

Bottoms up: great bustards use the sun to maximise signal efficacy

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Abstract

Visual displays are signals that may be selected to increase visibility. Light is a crucial component in the transmission of visual signals and white colour is very conspicuous when illuminated by sun and exhibited against darker backgrounds. Here we tested the hypothesis that orientation of sexual displays in males of great bustard *Otis tarda*, depends upon position of the sun, i. e. males direct their uplifted white tails towards the sun in order to maximise signal detectability to distant females. We recorded the orientation of 405 displays of males in relation to the sun and to females at 7 leks. Great bustard males signalled towards the sun more often than expected by chance in early morning, although this pattern was not obvious at other times of day, when males tended to directly display towards females. Our hypothesis was further supported by the fact that displays tended to be directed towards the sun only when the sun tended to be most visible. Males were more likely to direct their displays towards females during the most elaborate components of their courtship display, and when there were fewer males on the lek. Pointing white plumage to the sun may be a behaviour selected in species living in steppe-like open landscapes if individuals obtain net fitness benefit by increasing the likelihood of mating.

Keywords: animal communication, courtship, display, *Otis tarda*, white plumage.

Animal communication occurs through the exchange of information transmitted by signals (Maynard Smith and Harper 2003). Since the seminal work by Darwin (1871), some of the most impressive structures or behaviours in the animal kingdom, such as the peacock's tail, birdsongs, are considered to be signals that have evolved through strong inter- and intrasexual selection (Andersson 1994). Signals are more effective when they are conspicuous to a receiver (Fleishman and Persons 2001; Uy and Endler 2004). Increasing evidence supports that selection favours signal design and signalling behaviour that maximizes the signal detectability or contrast against the background (Fleishman and Persons 2001; Leal and Fleishman 2002; Fuller 2002; Uy and Endler 2004; and references therein). However, we might also expect a trade-off between increasing visibility to potential mates (driven by sexual selection) and reducing it to predators (natural selection) (Endler 1991; Heindl and Winkler 2003; Gómez and Théry 2004).

Increased conspicuousness of visual signals can be obtained in several ways but colour, brightness and contrast against the background are of particular relevance (e.g. Fleishman and Persons 2001; Uy and Endler 2004; Penteriani et al. 2007; Galván 2008). An achromatic visual signal such as white, which is formed by reflectance from all visible wavelengths, is very conspicuous when exhibited against darker terrestrial backgrounds (Beauchamp and Heeb 2001; Bókonyi et al. 2003). In fact, Galván (2008) has shown in a wide group of species (Pelecaniformes) that white plumage could increase the perception of sexual visual displays or the presence of the signaller. Animals can further enhance the effectiveness of the signal by behaviourally augmenting its conspicuousness (Uy and Endler 2004; Dakin & Montgomerie 2009).

Ambient light is a crucial component in the transmission of visual signals and seems to play a role in the evolution of colour patterns and signals (Marchetti 1993; Endler and Théry 1996; Fleishman and Persons 2001; Gomez and Théry 2004). Some evidence shows that animals can take advantage of particular lighting conditions to maximize visual contrasts of their displays

(Thery and Vehrencamp 1995; Endler and Thery 1996; Heindl and Winkler 2003; Uy and Endler 2004; but see Anciaes and Prum 2008). Recently it has been shown that one of the courtship displays of peacock males (*Pavo cristatus*) is oriented about 45° relative to the sun, with the females situated directly in front, probably to maximize the impact of iridescent eyespot feathers of the male erect train (Dakin & Montgomerie 2009). In this paper we explore how sunlight is used to increase signal efficacy during displays by great bustard *Otis tarda*.

Great bustards live in the wide open plains of the Palaearctic (del Hoyo et al. 1996), and are a good model to investigate signalling behaviour. Great bustards exhibit an impressive display that involves lifting their tail and rotating their wings in order to expose their white body feathers (Hidalgo de Trucios and Carranza 1990, 1991,), i.e. most of the white is on the back side of the bustard male (Fig. 6). This display can, under certain conditions, be seen by the naked eye from distances > 1km and is most obvious to humans when the sun shines directly onto the white feathers (pers. obs., Fig 6). From this observation we hypothesized that it would be advantageous for males to direct their white feathers towards the sun in order to maximise signal detection, especially by distant females. We expected this to be the case particularly in early morning and late evening, when directing the display to sun position would maximize signalling efficacy, and when courtship activity is maximal (early morning, Hidalgo and Carranza 1991; Martínez 2000). We tested the hypothesis that orientation of sexual displays depends upon position of the sun by watching displaying bustards in the plains of northern Spain. If the hypothesis is correct, we expected the direction of individual displays within the lek to follow the movement of the sun, especially in morning and evening (H1). We also predicted that males would orient their white tails towards the sun when the contrast against the background is higher to maximize signal detectability during display, to attract distant females. The alternative hypothesis was that orientation of displays of males relied of female position in the vicinity of the lek (H2), to attract these nearby females. Nonetheless, the two hypotheses could be not mutually exclusive, as females could position themselves where they have males

displaying both towards them and the sun. We therefore recorded the location and orientation of displaying males in relation to the sun and to the presence and distance of great bustard's nearest male and female/s, recording also other potential confounding factors (cloud cover, sun visibility, day period and number of males at the lek).

MATERIALS AND METHODS

Study species

The Great bustard inhabits steppes and agricultural habitats from Iberia to China (del Hoyo et al. 1996). Spain holds the largest population and highest densities of great bustards worldwide (del Hoyo et al. 1996; Palacin et al. 2004). It is a highly sexually dimorphic species with males being up to three times larger than females (Cramp and Simmons 1980; Hidalgo and Carranza 1990). They have a typical exploded lek mating system (Morales et al. 2001), with a lower level of male aggregation and larger male territories than classical leks (Morales et al. 2001). In exploded leks, females can potentially forage and even nest (Morales et al. 2001), although female choice is not based on territory quality, but only on male phenotype and age (Morales and Martin 2002; Magaña 2007).

