table 1). The remainder of the analyses compared the most common interactions, FPEs only and FPEs with fights.

### *3.1. The structure of aggressive interactions in sage-grouse*

If the FPE was the configuration adopted by the approaching bird, then it should arise from its movements even if the approached bird remained passive. This was not the case. In all 24 interactions analysed using EWMN, as one bird approached another, when at a distance of about one body length away, the bird being approached would turn towards its oncoming opponent and face it (see Supplementary Video 1 in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>). The combined movements of the two birds led to the FPE configuration, in which the birds stand anti-parallel to one another, between 0.5–1

**Table 1.**

The duration of different types of agonistic interactions are shown for males when on the lek.

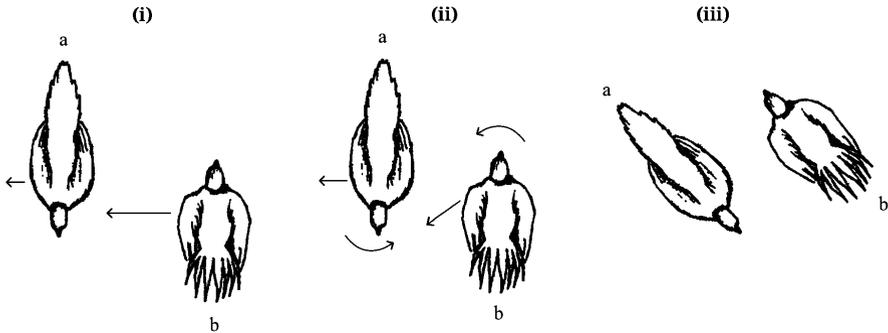
Interaction type	Number of interactions	Mean duration (min)	Median duration (min)	Min	Max
Interactions with only fighting (no FPE)	10	0.25	0.13	0.07	0.83
Interactions with only FPE (no fighting)	231	1.47	0.77	0.02	8.67
Interactions with both FPEs and fighting	98	3.68	2.50	0.10	21.17
Interactions with both FPEs and fighting (total duration spent in FPE posture)	98	3.34	2.08	0.03	20.73
Interactions with both FPEs and fighting where FPE occurs first (duration of pre-fighting FPE posture)	76	1.08	0.27	0.02	8.12

Data collected from hour-long samples of all agonistic interactions of 43 males visible on the lek in 2007; collected on 5 sample days (see Methods for details).

body length apart, with their heads or shoulders opposed. Once in this configuration, it was sustained by the compensatory movements made by one bird to those of its opponent (Figure 1).

From this anti-parallel configuration, fights began with one bird striking at its opponent's head with the wing closest to it. Wing strikes could be repeated in quick succession and the opponent could counter-attack with its own wing strikes at the initial attacker's head. In one of the 12 encounters, as the attacker began raising its wings, it jumped and grasped its opponent's beak with its foot and held on, while repeatedly striking the top of the other's head with its wing. In another encounter, the attacker grasped the side of its opponent's head with its beak as it manoeuvred to strike with its wing. While these two instances show the use of other body parts in attacking, they also show that they were used to secure the opponent for a subsequent wing strike to the head.

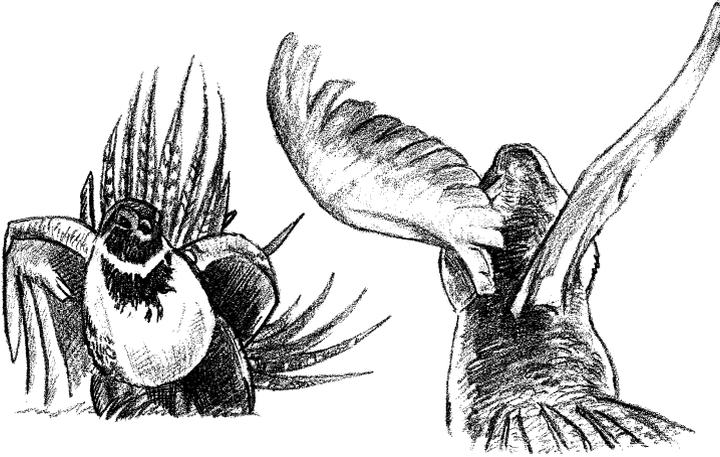
Hits that were made with the wrist seemed to provide the maximum amount of force in striking: in the two cases in the notated sequences in which such hits occurred, the recipient of the strike was knocked forward and



**Figure 1.** Drawn from an aerial perspective, the figure shows two birds moving and counter-moving during an encounter. In panel (i), bird *b* moves laterally towards bird *a*, which then moves laterally away. However, the movement by bird *b* is greater than that of bird *a*, leading to a reduced inter-animal distance at the end of their movements in panel (ii). Then, bird *b* rotates around its longitudinal axis, with its head moving towards bird *a*, and also begins to step obliquely backwards towards bird *a*. However, as it does so, bird *a*, also rotates around its longitudinal axis and steps laterally away, so that when the birds end their movements as shown in panel (iii), even though they have changed their position in space, they have maintained the same relative inter-animal configuration.

downward, to the ground (see Supplementary Video 2 in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>). Other such cases were also observed in the whole data set. The failure, by the attacker, to deliver such hits, appeared to arise from the defensive moves made by the recipient that kept its head further away from the attacker. As the attacker delivered the strike, the defender shifted its body weight away and partially squatted (Figure 2), thus withdrawing its head, and so protecting it from the strike. In turn, the defender could also retaliate with wing strikes of its own.

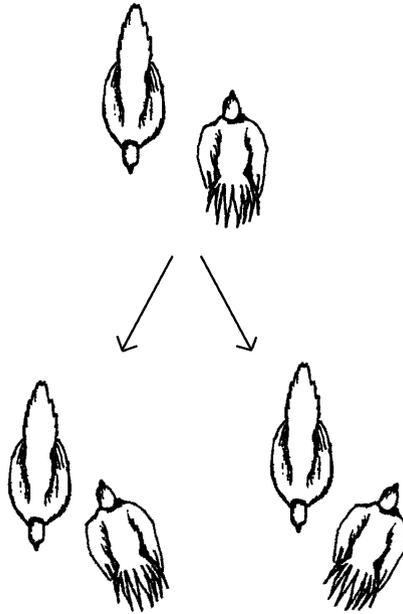
The circling that arises from one bird stepping forward and sideways away from its opponent, and the stepping backward and sideways toward by the other bird, suggests that, being at a slightly oblique angle, either a little forward of the shoulder-to-shoulder opposition facing towards the opponent, or a little further back from the shoulder-to-shoulder opposition and facing away from the opponent, provides an advantage to the attacker when performing wing strikes (Figure 3). When striking from this slightly off anti-parallel orientation, the attacker's wrist was closer to its opponent's head and the counter-strikes by the defender were not in alignment with the attacker's head. These counter-strikes either missed completely or just brushed the opponent's head with the tips of the flight feathers. Thus, while



**Figure 2.** The drawing, from an original video frame, shows the basic components of an attack. From an approximately anti-parallel orientation, the birds are standing with the shoulders/sides of their heads opposed. At about 0.5 body length distance, the attacker raises its wings and strikes, downwards, towards its opponent's head. As it does so, it moves laterally towards its opponent. As the strike is about to land, the defender can be seen shifting its weight away from the oncoming blow and so increasing the strike distance between its own head and its opponent's wing. Drawing by Devin Cahoon.

being slightly off the anti-parallel orientation is advantageous for attack, the fully anti-parallel orientation is advantageous for defence as it neutralises that advantage.

