

Notas Breves

FUNCTIONAL ANALYSIS OF THE BOWING DISPLAY OF COLLARED PRATINCOLES *GLAREOLA PRATINCOLA*

ANÁLISIS FUNCIONAL DE LA EXHIBICIÓN SOCIOSEXUAL DE LA CANASTERA COMÚN *GLAREOLA PRATINCOLA*

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In some birds, sexual displays are performed by both pair members once the pair formation period has concluded. To try to explain this behaviour several hypotheses have been developed. According to the sexual selection hypothesis, individuals continuously evaluate the quality of their mates, deciding whether to stay with the mate or to desert and the degree of parental investment to give (De Lope and Møller, 1993; Moreno *et al.*, 1994; Torres and Velando, 2003).

In addition, there are other hypotheses that have tried to explain the evolution of displays performed after pair formation. One of these hypotheses was formulated by classical ethologists, and refers to sociosexual displays as a behaviour carried out in order to strengthen the pair bonds, though its evolutionary logic is unclear (Wachtmeister, 2001 and cited references) and is not supported by empirical data (Hall, 2004 and cited references). Other hypotheses suggest that the function of this type of displays is the recognition of conspecifics to avoid hybridization (Johnson, 2000 and cited references), or the delimitation of a territory. However, the former cannot explain why the displays continue after egg laying, while the latter cannot explain why the displays seem direct-

ed only at the partner (see Wachtmeister, 2001 for a review).

The manipulation theory (Dawkins and Krebs, 1978; Krebs and Dawkins, 1984; Enquist and Arak, 1998) has been recently applied to sociosexual displays in monogamous species. Instead of transmitting information, signals may at least partly have evolved to persuade or manipulate other individuals' decision making (Wachtmeister and Enquist, 2000; Wachtmeister, 2001). In monogamous species conflicts exist after the partner has been chosen, and then an individual may use displays deceptively to elicit more investment from its partner so that it can reduce its own level of investment (Wachtmeister, 2001). Manipulation is possible by exaggerating certain aspects of the soliciting signal or stimulus, since there are response biases in the receiver's neural machinery (e.g., Enquist and Arak, 1998). Unfortunately, the manipulation theory has only been applied to pair displays from a theoretical point of view (Wachtmeister and Enquist, 2000).

One type of sociosexual display is the so called greeting ceremony, examples of displays not associated with pair formation that occur when both pair members meet after a

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period of separation (e.g., Torres and Velando, 2003). The collared pratincole *Glareola pratincola* is a monogamous wader species that performs greeting ceremonies at the breeding colonies. These ceremonies are known as “*bowing displays*”: the male approaches the female, each one placed in front of the other, and both bow their bodies, the heads almost touching the ground and the tails in a vertical position (Cramp and Simmons, 1983). However, the descriptive information given by these authors on this display is very scarce, something that can be applied to the rest of wader species (van de Kam *et al.*, 2004). Following this lack of information, in the present study a detailed description of the bowing display of collared pratincoles is made, with an emphasis in the form, variability and contexts in which this behaviour takes place in order to obtain some information that could help understanding its function.

The study was carried out in 2000 - 2001 at a colony (15 - 18 breeding pairs) of the collared pratincole located on a stubble field in Vilafranco del Gadiana (province of Badajoz, SW Spain, 38° 53' N, 06° 51' W) during the breeding period (April - July). Visits to the colony began in the second half of April, when the pratincoles arrive at the colonies (Dolz *et al.*, 1989; *pers. obs.*). A total of 32 observation days were equally distributed among the four months considered ($G_3 = 3.7$, $P > 0.25$). The earliest observation date was 19 April, coinciding with the beginning of the breeding activity of the species (Dolz *et al.*, 1989). The last observation date was 10 July. The first incubating birds were seen on 24 April, and the last on 19 May. The observations were made from elevated points on the edge of the colony. Data recording took place during the five hours prior to sunset. Each day of observation it was recorded whether there were incubating birds at the colony or not. The sex was identified by the breeding plumage characteristics of the birds (Cramp and Simmons, 1983; Hayman, 1986; Prater *et al.*, 1997).