Study area and field methods

Fieldwork was conducted in March 2007, when male display reaches its highest activity (March-April; Morales et al. 2003). The study area was located in farmland at Los Oteros (Northern Spain, 42° 30' N, 5° 15' W, 830 m a.s.l.). This area was selected because it supports one of the highest lekking male densities in Spain (Alonso et al. 2005). Bustards were observed over 4 days at 7 leks from sunrise to sunset, with a break in the middle of the day, when birds were less active (Hidalgo and Carranza 1990, 1991). Males move within and between leks and

thus size of studied leks fluctuated on an hourly basis. Leks were separated by 0.7-9.9 km and had a mean size of between 7 and 37.4 males (mean of the means = 29.8 males); the highest number of males registered at a single lek was 60. We estimated an overall population of 200-250 males in the 7 leks. Three observers were involved in this study, and we tried to minimize inter-observer differences by standardizing sampling criteria and performing training before data collection. During training, the three people observed simultaneously the same males and compared scores until uniform results were achieved. Each focal lek was sampled for 5-min observation periods. For each observation period, we observed leks from at least 400 meters with telescopes, and recorded compass directions from the observer to both the approximate centroid of the lek and to the sun (Fig. 1). This compass direction to the lek centroid was used later as the compass directions of all the focal males observed at the lek in that observation period. The estimated diameter of leks varied from 25 to 100 meters, so the formed angle between the lek centroid and one of the distal sides of the lek, observed from a distance of 400 meters, would be of 1.79°-7.13°. These angles would therefore be our maximum errors committed by assigning at each focal male the compass direction of the lek centroid. We recorded information from displaying adult males. Focal males were randomly selected from among all those that were engaged in display at the focal lek at the moment of starting data recording. For each displaying male within a lek we assigned them an identifier number and recorded beak orientation in relation to the observer, assigning it to one of the eight parts on which a 360° circle was divided (Fig. 1). If more than one orientation was observed of the same male in succession short of time (n=73), we considered only the first direction registered in order to avoid pseudoreplication (see below). Daytime, cloud cover (estimated to the nearest 10 % of sky covered by clouds), sun visibility (shining or obscured) and the number of males and females, were noted just prior to the beginning of each observation period in the lek. At the same time, we also drew an *ad hoc* map recording the position of each focal male at the lek and nearest female/s in and around the lek and noted the distance from focal male to the nearest neighbour (estimated in great bustard body size integers, see Martínez 1991 for a similar

procedure) and its sex, number of males and females in or around the lek. For each focal male we also recorded the display phase, considering three phases with increased exposure of white feathers; 1= lifting tail, performed by folding the tail feathers over the back, showing the white under tail-coverts (Fig. 6); 2= lifting tail and semi-lifting wings, white under tail-coverts exhibited, and wing contortion started, showing a greater number of white coverts. The gular pouch is inflated by successive intakes of air; 3= lifting tail and wings and rotating movement, corresponds to the so-called "full-display". In this phase, the white plumage of the wings and tail is fully shown and the gular pouch is completely inflated. For an extended description of the different display phases, see Hidalgo and Carranza 1990, 1991).

Data analysis

We collected 478 observations of displaying males over 4 days. Of these, 73 observations were known to be repeated displays from the same males observed over a short space of time (<30 minutes), so they were removed to avoid pseudoreplication. Yet, we could not totally rule out repeat sampling of the same individuals over longer time intervals, as birds were unmarked, but we attempted to minimise the potential for pseudoreplication by observing individually numbered and mapped males in different parts of the leks and in different leks. The possibility of repeat-sampling from one day to the next, however, was still possible, as leks, and males within leks, moved and changed position. Tail orientation in males is expected to be affected by multiple factors (see Results) and males orient their tails in multiple directions over relatively short periods of time (authors, pers. obs.). Therefore, we assume that tail orientation within males is independent from one day to the next (see Ruxton & Colegrave 2003, p.40-41 and radio-tracking studies for a similar approach; Erickson et al 2001, p.211). The potential for repeat-sampling was low (≤ 2.03 observations per male on average). Nonetheless, in order to assess the assumption of independence, we repeated the analysis with a subset of data from only one of the days sampled (27 March 2007, i.e. the day with higher number of observations, $n=138$, Online Resource1). For most analyses we used all displaying male observations ($n =$

405). However, because females were not always present in the leks, we used a reduced dataset for analyses relative to females ($n = 312$).

We regarded a focal male as directing their tail either towards the sun or a female whenever the tail was within the relevant 45-degree sector where the sun or the female was. Female positions were estimated from maps drawn for each 5-min observation period of the lek (see above). Female/s considered were the closest to the focal lek or the focal male. Results did not change when we considered either the proximity of the female to the lek or to the male. We knew male orientation and the relative positions of sun and focal males, enabling us to determine the orientation of the male tail relative to the sun and to the nearest female/s. Note that a male could also to orientate themselves towards both the sun and the female/s at the same time or to neither of them. To reduce possible sampling errors we also repeated analyses using an angle of 135° (i.e. 3 sectors of 45°). Results between 45° and 135° were very similar, but we state whenever these analysis yielded different results. For all analyses, daytime was divided in 4 periods (early morning: 8.00-10.00H, late morning: 10-12.00H; early evening: 17.00-19.00, late evening: 19.00-21.00).