One fight which did not begin in the typical manner actually confirms the configuration adopted for attack. The attacker approached from the rear and launched the wing strike  $45^\circ$  off parallel, but in a frontal oblique orientation, so facing the same general direction as the opponent — thus, opposite to the typical anti-parallel orientation. The closest wing was the right one, but, as it raised its wings and jumped forward, it pivoted, so that, as its wing struck, the attacker was approaching its opponent from the off anti-parallel orientation (rear oblique) and struck it with its left wing. Both the opponent and the attacker fell to the ground, and, once they had regained their standing posture, quickly adopted the anti-parallel, shoulder-to-shoulder opposition at  $1/2$  body distance. The next wing strike was from this configuration. Thus, even when attacks occurred from other configurations, the actual strikes tended to be channelled into the typical, anti-parallel, or slightly off anti-parallel, ones.



**Figure 3.** Aerial views of a pair of birds shown in three configurations. In the top panel, the birds are oriented in the typical anti-parallel configuration. When preparing to launch a strike with a wing, the attacking bird manoeuvres to a slightly off anti-parallel configuration, either pointing towards (left lower panel) or away (right lower panel) from its opponent. This off anti-parallel orientation allows the bird to place its wing in an optimal position for striking the top of its opponent's head with its wrist.

### 3.2. Quantitative tests of the predictions

#### 3.2.1. Prediction (i)

Prediction (i): Withdrawing from a FPE should be uncontested if the FPE is an index signal, but is likely to be contested if a combat tactic or a threat signal.

Once in the anti-parallel configuration, attempts by one bird to begin withdrawing were sometimes countered by a rapid movement towards by its opponent. This was especially evident in protracted interactions. Such a rapid approach, was, in turn, quickly countered with a re-orientation by the bird initiating the withdrawal back to the anti-parallel configuration. In many FPEs with fights, birds adopted the anti-parallel configuration both before and after wing strikes (Table 1). Therefore, to estimate the rate of attacks when attempting to disengage, FPEs with fights in which the termination was filmed and clearly visible were used. Moreover, to qualify for inclusion, be-

tween wing strikes and termination (i.e., the birds moved apart), there had to be at least 30 s of FPE preceding the withdrawal to ensure that the birds were indeed ensconced in the FPE configuration prior to an attempted withdrawal. Of the 19 fights that met these criteria, 42.1% involved one bird contesting the other's withdrawal. In most cases, this involved the bird rapidly moving towards its opponent, who, in turn, quickly adopted a defensive posture (and in one case running away). In two of these cases, the withdrawing bird was struck by its opponent.

### 3.2.2. *Prediction (ii)*

Prediction (ii): During FPEs only, additional defensive actions are not predicted if they are used for communication, but are predicted if the FPE arises from combat manoeuvres.

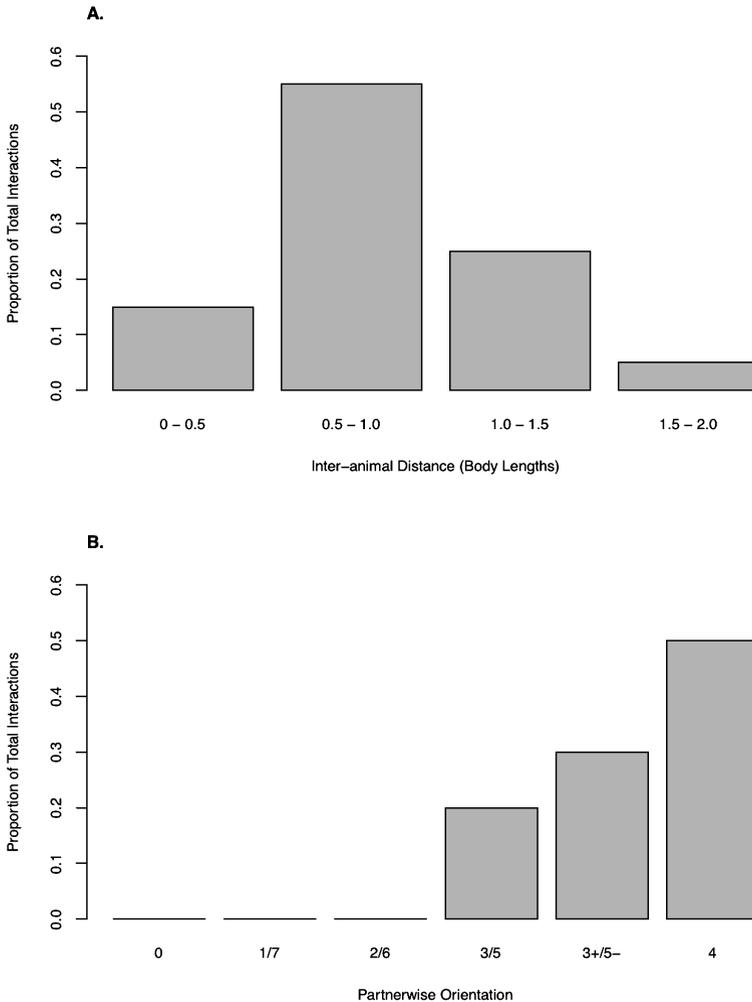
Defensive actions involving squatting and swerving were present in both FPEs only (91.7%) and FPEs with fighting (83.3%). Moreover, they were equally likely to occur in both types of interactions ( $\chi^2 = 0.38$ ,  $df = 2$ ,  $p > 0.05$ ).

### 3.2.3. *Prediction (iii)*

Prediction (iii): If the FPE configuration arises from the combined attack and defence manoeuvres of the opponents, then the anti-parallel orientation may not be the most effective position from which to launch an attack.