Continuous samplings were carried out on bowing displays and copulations (Martin and Bateson, 1986). In the bowing displays, the duration (by using a chronometer), type, distance between pair members and the number of bows made by males and females were recorded. Two types of display were considered: together or separated. In the first case, both pair members stayed close to each other, with the bills almost touching. In separated displays, the birds kept away from each other. These two types of display were differentiated during data recording in order to search for possible differences in the characteristics considered here.

During the displays, the body is maintained parallel to the ground before carrying out the bows, and both pair members approximate to each other. However, bows do not always take place after the approximation (see below). It was considered that the beginning of a bowing display (with or without bows) took place at the moment in which the birds adopted the horizontal posture. Sometimes it was seen that solitary pratincoles made only a single long bow when they arrived to the colony. In the analyses, only displays beginning with two pratincoles approaching with the horizontal posture described above were included.

The degree of exaggeration and frequency of the movements shows the motivation of the senders in many sociosexual displays (Wachtmeister, 2001) and is related to the probability of copulation (Torres and Velando, 2003). Furthermore, females are typically believed to have preferences for persistent males (Forstmeier, 2004 and cited references). Therefore, in the case of collared pratincoles the number of bows during the display may be considered as a measure of the intensity of displays.

The birds were not individualized with marks, but each day of observation all the pairs of the colony could be observed, and thus it was considered that the effects of pseudoreplication were not significant for the interpretation of results.

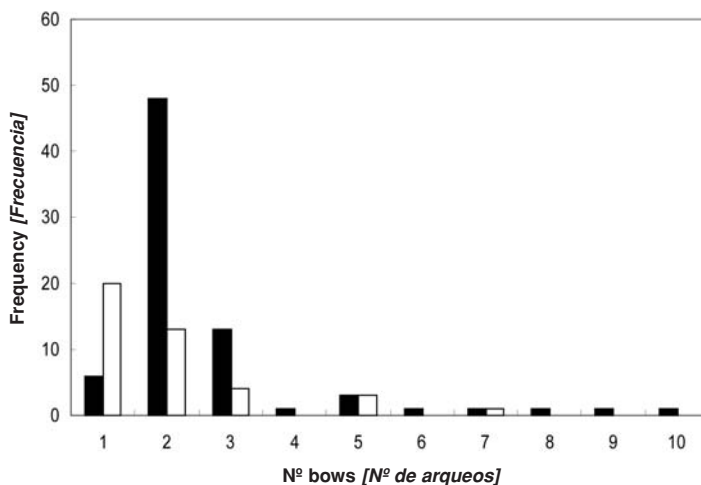


FIG. 1.—Frequency distribution of the number of bows made by male (black bars) and female (white bars) collared pratincoles during displays.

[Distribución de frecuencias del número de arqueos realizados por el macho (barras negras) y la hembra (barras blancas) de canastera común durante las exhibiciones.]

Distances between birds were recorded in order to search for possible effects of this variable on the display performance, and were estimated using landmarks as reference points.

In the analyses of frequencies G -tests were used. Correlations with Spearman's rank tests were made. When data were normally distributed and the condition of homoscedasticity was fulfilled (using Kolmogorov-Smirnov and Levene's tests), t -tests were carried out to compare means. When this was not possible, Mann-Whitney's U -tests were used instead to compare medians. All the tests are two-tailed. Means are expressed with the corresponding standard errors (Zar, 1999).

Bowing displays were observed during April, May and June, with a lower frequency in June ($G_2 = 42.80$, $P < 0.001$). A total of 80 displays were observed. The duration could be determined in 58 (72.5 %) of them, with a mean value of 27.6 ± 3.6 s (range 2 - 140 s).

When the bowing displays were performed with both sexes separated, the distance between them was determined in 30 cases, with a mean value of 3.5 ± 0.7 m. Displays were only

performed by one male and one female, except in two cases in which two males were seen displaying toward a single female. The duration of one of these displays was long (60 s), and the other one was the longest of all the observed displays (140 s).