To compare frequencies between day periods, we used chi-square tests. To compare proportion observed to that expected by chance we used a binomial test (Note that 12.5% would be expected under a random orientation, i.e. $100\% / 8 \text{ sectors} = 12.5\%$). Directional data were analysed using circular statistics (Batschelet 1981). In order to analyze orientations of male tails towards the sun, we used Rayleigh's test for circular uniformity, i.e. if displaying male orientations were uniformly distributed around the circle. To test that the directions of male tails were non-randomly distributed, but had an expected mean direction instead, we used V test , which is a modified Rayleigh test for testing circular uniformity *versus* nonuniformity and a specified mean direction (Zar 2010, p. 626). The expected directions were those of the sun in each day period (see above), i.e. at early morning it was the mean position of the sun (azimuths in degrees) averaging all observations done between 8:00 and 10.00 H ($n = 137$), so the mean position of the sun in early morning was 97.8°; in late morning, the expected mean direction was

109.0° (n=99); at early evening 250.6° (n=103) and 262° (n=66) at late evening. Exact positions of the sun (azimuths, in degrees) at the nearest minute were obtained from NOAA (National Oceanic & Atmospheric Administration, USA:

<http://www.esrl.noaa.gov/gmd/grad/solcalc/>).

We used generalized linear mixed models (GLMM) to look at factors affecting displaying male tail orientated towards the sun (1) or not (0) (dependent variable), with binomial error link and lek as random effect. The latter allowed us to control for the possibility that male display orientation might vary due to factors related to the lek itself, such as geographical features or sources of disturbance, whose effects are not take into account in the fixed effects (see below). Random effects allow us also control for the fact that males within same lek could be pseudo-replicates, i.e. behaviour of males could be more similar within the same lek than among leks. Importantly, considering the lek as a random effect, our results can thus be extrapolated to a population of leks from which our sample (7 leks) was drawn. In these models we tested for the fixed effects of whether the sun was visible or not, female position relative to focal male, male density, cloud cover, distance to the nearest neighbour and its sex, the display phase, day period and observation day. Non-significant effects were removed from saturated models in a stepwise progression up to obtain minimal adequate models. Models including day and lek as random effects were also performed in order to account for possible dependence of observations between days. We also performed a similar procedure (binomial GLMM) to analyze factors affecting displaying male tail orientated towards female position (1) or not (0). Interactions formed by two variables with biological sense were tested (sun*day period, sun*display phase, sun*number of females, sun*number of males, display phase*day period, display phase*cloud cover). We used the lme4 package (Bates et al., 2008) for modelling using the R statistical software (R Development Core Team, 2008). Analysis of circular data including rose diagram were performed in ORIANA 3.0 software (Kovach Computing Services, Wales, UK).

RESULTS

Most of our observations were males displaying in phase 3 (72.1%), compared with the other phases (phase2: 21.0%, phase 1: 6.9% ($\chi^2 = 285.9$; $df = 2$, $P < 0.0001$). Phases of display followed a similar pattern throughout day. The proportion of male displays directed towards the sun was non-randomly distributed with respect to time of day ($\chi^2 = 16.31$; $df = 3$, $P < 0.001$; Fig 2 and 4, Table 1). It was very high at early morning (31.4%), diminished until early evening (10.7%) and slightly increased at late evening (16.7%, Fig. 2 and 4). In early morning, the distribution of male tail orientations was significantly different from random (Rayleigh test, $Z = 16.67$; $p < 0.001$, $n = 137$), and they orientated significantly towards the expected mean direction of the sun position, i.e. 97.8° (orientation mean angle $\pm$ SE: $84.05^\circ \pm 9.61^\circ$; V-Test, $V = 0.34$, $u = 5.60$, $p < 0.001$; Fig 2a). In late morning males tended to point their tails towards southeast (Fig. 2b), but there was not a significantly predominant direction (mean $\pm$ SE: $106.9^\circ \pm 31.0^\circ$; Rayleigh test, $Z = 1.69$; $p = 0.18$, $n = 99$). In early evening, orientation of males was not significantly different from random (Rayleigh test, $Z = 0.002$; $p = 0.99$, $n = 99$). In late evening, males orientated their tails non-randomly, and in a northerly direction ($352.9^\circ \pm 23.5^\circ$; Rayleigh test, $Z = 2.90$; $p = 0.055$, $n = 66$), but it was far from the expected mean direction of 262° (V-Test, $V = 0.000007$, $u = 0.00008$, $p = 0.50$; $n = 66$; Fig 2d). Results for only one day were similar to that of the whole study period, i.e., males orientated their tails following position of the sun at the morning (Online Resource1).

The frequency of observations of males pointing with their tails to females was low in early morning (10.3%), and increased in late morning (25.0%) and evening (16.1 and 22.6%, Fig. 4). The percentage of males directing their tails towards females was not significantly different from random for any of the day periods (Rayleigh test, $Z = 0.77$ - 2.57 ; $p > 0.05$ in all the four cases) (Figure 3).

Only 7 (2.24%) of 312 observations had coincident directions towards the sun and female position (i.e. females were between the sun and the focal male). After controlling for these seven observations and orientation to females (Fig. 4), males displayed their tails towards the

sun 3.5 times more often than to females at early morning (29.5 % vs 8.4% - binomial test, $p < 0.001$), but there were no significant differences in the other periods (12.3%, 10.9%, 14.8%, $p = 0.99$, $p = 0.75$, $p = 0.56$, in late morning, early and late evening, respectively). The proportion of male displays oriented towards females was not significantly different from that expected by chance alone in early morning (8.42%; binomial test, $p = 0.27$), late morning (21.1%; $p = 0.068$), and early evening (15.2%, $p = 0.43$), but more often than expected by chance in late evening (21.3%, $p = 0.050$).

Mixed models suggested that male displays towards the sun were influenced strongly by day period (Fig. 2 and 4), positively by visibility of sun (45° models; Table 1), and negatively by cloud cover (135° models; Table 1). Models including day and lek as random effect yielded qualitatively similar results (Online Resource1). Displays orientated towards females were influenced by day period (Fig. 3 and 4), number of males at the lek (Table 2) and phase of display (Fig. 5). Males were more likely to direct their tails towards females during the higher phases of their display, and when there were fewer males present on the lek. No interactions were significant.