The configuration adopted at the moment of launching a wing attack showed that not all inter-animal positions were equally likely (distance:  $\chi^2 = 10.2$ ,  $df = 4$ ,  $p < 0.05$ ; partner-wise orientation:  $\chi^2 = 15.96$ ,  $df = 5$ ,  $p < 0.01$ ). The same was the case for the opposition between the birds with all cases involving shoulder-to-shoulder (40%), side of head-to-shoulder (30%) or side of head-to-side of head (30%) oppositions, but not other possibilities, such as side of head-to-lower flank, side of head-to-side of tail and side of tail-to-side of tail ( $\chi^2 = 11.72$ ,  $df = 5$ ,  $p < 0.05$ ). As predicted by both the combat and threat hypotheses, the distance when striking was between 1/2 and one body length (Figure 4A), the optimal distance for delivering a wing strike, and the body areas opposed were typical of the position adopted in FPE. However, that nearly half the strikes were performed when in the slightly off anti-parallel orientation (Figure 4B) is not consistent with the threat hypothesis, but it is consistent with the combat hypothesis.

In all cases, the location of the wing strike was the head (head (+) versus non-head (-):  $x = 0$ ,  $N = 20$ ,  $p < 0.001$ ). Thirteen of the strikes were to the



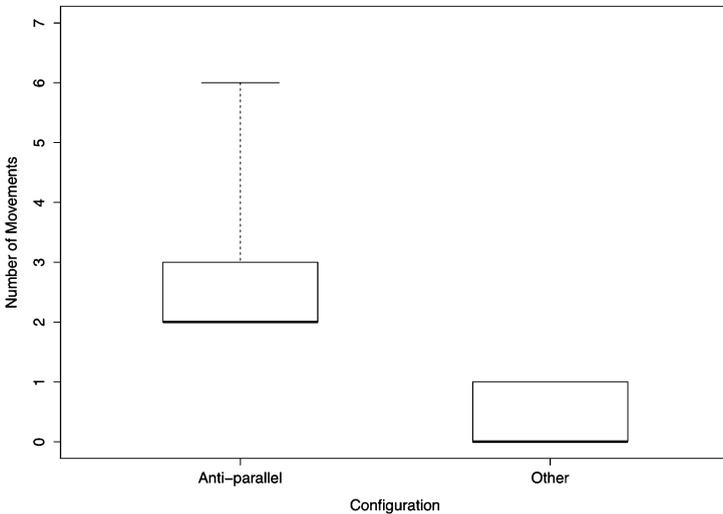
**Figure 4.** The inter-animal configuration is shown at the frame in which the wing of the attacker strikes its opponent. (A) Inter-animal distance (in body lengths). (B) Partner-wise orientation between the opponents. For the partner-wise orientation, the numbers represent the orientation of the longitudinal axes between the opponents: 0 = the longitudinal axes are facing directly in the same direction, 4 = the longitudinal axes are facing directing in the opposite direction (i.e., the anti-parallel orientation), 2/6 = the longitudinal axis of one bird faces the direction of the other's longitudinal axis from a perpendicular angle (i.e., at 90°), 1/7 = frontal oblique (i.e., 45° from 0), 3/5 = rear oblique (i.e., 45° from 4), and 3+/5- = rear oblique (i.e., 22.5° from 4 — the slightly off anti-parallel orientation). The positions, showing two values (e.g., 2/6), signify the right and left side of the body (see Appendix A for further details).

top of the head and the remaining seven were to the side of the head or to the front, including the top of the beak. Moreover, the seven hits not directly on top of the head were glancing ones, involving the tips of the anterior primary flight feathers. While this was also true for many of the strikes to the top of the head, some involved hits with the wrist, in which the strike caused the recipient to be pushed forward and downward, usually falling onto its chest then side. As indicated above, the hits most likely to unbalance the recipient were ones to the top of the head that were delivered at close quarters (0.5 body length) and, critically for the combat hypothesis, from a slightly off anti-parallel orientation.

#### 3.2.4. Prediction (iv)

Prediction (iv): If the FPE arises as the birds position themselves for attack and defense, then this configuration, but not others, should be actively maintained.

The number of matched movements were more frequent when the birds were approximately in the anti-parallel configuration than when in another configuration (Figure 5) (Wilcoxon matched-pairs test:  $T_{12} = 0$ ,  $p < 0.01$ ). Comparison of the six matched samples for the pair that was scored re-



**Figure 5.** The number of correlated movements (i.e., movements by one bird that are countered by movements of the other bird which lead them to maintain the same inter-animal configuration) in which the birds are in the typical anti-parallel configuration versus other configurations during FPE encounters. The median, quartiles and ranges are shown.

peatedly showed the same pattern ( $T_6 = 0$ ,  $p < 0.05$ ). The relatively low frequency is in itself revealing. In all encounters, the birds approached one another, and, as they came to within one body length, adopted the anti-parallel configuration. Most of the jockeying for position occurred within the first 10 s of attaining that configuration. The birds then remained stationary in this position, with only the occasional movement and counter-movement. In contrast, once out of the anti-parallel configuration, the birds were more likely to move for more of the 60-s sample, but even though they moved more often, the movements were less likely to counteract those of their opponent.

### 3.2.5. Prediction (v)

Prediction (v): If the movements performed during FPEs are for communication, then added elements of signalling could enhance such a function and so should be prevalent in both FPEs only and FPEs with fights.

Actions not involving combat-related movements were present in both the FPEs only (100%) and FPEs with fights (91.7%), and they were equally likely to occur in both types of interactions ( $\chi^2 = 1.92$ ,  $df = 2$ ,  $p > 0.05$ ).

## 4. Discussion

The present data are consistent with Wiley (1973b) in showing that facing past encounters (FPEs) not leading to fights are more frequent than FPEs with fights. Also, the data show that FPEs with fights last longer than FPEs only (Table 1), supporting the possibility that FPEs are used for communication of threat or fighting strength, with escalation arising from a failure to resolve the encounter via communication. However, overall, the results of the detailed analyses of aggressive encounters support the combat hypothesis that the FPE arises from one bird manoeuvring to gain a vantage point from which to launch an attack and the opponent manoeuvring to position itself in an orientation favourable for defence and counter-attack. Indeed, in encounters with both FPE behaviour and combat, more than twice as much time is spent in the FPE posture after the initial bout of combat than preceding it (Table 1). This suggests that the FPE does not function primarily to resolve the conflict with communication before escalation to combat. The difficulty in disengaging from the FPE configuration is particularly damaging to the index signal hypothesis (Prediction (i)). Our observations are, moreover, consistent with those made by Wiley (1973b), who reported that, during the termination

process, one of the opponents may slowly sidle away, then finally turn and leave, but that often, the other bird would lunge at its disengaging opponent.