No significant differences were found in the frequency of displays performed with both sexes together and separated ($G_1 = 0.80$, $P > 0.25$), nor in their duration (together: 24.3 ± 3.3 s; separated: 31.0 ± 6.7 s; $Z = -0.53$, $P = 0.60$).

The number of bows made during the displays could be determined in 76 (95 %) cases for males and 41 (51 %) cases for females. Males made more bows than females (males: 1.7 ± 0.2 bows; females: 1.3 ± 0.3 bows; $Z = -3.64$, $P < 0.001$). The frequency distribution of bows was unimodal for both sexes, but the males only made one bow in the majority of the cases ($G_0 = 154.40$, $P < 0.001$; Fig. 1), while the mode was located at 0 in the females ($G_4 = 30.91$, $P < 0.001$; Fig. 1). The level of display performance, determined by means of the number of bows, did not differ between both sexes (Levene's test = 0.52, $P = 0.471$). Except

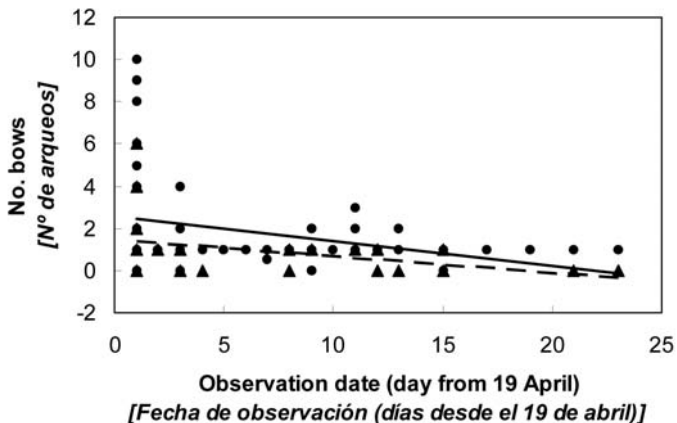


FIG. 2.—Relationship between the number of bows made during the displays and the elapsed time since the beginning of the breeding period (which coincides with the beginning of the observation period) in male (circles) and female (triangles) collared pratincoles. Regression lines are showed.

[Relación entre el número de arqueos realizados durante las exhibiciones y el tiempo transcurrido desde el inicio del período reproductor (coincidente con el inicio del período de observación) en machos (círculos) y hembras (triángulos) de canastera común. Se muestran las rectas de regresión.]

in two cases in which no bows were observed, the displays always contained bows. The males always made the first bow.

The number of bows per display decreased from the beginning of the breeding period (males: $r_s = -0.42$, $n = 76$, $P < 0.001$; females: $r_s = -0.42$, $n = 41$, $P = 0.006$; Fig. 2). The same was found in the duration of displays ($r_s = -0.38$, $n = 58$, $P = 0.003$).

The number of bows did not differ between displays performed with both sexes together and separated, in males (separated: 1.8 ± 0.3 bows; together: 1.5 ± 0.3 bows; $Z = -0.31$, $P = 0.758$) and females (separated: 1.5 ± 0.5 bows; together: 0.7 ± 0.2 bows; $Z = -1.27$, $P = 0.202$).

Bivariate correlations between the features of the bowing displays analysed here (number of bows made by males and females, duration of display and male-female distance) did not show significant results (all $P > 0.05$), except between the number of bows made by males and the display duration ($r_s = 0.41$, $n = 57$, $P = 0.002$).

It has been reported that pair formation in collared pratincoles begins in the wintering

quarters (Cramp and Simmons, 1983 and cited references). The bowing displays were observed here during April, May and June, and they were probably performed after the pair formation. No clutches are found at the colonies in June (Dolz *et al.*, 1989; *pers. obs.*). Thus it is difficult to associate the displays with the formation of new pairs. The last day in which the presence of incubating birds at the colony could be confirmed was 19 May, indicating that the bowing displays continue so late in the season that it is probably impossible to successfully rear a new clutch of eggs with a new partner. Although these results must be taken with caution because no birds were marked, the fact that greeting ceremonies occur after pair formation in many species (Wachtmeister, 2001) lends support to this idea. Both male and female were active during the displays, and the copulations were observed during the same period. The fact that the observation frequency of bowing displays was lower in June and no displays were observed in July suggests that this behaviour takes place during the first phases of the reproductive cycle.