DISCUSSION

Our observations indicated that great bustard males do indeed tend to display towards the sun in the morning, particularly during early morning hours, but this pattern was not obvious at other times of day. In late evening, males tended to display towards females. Thus, we found evidence supporting both hypotheses. Our initial hypothesis (H1) was further supported by the fact that cloud cover and sun visibility affected the probability of orientating the display to the sun direction. Displays tended to be directed towards the sun only when the sun was more visible. Females are known to move over a large area, including several leks, during courtship season (home range > 1,000 hectares) and, during daylight hours, they approach leks in order to mate (Morales et al. 2001; Hidalgo and Carranza 1990, 1991). Our results suggest that males orient

their displays differently according to the time of day: in the morning, they direct their displays towards the sun, possibly to attract distant females, whereas later in the day displays may be oriented to attract specific females close to the leks. It is well known that great bustard courtship activity is maximal during early morning (Martínez 2000), when bustards maximized signal efficacy. Maximizing signal detectability at long distances may be particularly important during early morning, when females leave roosting sites, having the rest of the day to approach the leks. Perhaps maximizing long-distance signal efficacy is less profitable in terms of attracting females during the last hours of the day, when, additionally, signalling to long distances could be a risky activity attracting nocturnal mammal predators (Casas et al. unpublished data). Thus, perhaps these behavioural differences associated with time of day may be due to a trade-off between maximizing female attraction and reducing predation risk.

Our study was based on a short 4-day snapshot and further information is required to explore patterns throughout the display period. Nonetheless, our prediction is that the trade-offs will vary depending on seasonality and the timing of breeding, i.e. males will need to display to females more when they are becoming fertile. We studied an unmarked bustard population through time and thus there was a potential for temporal and spatial pseudoreplication, i.e. multiple observations of the same individuals, as well as the same sites (Crawley 2007, pp 629). However, we have dealt with this potential problem in various ways and are confident that it has not significantly affected our results. In many ways, whether or not there is a pseudoreplication problem relies of the biology of the study system (Ruxton & Colegrave 2003, p 40-41). In our case, multiples factors are expected to affect orientation of tails. Consequently, bustard males can orient their tails in any direction in relatively short periods of time (pers. obs.), so it seems unlikely that tail orientation at one point on one day affects orientation in subsequent days. The likelihood of re-sampling is low in this study (average 2.03 observations), and those are expected to be randomly distributed (unbiased) throughout the studied population. Therefore, the assumption we adopted that observations of male orientation taken in different days were

independent samples was reasonable (see Ruxton & Colegrave 2003, Erickson et al 2001, p.211) and it seemed not to affect our results. Finally, spatial pseudoreplication was dealt with using mixed models including lek as a random effect (see Crawley 2007; Olea 2009).

We propose that directing a white patch to the sun by great bustard males is a way of improving the efficiency of sexual communication through increasing visibility to attract the attention of conspecifics and/or indicate male location. In an open landscape where several leks and dozens of males exhibit their white patches, a more conspicuous signal could elicit the attention of females. It has been shown in vertebrates that stimulus detection and stimulus recognition can occur as distinct sequential steps (Fleishman and Persons 2001). Therefore, once females have been initially stimulated from distant places by the brightness of the white signal sent by males, females then could focus attention on specific stimuli, such as male display rate, or ornaments (such as moustache feathers, or neck plumage development; Morales et al. 2003). This would suggest that different sexual cues may operate at different stages of the mating process (Mateos 1998). Females could benefit by rapidly locating and evaluating leks or potential males from distant places, visiting only more attractive leks, and thus saving travel time, energy expenditure, predation risk and interference from unwanted males.

We also found that signalling towards females was more common during higher phases of male display (i.e. phase 3, Fig. 5), consistent with the idea that the full display is used by males to exhibit to females at short distances (Hidalgo and Carranza 1991). However, there was not a phase of display (phase 1-3) on which males preferred pointing the tail to the sun (Fig. 5), suggesting that either the three display levels would exert similarly well the function of convey the message. Therefore, it seems that the signal sent to conspecifics when pointing to the sun depends on showing a bright white patch rather than the amount of exposed white surface.

If displaying towards the sun is advantageous, why don't all males do it? Bustard displays are a highly elaborate, energetically costly activity, and male display rates are positively related to male body condition, attractiveness, number of females attracted and copulation attempts (Morales et al. 2003), suggesting that the display rate may constitute a honest indicator of individual condition. White plumage can be costly to produce and maintain, and it may be condition-dependent (McGlothlin et al. 2007). According to the handicap principle, many aspects of such stereotypical behaviour could serve to increase the cost of the signal (Zahavi 1977; Redondo 1994). Therefore, such sexual displays could be a difficult skill, and the ability to perform the display towards the sun could be a costly, varying skill among males, i.e there might be variation among males in the ability to efficiently develop this task. Orientation towards the sun could be particularly costly because it could require careful co-ordination. Doing courtship display is already *per se* difficult, as shown by young males who do not perform the displays the same way as adults (pers. obs.), suggesting that displays take time and experience to develop. The display must also be combined with directing it towards a particular direction, the sun position. Future work could examine if males in better condition or "attractiveness" to females, besides showing a higher display rate (Morales et al. 2003), direct their tails more frequently to the sun in order to establish if it is an honest communication signal. Alternatively, the behaviour of orientating the white tail towards the sun might be a signal amplifier (sensu Hasson 1989) —a kind of signals which could improve the ability of the receiver to assess pre-existing quality cues— by which females could better discriminate the quality of displaying males (Barber and Folstad 2000; Ljetoff et al. 2007).