The present data show that, whether leading to fights or not, FPEs contain (1) defensive manoeuvres (e.g., squat, swerve away) to counter the movements of one's opponent (Prediction (ii)), (2) countermoves to maintain the FPE configuration (Prediction (iv)), and (3) attempts to achieve a position slightly at an angle to the FPE to deliver the most effective wing strikes (Prediction (iii)). All are consistent with the combat hypothesis. However, the presence of apparent signals (e.g., tail fanning, staccato calls) in both FPEs only and FPEs with fights supports the communication hypotheses, whereby the FPE is adopted to facilitate threat or assessment (Prediction (v)).

#### *4.1. Caught in the vortex of attack and defence*

While in most encounters (FPEs only and FPEs with fights) the birds maintained the typical anti-parallel orientation (Figure 1), this was not the most advantageous position from which to launch a wing attack. The most successful wing strikes, in which the attacker hits the top of the defender's head with its wrist, were those that occurred when it managed to stand about 20–25° off anti-parallel (Figure 3), an orientation which also reduced the capacity for the defender to retaliate with a successful counter-strike. However, most attempts by birds to gain this advantageous orientation were countered by movements of their opponents, which would then bring them back into the typical, anti-parallel orientation. In this regard, this configuration was a compromise position created by the actions of both animals, as each countered the other's attempts to move into a configuration more advantageous for attack. That is, although the anti-parallel orientation was an optimal orientation from which to defend and retaliate against one's opponent's attempted attacks, the off anti-parallel orientation was the optimal one from which to launch attacks. Hence, when neither animal succeeded in gaining a slight advantage to initiate an attack, there was a stalemate, and no attack took place; this seems to account for many of the FPEs that failed to escalate to a fight.

That defensive actions played a major role in the final configuration adopted is supported by the finding that when fights did occur, defensive manoeuvres attenuated the severity of the strikes (Figure 2), and, indeed, fights are rarely reported to cause damage (Wiley, 1973b). The role of defensive actions by the opponent in reducing the risk of injury (e.g., Blanchard et al., 1977; Geist, 1978; Pellis & Pellis, 1987) is further supported by unpublished

observations. Even though rare, males have been found to suffer fractures or to have died after having been observed to engage in combat (Tom Christiansen, Wyoming Game and Fish Dept., pers. commun.), and bruising of both the head and the wings appears to be quite common (A.H.K. and G.L.P., pers. obs.). Therefore, it is likely that, in the fights, while the attacking birds are attempting to do their best to inflict damage, the relative rarity of severe damage is due to the defensive actions taken by the opponent.

Once in the typical anti-parallel orientation, the manoeuvring and counter-manoevring to gain a vantage point for attack, contributed to the tendency for many FPEs and fights to be of long duration (up to as much as 20 min — see Table 1). Obviously, in order to strike an opponent, the inter-animal distance has to be closed to within striking distance, but, in doing so, it also affords the opponent a greater ability to detect and counter the other's movements.

That there is such an information gathering and protective gain from proximity has been reported for encounters with predators, with prey sometimes closing the distance rather than increase it (e.g., Godin & Davis, 1995; Lingle, 2001; Eilam, 2005). The advantage of such proximity is that the movements of the opponent may be easier to detect and so counter. However, once within striking range, the problem becomes one of disengagement — how to leave without inviting attack. Such a case of stalemate has been reported for intra-specific combat in stomatopods (i.e., mantis shrimps). These marine crustaceans fight by approaching tail-to-tail to within striking distance. Fighting involves using the claws to strike the opponent's tail (Caldwell & Dingle, 1975; Patek & Caldwell, 2005). They jockey for a position that is not too close (i.e., too short a distance to discharge the full energy at impact) or too far (i.e., an insufficient mass hits the opponent). A phenomenon seen in several species of mantis shrimp is that, once the optimal strike distance is gained, the animals appear to have difficulty in disengaging. As one shrimp begins to withdraw, the other can initiate a strike, so that the shrimp become seemingly stuck in this ready-to-strike distance for 2–3 min before finally disengaging (Roy Caldwell, pers. commun., 2012).

Similarly, the difficulty in disengaging from the anti-parallel orientation by sage-grouse may be accounted for by the problem of how to move away without creating an opportunity to be attacked. The impression gained from the present analyses is that, in prolonged encounters, disengagement occurred after a long period in which the birds were quiescent, often in an

FPE configuration (Table 1) — that is, when they stopped manoeuvring for advantage. A formal analysis is needed to test this assertion, but, if correct, perhaps such long periods of quiescence are needed to inform an opponent that no attack is likely on withdrawal. That is, some communication takes place to inform an opponent as to when it is safe to withdraw.

#### 4.2. Roles for communication

While FPEs arise from the coordinated attack and defence manoeuvres of the fighting pair, there is also support for the hypothesis that once engaged in an FPE, the opportunity arises to gain a tactical advantage by the use of threat signals (the threat signals hypothesis). Indeed, non-combat signals were prevalent in both FPEs only and FPEs with fights (see Prediction (v)). Thus, the FPE may be a positive handicap — with birds assuming the position that will give them an advantage in combat as a signal of willingness to fight (Hurd & Enquist, 2001; Számadó, 2003; Bradbury & Vehrencamp, 2011). Indeed, such threats may be another reason for why many FPEs do not escalate to fighting (Table 1).

Unlike the parallel walk of the red deer, this study does not support the hypothesis that the FPE *per se* is used by sage-grouse as an index signal or that FPEs function to facilitate such signalling. Nonetheless, once in the FPE configuration, there may be opportunities for the opponents to use signals to inform each other of potential fighting capabilities. This possibility is supported by the findings that, during both FPEs only and FPEs with fights, sage-grouse frequently incorporate signalling gestures associated with the strut display (e.g., chest-raised posture, tail fanning), as well as signals unique to agonistic interactions (e.g., staccato vocalisations, tail rattling) (Wiley, 1973a, b). While we could not test this hypothesis directly with the available data, the vigour of these movements or the frequency of these staccato vocalisations may provide the opponent with some information about body size and stamina. Thus, these signals — as well as information about fight performance gathered during combat — could be used to assess one's opponent and decide how long to persist in the interaction (Enquist & Leimar, 1983). Indeed, the information provided may be subtler, such as indicating when it is safe to withdraw (see above). Conversely, the counter moves by the resident may inform the potential opponent of the resident's tolerance, or lack thereof, to the encroachment (Senar, 1990).