To our knowledge, the great bustard, along with the Anna's hummingbirds (*Calypte anna*) (Hamilton 1965), and the peacock (Dakin & Montgomerie 2009), are the only bird species reported showing directional displays oriented relative to the direction of sunlight. Peacock and great bustard are the only ones reported showing a sunflower-like behaviour during the courtship. Interestingly, other bustard species inhabiting steppe-like landscapes show large

patches of white feathers during the courtship (e.g. Houbara *Chlamydotis undulate* and kori *Ardeotis kori*), and both show also an exploded lek mating system (Morales et al. 2001). White objects in the green habitat of bustards during the courtship are practically absent. Pointing white plumage to the sun may be a behaviour selected in some species living in steppe-like open landscapes if individuals obtain net fitness benefits by increasing the likelihood of mating. Further work is needed to explore whether display behaviour using the light sun is present in other great bustard populations and in other steppe-land bird species.

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REFERENCES

- Alonso JC, Palacín C, Martín CA (2005) La Avutarda Común en la península Ibérica: población actual y método de censo. Madrid, Spain: SEO/BirdLife.
- Anciaes M, Prum RO (2008) Manakin display and visiting behaviour: a comparative test of sensory drive. *Anim Behav* 75:783-790.
- Andersson M (1994) Sexual selection. Princeton, USA. Princeton University Press.
- Barber I, Folstad I (2000) Schooling, dusk flight and dance: social organisations as amplifiers of individual quality? *Oikos* 89:191-194.
- Bates D, Maechler M & Dai B (2008) The lme4 Package. <<http://lme4.r-forge.r-project.org/>>.
- Batschelet, E. (1981): Circular statistics in biology. London. Academic Press.
- Beauchamp G, Heeb P (2001) Social foraging and the evolution of white plumage. *Evol Ecol Res* 3: 703-720.
- Bókony V, Liker A, Székely T, Kis J (2003) Melanin-based plumage coloration and flight displays in plovers and allies. *Proc R Soc B* 270: 2491-2497.
- Cramp S, Simmons KEL (1980) *The Birds of the Western Palearctic*. Vol. II. Oxford, UK: Oxford University Press.
- Crawley M J (2007) The R book. West Sussex, England: John Wiley & Sons Ltd.
- Dakin R, Montgomerie R (2009) Peacocks orient their courtship displays towards the sun. *Behav Ecol Sociobiol* 63: 825-834.
- Darwin, CR (1871) *The Descent of Man, and Selection in Relation to Sex*. London. John Murray.

409 del Hoyo J, Elliott, A, Sargatal J (1996) *Handbook of the Birds of the World, Vol. III. Hoatzin to Auks.*
 410 Barcelona, Spain: Lynx Edicions,.
 411
 412 Doucet SM, Mennill DJ, Montgomerie R, Boag PT, Ratcliffe LM (2005) Achromatic plumage reflectance
 413 predicts reproductive success in male black-capped chickadees. *Behav Ecol* 16: 218-222.
 414
 415 Endler JA (1991) Variations in the appearance of guppy color patterns to guppies and their predators
 416 under different visual conditions. *Vision Res* 31: 587–608.
 417
 418 Endler JA, Thery M (1996) Interacting effects of lek placement, display behavior, ambient light, and
 419 color patterns in three Neotropical forest-dwelling birds. *Am Nat* 148:421–452.
 420
 421 Erickson, WP, McDonald, TL, Gerow KG, Howlin S & Kern JW (2001) Statistical issues in resource
 422 selection studies with radio-marked animals, p 209-242. In : Millspaugh JJ & Marzluff JM (Eds) *Radio*
 423 *Tracking and Animal Populations*. Academic Press, San Diego, USA
 424
 425 Fleishman LJ, Persons M (2001) The influence of stimulus and background colour on signal visibility in
 426 the lizard *Anolis cristatellus*. *J Exper Biol* 204: 1559-1575.
 427
 428 Galván I (2008) The importance of white on black: unmelanized plumage proportion predicts display
 429 complexity in birds. *Behav Ecol Sociobiol*. 2008 63: 303-311.
 430
 431 Gómez D, Théry M (2004) Influence of ambient light on the evolution of colour signals: comparative
 432 analysis of a Neotropical rainforest bird community. *Ecol Let* 7: 279-284.
 433
 434 Hamilton WJ (1965) Sun-oriented display of the Anna's hummingbird. *Wilson Bulletin* 77: 38–44
 435
 436 Hasson O (1989) Amplifiers and the handicap principle in sexual selection: A different emphasis. *Proc R*
 437 *Soc Lond Ser B* 235: 383-406.

438

439 Heindl, M, Winkler, H (2003) Interacting effects of ambient light and plumage color patterns in
 440 displaying wire-tailed manakins (Aves, Pipridae). Behav Ecol Sociobiol. 53: 153-162.
 441

442 Hidalgo SJ, Carranza J(1990) Ecología y comportamiento de la avutarda (*Otis tarda* L.). Cáceres, Spain:
 443 Servicio de publicaciones Universidad de Extremadura.
 444

445 Hidalgo SJ, Carranza J (1991) Timing, structure and functions of the courtship display in male great
 446 bustard. Ornis Scand 22: 360-366
 447

448 Ljetoff M, Folstad I, Skarstein F, Yoccoz NG (2007) Zebra stripes as an amplifier of individual quality?
 449 Ann Zool Fenn 44: 368-376.
 450

451 Magaña M (2007) Comportamiento reproductivo de la Avutarda Común [dissertation].Madrid.
 452 Universidad Complutense.
 453

454 Marchetti K (1993) Dark habitats and bright birds illustrate the role of the environment in species
 455 divergence. Nature 362:149–152.
 456

457 McGlothlin JW, Duffy DL, Henry-Freeman JL, Ketterson ED (2007) Diet quality affects an attractive
 458 white plumage pattern in dark-eyed juncos (*Junco hyemalis*). Behav Ecol Sociobiol 61:1391-1399.
 459