On leks, many birds are clustered in a relatively small space (Wiley, 1973a; Bradbury et al., 1986, 1989), so that the neighbours of the two interacting birds are often within visual range, and, given that altercations occur with neighbours (Wiley, 1973b), what happens in one encounter could influence subsequent encounters with other neighbours. That is, the lek may form an eavesdropping network (Peake, 2005), in which eavesdropping can influence the likely outcomes of subsequent encounters within that network (e.g., Early & Dugatkin, 2002). The changing pattern of increasing familiarity with neighbouring male opponents and the variable presence of females during the altercations could produce a rich social context from which the communicatory aspects of the FPEs could be used in highly variable ways, even if the FPEs arise from failed attacks or fights which ended in stalemates. Such network and relationship effects have been reported in other species (e.g., Dzieweczynski et al., 2012; Mouterde et al., 2012) and could well apply to leks (Noë & Hammerstein, 1995; Patricelli et al., 2011).

#### *4.3. Conclusion*

The present analysis supports the findings of other studies of animal combat, in which the dynamic inter-play between opponents is taken into account, showing that actions that superficially seem to have evolved primarily as signals or communicatory displays are often better explained as tactics of attack and defence (Geist, 1971, 1978; Blanchard & Blanchard, 1994; Pellis, 1997). The present findings also suggest that FPEs, or aspects of FPEs, have been co-opted into an additional communicatory function, a conclusion consistent with the finding that the signalling function of tactical threat emerges because the same behaviour is used in combat (Hurd & Enquist, 2001; Számadó, 2003; Bradbury & Vehrencamp, 2011). Irrespective of these added communicatory functions, however, the present paper suggests that the primary function of the FPE configuration arises from the combat manoeuvres of the opponents. The signalling function of FPEs when combined with combat may explain why these interactions can be so protracted in duration (Wiley, 1973b). FPEs that have continued for 45 min or more have been observed (G.L.P. and A.H.K., pers. obs.). In some of the most protracted interactions, males hunker down in the anti-parallel position, with no evidence of active signalling or manoeuvring for combat. In these cases, males may truly be stuck in the vortex, unable to disengage lest they risk inciting a wing strike.

## Acknowledgements

For advice and help in data collection and analysis, we thank the Lander offices of the BLM and Wyoming Game and Fish Department, Tom Christiansen, Mary Clapp, Erin Hannelly, Stan Harter, Daniel Lipp and Sue Oberlie. We thank Jack Bradbury for use of his high-speed video camera and Marc Dantzker for design and use of his audio-video synchronisation system. We thank Devin Cahoon for providing the drawing of the grouse fighting. Data collection was supported by provided by UC Davis and an NSF grant (IOS-0925038) to G.P. and A.K. The analysis was supported by a Discovery grant from the Natural Sciences and Engineering Research of Canada to S.P. H.B. was supported by a scholarship from the Alberta Innovates Health Services and Melissa Blundell by the National Science Foundation Graduate Research Fellowship under Grant No. DGE-1148897.

## References

- Archer, J. & Huntingford, F. (1994). Game theory models and escalation of animal fights. — In: Dynamics of aggression. Biological and social processes in dyads and groups (Potegal, M. & Knutson, J.F., eds). Lawrence Erlbaum Associates, Hillsdale, NJ, p. 3-31.
- Blanchard, R.J. & Blanchard, D.C. (1994). Environmental targets and sensorimotor systems in aggression and defence. — In: Ethology and psychopharmacology (Cooper, S.J. & Hendrie, C.A., eds). Wiley, New York, NY, p. 133-157.
- Blanchard, R.J., Blanchard, D.C., Takahashi, T. & Kelly, M.J. (1977). Attack and defensive behaviour in the albino rat. — *Anim. Behav.* 5: 622-634.
- Bradbury, J.W. & Vehrencamp, S.L. (2011). Principles of animal communication, 2nd edn. — Sinauer Associates, Sunderland, MA.
- Bradbury, J.W., Gibson, R.M., McCarthy, C.E. & Vehrencamp, S.L. (1989). Dispersion of displaying male sage grouse. II. The role of female dispersion. — *Behav. Ecol. Sociobiol.* 24: 15-24.
- Bradbury, J.W., Gibson, R.M. & Tsai, I.M. (1986). Hotspots and the dispersion of leks. — *Anim. Behav.* 34: 1694-1709.
- Bruski, C.A. & Dunham, D.W. (1987). The importance of vision in agonistic communication of crayfish *Orconectes rusticus*. I. An analysis of bout dynamics. — *Behaviour* 103: 83-107.
- Caldwell, R.L. & Dingle, H. (1975). Ecology and evolution of agonistic behavior in stomatopods. — *Naturwissenschaften* 62: 214-222.
- Charlton, B.D., Reby, D. & McComb, K. (2007). Female red deer prefer the roars of larger males. — *Biol. Lett.* 3: 382-385.
- Clutton-Brock, T.H. & Albon, S.D. (1979). The roaring of red deer and the evolution of honest advertisement. — *Behaviour* 69: 145-170.

- Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. & Guinness, F.E. (1979). The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus L.*). — Anim. Behav. 27: 211-225.
- Clutton-Brock, T.H., Guinness, F.E. & Albon, S.D. (1982). Red deer. Biology and ecology of two sexes. — University of Chicago Press, Chicago, IL.
- Connelly, J.W., Gratson, M.W. & Reese, K.P. (1998). Sharp-tailed grouse (*Tympanuchus phasianellus*). — In: The birds of North America online (Poole, A., ed.). Cornell Lab of Ornithology, Ithaca, NY. Available online at <http://bna.birds.cornell.edu/bna/species/354> (accessed 22 October 2012).
- Dziewieczynski, T.L., Gill, C.E. & Perazio, C.E. (2012). Opponent familiarity influences the audience effect in male–male interactions in Siamese fighting fish. — Anim. Behav. 83: 1219-1224.
- Earley, R.L. & Dugatkin, L.A. (2002). Eavesdropping on visual cues in green swordtail (*Xiphophorus helleri*) fights: a case for networking. — Proc. Roy. Soc. Lond. B: Biol. 269: 943-952.
- Eilam, D. (2005). Die hard: a blend of freezing and fleeing as a dynamic defense — implications for the control of defensive behaviour. — Neurosci. Biobehav. Rev. 29: 1181-1191.
- Eilam, D. & Golani, I. (1988). The ontogeny of exploratory behavior in the house rat (*Rattus norvegicus*): the mobility gradient. — Dev. Psychobiol. 21: 679-710.
- Enquist, M. & Jakobson, S. (1986). Decision making and assessment in the fighting behavior of *Nannacara anomala* (Cichlidae, Pisces). — Ethology 72: 143-153.
- Enquist, M. & Leimar, O. (1983). Evolution of fighting behaviour: decision rules and assessment of relative strength. — J. Theoret. Biol. 102: 387-410.
- Eshkol, N. & Wachmann, A. (1958). Movement notation. — Weidenfeld & Nicholson, London.
- Geist, V. (1971). Mountain sheep: a study in behavior and evolution. — University of Chicago Press, Chicago, IL.
- Geist, V. (1978). On weapons, combat and ecology. — In: Advances in the study of communication and affect, Vol. 4, Aggression, dominance and individual spacing (Krames, L., Pliner, P. & Alloway, T., eds). Plenum, New York, NY, p. 1-30.
- Gibson, R.M. & Bradbury, J.W. (1985). Sexual selection in lekking grouse: phenotypic correlates of male strutting success. — Behav. Ecol. Sociobiol. 18: 117-123.
- Gibson, R.M. (1996). Female choice in sage grouse: the roles of attraction and active comparison. — Behav. Ecol. Sociobiol. 39: 55-59.
- Godin, J.-G. & Davis, S. (1995). Who dares, benefits: predator approach behaviour in the guppy (*Poecilia reticulata*) deters predator pursuit. — Proc. Roy. Soc. Lond. B: Biol. 259: 193-200.
- Golani, I. (1976). Homeostatic motor processes in mammalian interactions: a choreography of display. — In: Perspectives in ethology, Vol. 2 (Bateson, P.P.G. & Klopfer, P.H., eds). Plenum, New York, NY, p. 69-134.
- Grafen, A. (1990). Biological signals as handicaps. — J. Theor. Biol. 144: 517-546.
- Hasson, O. (1989). Amplifiers and the handicap principle in sexual selection: a different emphasis. — Proc. Roy. Soc. Lond. B: Biol. 235: 383-406.
- Hurd, P.L. & Enquist, M. (2001). The threat displays of birds. — Can. J. Zool. 79: 931-942.

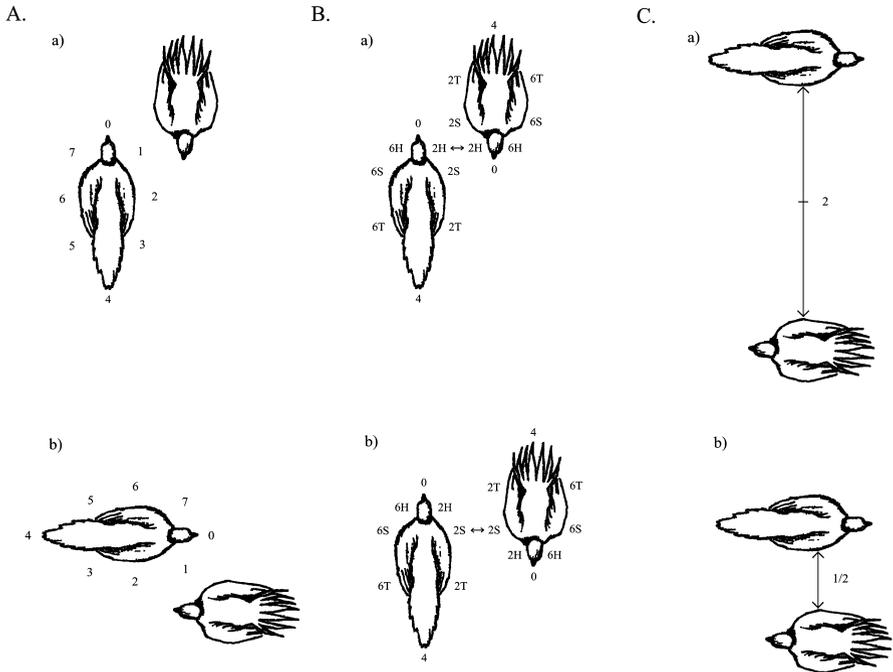
- Hurd, P.L. & Enquist, M. (2005). A strategic taxonomy of biological communication. — *Anim. Behav.* 70: 1155-1170.
- Jennings, D.J., Gammell, M.P., Carlin, C.O.M. & Hayden, T.J. (2003). Is the parallel walk between competing male fallow deer, *Dama dama*, a lateral display of individual quality? — *Anim. Behav.* 65: 1005-1012.
- Johnsgard, P.A. (1983). *The grouse of the world*. — University of Nebraska Press, Lincoln, NE.
- Lingle, S. (2001). Antipredator strategies and grouping patterns in white-tailed deer and mule deer. — *Ethology* 107: 295-314.
- Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. — *J. Theor. Biol.* 47: 209-211.
- Maynard Smith, J. (1982). *Evolution and the theory of games*. — Cambridge University Press, Cambridge.
- McComb, K.E. (1991). Female choice for high roaring rates in red deer, *Cervus elaphus*. — *Anim. Behav.* 41: 79-88.
- Moran, G., Fentress, J.C. & Golani, I. (1981). A description of relational patterns of movement during 'ritualized fighting' in wolves. — *Anim. Behav.* 29: 1146-1165.
- Mouterde, S.C., Duganzich, D.M., Molles, L.E., Helps, S. & Waas, J.R. (2012). Triumph displays inform eavesdropping little penguins of new dominance asymmetries. — *Anim. Behav.* 83: 603-611.
- Noë, R. & Hammerstein, P. (1995). Biological markets. — *Trends Ecol. Evol.* 10: 336-339.
- Patek, S.N. & Caldwell, R.L. (2005). Extreme impact and cavitation forces of a biological hammer: strike forces of the peacock mantis shrimp *Ondontodactylus scyllarus*. — *J. Exp. Biol.* 208: 3655-3664.
- Patricelli, G.L. & Krakauer, A.H. (2010). Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. — *Behav. Ecol.* 21: 97-106.
- Patricelli, G.L., Krakauer, A.H. & McElreath, R. (2011). Assets and tactics in a mating marker: economic models of negotiation offer insights into animal courtship dynamics on the lek. — *Curr. Zool.* 57: 225-236.
- Peake, T.M. (2005). Eavesdropping in communication networks. — In: *Communication networks* (McGregor, P.K., ed.). Cambridge University Press, Cambridge, p. 13-37.
- Pellis, S.M. (1982). An analysis of courtship and mating in the Cape Barren goose *Cereopsis novaehollandiae* Latham based on Eshkol-Wachman Movement Notation. — *Bird Behav.* 4: 30-41.
- Pellis, S.M. (1989). Fighting: the problem of selecting appropriate behavior patterns. — In: *Ethoexperimental approaches to the study of behavior* (Blanchard, R.J., Brain, P.F., Blanchard, D.C. & Parmigiani, S., eds). Kluwer, Dordrecht, p. 361-374.
- Pellis, S.M. (1997). Targets and tactics: the analysis of moment-to-moment decision making in animal combat. — *Aggress. Behav.* 23: 107-129.
- Pellis, S.M. (2011). Head and foot coordination in head scratching and food manipulation by purple swamp hens (*Porphyrio porphyrio*): rules for minimizing the computational costs of combining movements from multiple parts of the body. — *Int. J. Comp. Psychol.* 24: 255-271.