460 Mateos C (1998) Sexual selection in the ring-necked pheasant: a review. *Ethol Ecol Evol*.10: 313-332.
 461

462 Martínez C (1991) Relaciones espaciales en una población de avutarda (*Otis tarda*) del noroeste de
 463 España. Ardeola 38: 265-276.
 464

465 Martínez C (2000) Daily activity patterns if great bustards *Otis tarda*. Ardeola 47: 57-68.
 466

467 Mateos C, Carranza J (1997) The role of bright plumage in male-male interactions in the ring-necked
 468 pheasant. *Anim Behav.* 54: 1205-1214.
 469
 470 Maynard Smith, Harper D (2003) *Animal Signals* Oxford, UK: Oxford University Press,
 471
 472 Morales MB, Jiguet F, Arroyo B (2001) Exploded leks: what bustards can teach us. *Ardeola* 48: 85-98
 473
 474 Morales MB, Martín CA (2002) Great bustard. In: BWP update. The birds of the western Palearctic, vol 4,
 475 no 3. Oxford, UK: Oxford University Press.
 476
 477 Morales MB, Alonso JC, Martín C, Martín E, Alonso J (2003) Male sexual display and attractiveness in
 478 the great bustard *Otis tarda*: the role of body condition. *J Ethol* 21: 51-56.
 479
 480 Olea PP, (2009) Analysing spatial and temporal variation in colony size: an approach using
 481 autoregressive mixed models and information theory. *Pop Ecol* 51: 161–174.
 482
 483 Palacín C, Alonso JC, Martín CA, Alonso JA, Magaña M, Martín B (2004) Avutarda Común (*Otis tarda*).
 484 In: Madroño A, González C, Atienza JC (eds). Libro rojo de las aves de España, p. 209-213.
 485 SEO/BirdLife and Dirección General de Conservación de la Naturaleza, Ministerio de Medio Ambiente.
 486 Madrid.
 487
 488 Penteriani, V., Delgado, M. M., Alonso-Álvarez, C. and Sergio, F (2007) The importance of visual cues
 489 for nocturnal species: eagle owls signal by badge brightness. *Behav. Ecol.* 18, 143-147.
 490
 491 R Development Core Team, (2008) *R: A Language and Environment for Statistical Computing*. R
 492 Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org>>.
 493
 493 Redondo T (1994) Comunicación: teoría y evolución de las señales. In: *Etología*, Carranza J, editor.
 494 Cáceres, Spain: Universidad de Extremadura. p. 255-298.

495 Ruxton GD & Colegrave N (2003) Experimental design for the life sciences, New York: Oxford
 496 University Press Inc.

497 Théry, M. and Vehrencamp, S L (1995) Light patterns as cues for mate choice in the lekking white-
 498 throated manakin (*Corapipo gutturalis*). *Auk* 112, 133-145.
 499

500 Uy JAC, Endler JA (2004) Modification of the visual background increases the conspicuousness of
 501 golden-collared manakin displays. *Behav Ecol* 15: 1003-1010.

502 Zahavi A (1977) Cost of honesty - (further remarks on handicap principle). *J Theor Biol* 67:603-605.

503 Zar, JH (2010) *Biostatistical analysis. Fifth Edition*. New Jersey, USA. Prentice Hall, Inc
 504

Table1.- Minimal adequate models for whether or not male bustard displays were orientated towards the sun, considering an angle of 45° or 135° (see methods for details, N=405). Lek was included as a random effect. SUN: sun visible or not; SKYCOVER: percentage of sky covered by clouds.

	Parameter	<i>SE</i>	<i>z-value</i>	<i>P</i>
“Tail to sun ” 45° model	estimate			
Intercept	-1.669	0.470	-3.550	0.0004
LATE MORNING	-0.477	0.318	-1.502	0.133
EARLY EVENING	-1.566	0.385	-4.072	0.00004
LATE EVENING	-1.039	0.393	-2.645	0.008
SUN	0.591	0.282	2.091	0.037
“Tail to sun ” 135° model				
Intercept	0.567	0.210	2.696	0.007
LATE MORNING	-0.611	0.269	-2.274	0.023
EARLY EVENING	-0.596	0.371	-1.605	0.108
LATE EVENING	-0.541	0.408	-1.327	0.184
SKYCOVER	-0.008	0.005	-1.712	0.087

Table 2.- Minimal adequate model explaining displaying male's tail directed towards the nearest female/s or not, considering an angle of 45° (N=312) . Lek was included as a random effect. No.MALES: number of males at the lek; DISPLAY: Phase of displaying males.

	Parameter estimate	<i>SE</i>	<i>z-value</i>	<i>P</i>
Intercept	-3.313	1.055	-3.140	0.0017
LATE MORNING	1.073	0.461	2.329	0.020
EARLY EVENING	0.496	0.445	1.116	0.264
LATE EVENING	0.856	0.460	1.863	0.063
No.MALES	-0.026	0.011	-2.344	0.019
DISPLAY	0.696	0.351	1.982	0.048

Figure 1. Procedure followed to take measures of sun position (compass direction from north, azimuth) and of the lek centroid from observer position. A circle with 8, 45° sectors was used to assign the direction of the beak-tail of the bustard males relative to the observer position. I was always the sector furthest away from the observer. Beak-tail orientations in relation to the observer were then assigned to one of the eight sectors. The coloured bustard represented at the lek has the beak-tail orientated towards sectors 8-4 and thus its tail orientated towards the sun position.

Figure 2. Orientation of displaying males (percentage of observations) through day (from early morning to late evening) relative to the sun (2a-2d). Mean angle of orientation (black solid line from centre to edge of the circle) and 95% confidence interval (bars) are shown (computed in ORIANA 3.0 software).

Figure 3. Orientation of displaying males (percentage of observations) through day (from early morning to late evening) relative to the female/s position (3a-3d). Mean angle of orientation (black solid line from centre to edge of the circle) and 95% confidence interval (bars) are shown (computed in ORIANA 3.0 software).