- Pellis, S.M. & Pellis, V.C. (1987). Play-fighting differs from serious fighting in both target of attack and tactics of fighting in the laboratory rat *Rattus norvegicus*. — *Aggress. Behav.* 13: 227-242.
- Reby, D. & McComb, K. (2003). Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. — *Anim. Behav.* 65: 519-530.
- Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W.T. & Clutton-Brock, T. (2005). Red deer stags use formants as assessment cues during intrasexual agonistic interactions. — *Proc. Roy. Soc. Lond. B: Biol.* 272: 941-947.
- Schroeder, M.A., Young, J.R. & Braun, C.E. (1999). Sage grouse: *Centrocercus urophasianus*. — *Birds of North America* 425: 1-28.
- Senar, J.C. (1990). Agonistic communication in social species: what is communicated? — *Behaviour* 112: 270-283.
- Siegel, S. & Castellan, N.J.J. (1988). Nonparametric statistics for the behavioral sciences. — McGraw-Hill, New York, NY.
- Számádó, S. (2003). Threat displays are not handicaps. — *J. Theor. Biol.* 221: 327-348.
- Számádó, S. (2008). How threat displays work: species-specific fighting techniques, weaponry and proximity risk. — *Anim. Behav.* 76: 1455-1463.
- Waas, J.R. (1991). The risks and benefits of signalling aggressive motivation: a study of cave-dwelling little blue penguins. — *Behav. Ecol. Sociobiol.* 29: 139-146.
- Waas, J.R. (2006). How do little blue penguins “validate” information contained in their agonistic displays? — *Adv. Stud. Behav.* 36: 397-447.
- Walther, F.R. (1984). Communication and expression in hoofed mammals. — Indiana University Press, Bloomington, IN.
- Wiley, R.H. (1973a). The strut display of male sage grouse — a ‘fixed’ action pattern. — *Behaviour* 47: 129-152.
- Wiley, R.H. (1973b). Territoriality and non-random mating in sage grouse, *Centrocercus urophasianus*. — *Anim. Behav. Monogr.* 6: 85-169.
- Zahavi, A. (1977). The cost of honesty (further remarks on the handicap principle). — *J. Theor. Biol.* 67: 603-605.

## Appendix A

### A.1. Description of how EWMN was used

In EWMN, the body is treated as a system of articulated axes (i.e., body and limb segments). A limb is any part of a body that either lies between two joints or has a joint and an extremity. These are imagined as straight lines (axes), of constant length, which move with one end fixed to the centre of a sphere (Eshkol & Wachman, 1958). The body is represented on a horizontally ruled page into columns that denote units of time (e.g., frames of a video). The signs for movement are read from left to right and from bottom to top. Movements by any limb segment, or the body as a whole, can



**Figure A.1.** The figure illustrates the three, simplified, horizontal coordinates derived from EWMN that were used to record inter-animal configuration during interactions. (A) Partner-wise orientation: In this case, even though the birds change their position in space, the relative orientation of their longitudinal axes remains the same. (B) Opposition: In this case, as the animals move, they switch from an opposition that is head-to-head to one that is shoulder-to-shoulder. Relative distance: In this case, as the birds move, they decrease their relative distance to one another.

be described as the distal end moves across the surface of the sphere, with the proximal end being anchored in the centre of the sphere. Typically, the locations on the sphere (horizontal and vertical) are at  $45^\circ$  angles (see Figure A1), but the unit of angular measurement can be reduced (e.g.,  $22.5^\circ$ ) if finer grain comparisons are needed. An important feature of EWMN is that the same movements can be notated in several polar coordinate systems. The coordinates of each system are determined with reference to the environment, to the subject's body's midline axis, and to the next proximal or distal limb or body segment. Critical for studying interactions between animals, the movement by one animal can be described relative to the body of the other animal. By transforming the description of the same behaviour from one coordinate system to the next, invariance in the behaviour may emerge

in some coordinates but not others. Thus, the behaviour may be invariant in relation to some or all of the following — the subject's longitudinal axis, gravity, body-wise in relation to the next proximal or distal segment (Golani, 1976), or to some aspect of the opponent, such as the animal-animal orientation or the body location of closest proximity or contact (e.g., Moran et al., 1981; Pellis, 1982).

For the current study, the EWMN score was limited to the horizontal plane, as most of the positioning and manoeuvring occurred within a limited vertical domain. To keep track of the relationship between the two birds during interactions, the bodies of the two interacting birds were described on three coordinate systems (see Figure A1). Partnerwise orientation: the relationship of the longitudinal axis of one bird relative to the other. One bird is selected as the focal animal and the 45° units are situated in a circle around the longitudinal axis (0–7), with 0 being situated in the direction in which the bird is facing, and continues to be so situated even as the bird changes position in space. The longitudinal axis of the other bird is superimposed over the longitudinal axis of the focal animal and the value pointed at by the anterior of the opponent is given that numerical label. For example, in Figure A1A, panel a, the focal animal is facing towards the top of the page and the opponent to the bottom of the page, so that if the opponent is imagined to be sitting on top of the focal bird, its bill would be facing past the tail end to value 4, and so would be labelled {4} (with {} signifying coordinates for partner-wise orientation). In panel b, the two birds have moved, with the focal bird rotating its longitudinal axis by 90° to the right, but so has the opponent, which means that, although both birds have changed their position in space, their relationship to each other remains the same. Since in partner-wise notation the circle of coordinate values moves with the focal animal, the partner-wise orientation continues to be designated as {4}. Opposition: the part of the body of one bird closest to the other is scored. To score this, imagine the EWMN sphere being deflated, so that it is wrapped around the animal's body. The front of the sphere (taking the horizontal value only) would be 0 and this value would be attached to the tip of the bird's beak, and the most posterior point would be 4. Similarly, each side of the bird's body (head, shoulder, torso) would be labelled 2 for the right side and 6 for the left side. In Figure A1B, panel a, the two birds are shown, with their respective labels attached, standing, in an anti-parallel orientation, and with their heads in closest proximity to one another.