Figure 4. Percentage of males with tails orientated towards the sun (black bars), females (white bars) or both (sun and females in the same direction, grey bars) through day time (Note that under random orientation, we would expect 12.5% of male displays (i.e. 100%/ 8 sectors = 12.5%) to be orientated towards the sun or towards the female,

Figure 5. Percentage of males with tails orientated towards the sun (black bars) and towards females (white bars) for different phases of display.

547 **Figure 6.** Display of great bustard male (phase 1) orientating the white tail towards the sun
548 direction
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Fig. 2

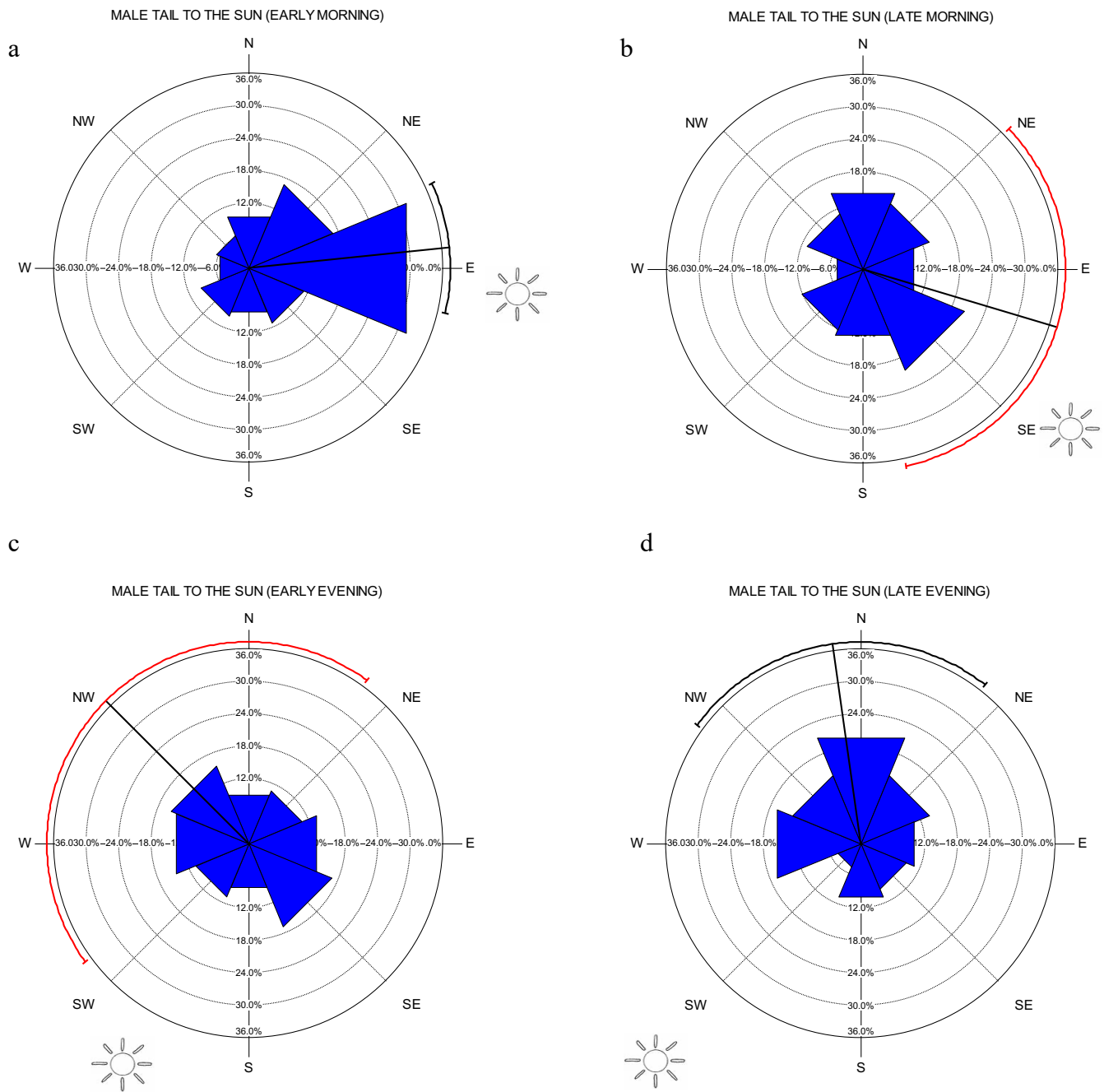


Fig. 3

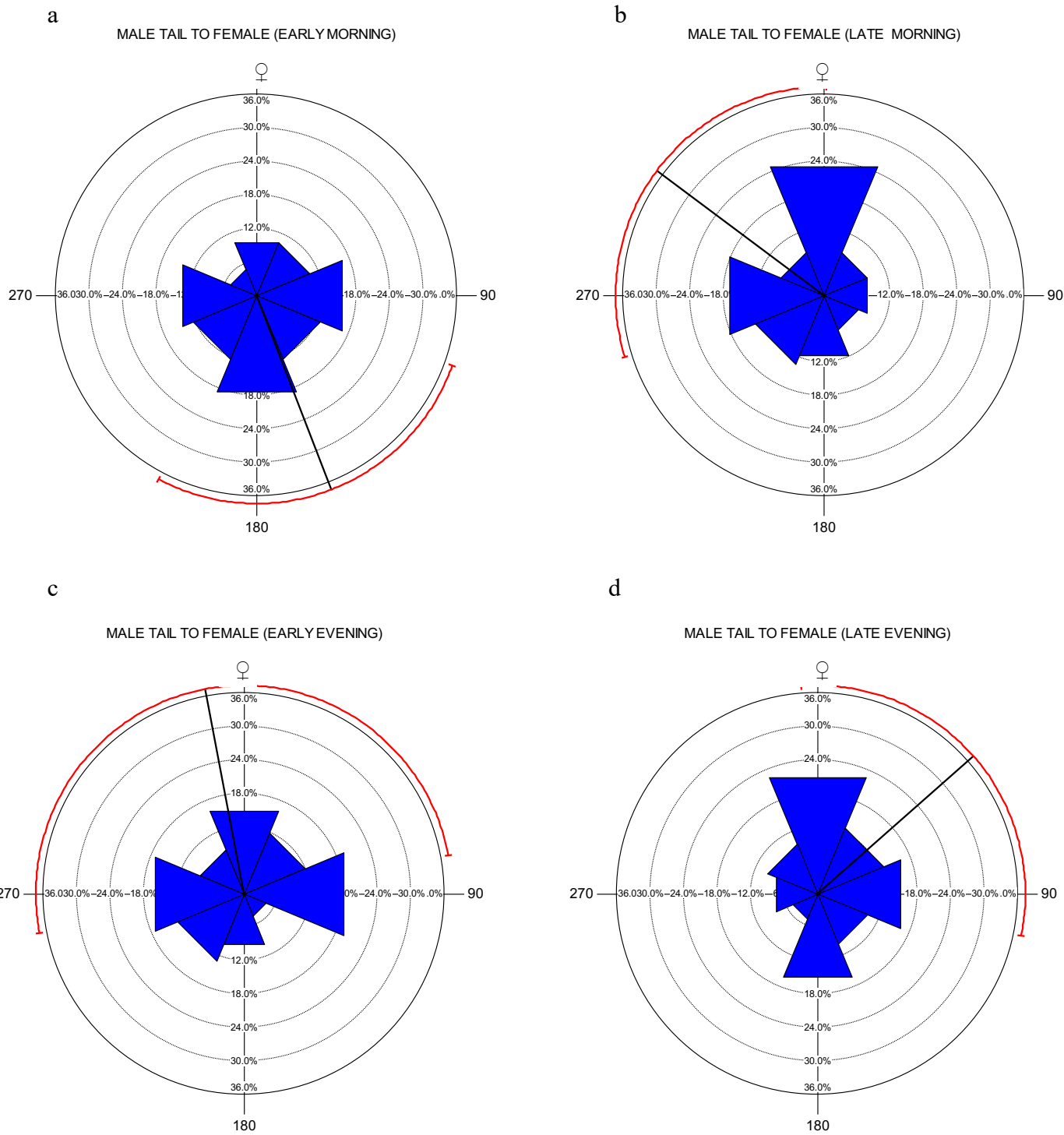
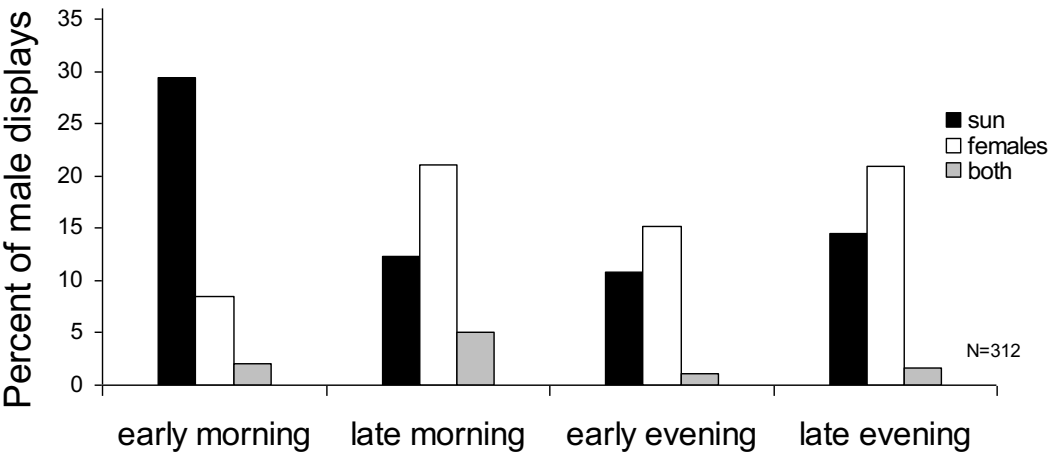
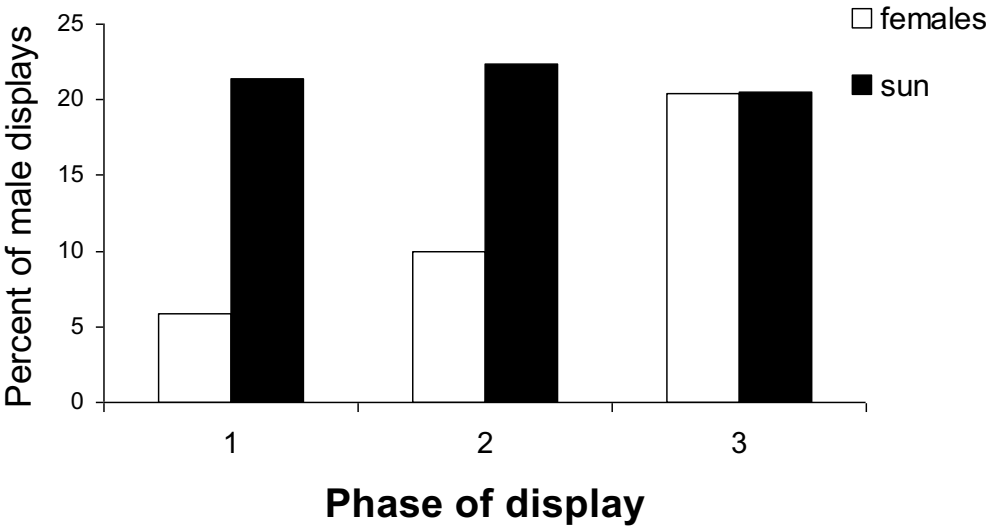


Figure 4



628 Figure 5



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644 Figure 6



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