The opposition between the two birds would be designated at 2H/2H, as the sides of their heads would be in closest proximity. In panel b, the birds move forward, relative to one another, which result in their shoulders being in closest proximity (2S/2S). Relative distance: given that videotapes were not taken with a measurable frame of reference, the absolute distance in a metric, such as centimetres, was not possible, but the distance in terms of bird lengths (i.e., from the tip of bill to the base of the tail when the bird is standing upright in a relaxed posture) could be used to track the relative distance, during encounters, between the birds. For example, in Figure A1C, panel a, the two birds are side-by-side, but are two body lengths apart. Then, following some movement, in panel b, the two birds have closed the gap between them to about 0.5 a body length. Together, these three coordinates create a space within which the relationship between the two animals can be traced throughout the encounter (Moran et al., 1981; Pellis, 1982).

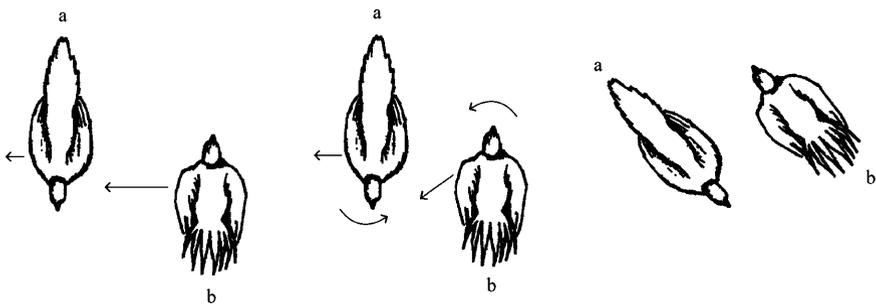
By using different aspects of the EWMN to record the whole body movements of the individual birds during these encounters, it is possible to determine which of the birds are contributing to changes in the inter-animal relationships (Pellis, 1989). For this study, whole body movements were recorded in two ways. First, changes in the orientation of the longitudinal axis of the body were recorded as rotations in absolute space. For example, in Appendix Figure 1A, the focal animal rotates its body axis 90° to the right, and for this, the sphere (or, in this case, its horizontal dimension) is viewed as remaining stationary as the bird moves within it. If the absolute coordinate in this case involves the front of the sphere being closest to the top of the page, then the bird would be facing (0), and, after rotating, faces (2) (in which () signifies movements in absolute space). In contrast, the opponent in Figure A1 begins at (4) and ends at (6). Rotation in space is designated U for clockwise movements, and an inverted U for anti-clockwise movements. These rotational changes of the body axis in absolute space are called changes in 'Front'.

Second, the movement of the whole body in space can be accomplished by shifting the body's centre of mass in a particular direction, which may or may not involve stepping. These bodily movements were scored, again, only in the horizontal plane, and in a body-wise frame of reference. That is, if the bird leans to its right, it would be designated as [2] and if backwards, [4] (in which [] signifies body-wise notation). This designation would remain the same, irrespective of the bird's position in absolute space — a body shift to

the right would be [2], no matter whether the bird was pointing towards (0) or (6) in absolute space. If the shift of body weight involved stepping, then the direction of the shift would be accompanied with the appropriate stepping symbol, S. These shifts in body mass are referred to as changes in ‘Weight’ (Eshkol & Wachman, 1958).

To illustrate how the notation works, the example of the birds moving and counter moving shown in Figure 1 of the paper is shown again here, but this time, each of the three panels is matched to their respective moments in the notated score that describes the movements (see Figure A2). It shows how an EWMN analysis can detect and record movements that are correlated between the opponents. The left hand column shows the rows for the movements in space (Front and Weight) for both birds *a* and *b*, and, in between, the three coordinates that are used to track the inter-bird relationship (i.e., partner-wise orientation, opposition, relative distance in bird lengths). At the start of the EWMN score, the positions of the birds are shown, from a dorsal perspective, on the far left (under (i)). Starting from the anti-parallel

Frames	0	6	7	11	20	23	25	32
a. Front	(4)						<u>U</u>	(3)
Weight			S [2]			S [2]		
Partner wise	{4}							
Opposition	2S/2S							
Distance	1.5		1					0.5
b. Front	(0)					<u>U</u>		(7)
Weight		S [6]				S [5]		
	(i)			(ii)				(iii)



**Figure A.2.** A short sequence, around one second, embedded within a fight, in which two clusters of movements by the two opponents are illustrated. (Top panel) The notated score for the movements. (Bottom panel) Drawings from a dorsal view of the relative positions of the birds at specific moments in the score (same as in Figure 1).

configuration with their shoulders opposed and standing at about 1.5 bird lengths apart (i), bird *b* moves laterally toward the bird *a*. This movement is followed by *a* laterally stepping in the opposite direction (as shown by the arrows next to the drawings of the birds). Therefore, at the end of the movements, because *b* makes a bigger lateral displacement than *a*, even though the distance has closed between them to one body length, they remain in the same opposition and partner-wise orientation (ii). Bird *b* then makes another set of movements, stepping obliquely backwards and rotating towards its opponent, followed by *a* stepping away and then rotating laterally towards *b*. At the end of the sequence of movements, the birds' orientation in absolute space has changed, as has inter-animal distance, which has been reduced to half a body length, but their partner-wise orientation and opposition has remained the same (iii). By simply looking at the arcs designating the duration of the movements by each bird illustrate how the notation score can be used to identify how the movements between the two birds are correlated and which of these movements lead to changes in the inter-animal configuration. Moreover, the movements by one bird can be seen to counteract the changes that would otherwise be imposed by the movements of the other bird.

#### *A.2. Intra- and inter-observer reliability*

Two methods were used to verify consistency in the qualitative and quantitative analyses. First, for reliability of the qualitative descriptions, 12 of the EWMN scores produced by one observer (SMP) were randomly selected and read by another (VCP), who had not previously seen the actual videotaped sequences. The reader provided a verbal/written description of the sequences and these were then compared to what the birds actually did. In all cases, the naïve reader recreated the actual movements performed, confirming that the EWMN scores were an accurate descriptive representation of the birds' behaviour.

Second, for consistency in the quantitative scores, an independent observer (HCB) rescored the same 20 sequences scored by the first observer (SMP). There were no significant differences between the scores from the two observers (Wilcoxon matched pairs tests:  $p > 0.05$ ). The concordance between scores for the inter-observer scores was 60–100%. The lowest concordance occurred when attempting to make finer distinctions, such as the inter-animal distance in which an ordinal scale was used. However, when the scores were grouped to the nearest 0.5 bird length, the concordance was

closer to 80%. Thus, the more crude categorical and ordinal measures are reasonably reliable across observers. Video taken from an aerial view would be needed to ascertain, objectively, whether one observer's tendency to score closer to one bird length relative to the other's tendency to see the distance closer to 0.5 body length, was more accurate. What is consistent is that both observers detected a reliably, consistent, non-random distribution in the scores and those scores were not statistically significant between observers.