Behavioural characteristics reflecting individual quality are unimodal but not highly variable (Dale *et al.*, 2001). In this case, the number of bows (the main behavioural category used here to describe bowing displays) was unimodal, but relatively variable in both males and females. In particular, the number of bows was highly variable in the case of males (10 different values), which seem to be the senders of the signal during the displays (see below). Bowing displays were more frequently observed at the beginning of the breeding period, and the intensity of the displays also decreased with the breeding period.

Studies that have found a territorial role in sexual displays have detected changes in the orientation of the males, which not only direct their displays to females but also to other males (e.g., Davis, 1997). Here, the pratincoles only made vertical movements (i.e., bows), and never oriented the displays to other birds except for the partner (i.e., the bird with which the display was being performed at that time). Birds of the same sex were never seen displaying, which is not consistent with the idea of territoriality because, in monogamous birds, the territory defence is mainly assumed by the male (but see Negro and Grande, 2001), which means that the majority of interactions (displays) take place between two males (e.g., Kinkel Southern, 1981; Butler and Janes-Butler, 1982; Moreno *et al.*, 1995; Viñuela *et al.*, 1995). This suggests that bowing displays could thus not be related to territoriality.

At least in birds, the general pattern is that the later in the breeding season that reproduction is started, the lower the breeding success (Klomp, 1970). Therefore, male pratincoles would obtain lower benefits from persuading females to start reproduction late in the season. If higher numbers of bows correspond to higher intensities of display, then the negative correlation found between the number of bows made by the males and the observation date is according with that. In response, the females also made a lower number of bows. According

to these results, the display duration also decreased with the season. On the other hand, the manipulation theory assumes that pair displays have evolved as a consequence of the males' effort to manipulate females to start reproduction before the optimal moment for females, when there are greater possibilities of cuckoldry for males (Wachtmeister and Enquist, 1999, 2000). In accordance with that, the bowing displays of collared pratincoles were observed at the beginning of the breeding period, since the majority of displays were observed in April and May, when there are still clutches in the colonies (Dolz *et al.*, 1989).

A relationship between the duration of displays and the number of bows that the males made during them was found. Furthermore, the first bow was always made by the males. Thus, similar to Levin (1996), the males seemed to be the senders during the displays, while the females acted in response to the activity of the males. However, the correlation between the duration of displays and the number of bows made by the females was only marginally significant ($P = 0.05$). This means that a clear direction of the signal between actors and receivers can not be categorically established in relation to sex, but the stronger correlation between display duration and number of male bows suggests that the behaviour of males was more important for the performance of this activity than that of females. The fact that the number of bows made by males and that made by females were not correlated indicates that the activity of each sex could have differential effects on the duration of displays. Future studies should consider this possibility.

The manipulation theory suggests that for the males have success in their try of exploitation of the neurologic system of the females, the emitted signal (that made by the males; see above) must be variable (Wachtmeister and Enquist, 2000). The number of bows made by male pratincoles showed 10 different values, being the mode much more frequent than the rest. This non-random distribution of the num-

ber of bows suggests that the ritualized sequence of the display is that in which only one bow is made by the male. If higher numbers of bows correspond to higher intensities of displays, this low frequency of high intensity displays would allow the maintaining of the equilibrium and the function of the signal (Redondo, 1994; Johnstone, 1998).

Although the results of the present study can not be used to support or discard any hypothesis dealing with the function of sociosexual displays, it is possible that some of them are in agreement with the manipulation theory, which seems to be the best explanation of this behaviour to date (Wachtmeister, 2001). Thus, further research should be made of the sociosexual displays of collared pratincoles and other species, considering all the possibilities (including that this behaviour has no function) but with especial attention to this theory. As commented before, sometimes solitary pratincoles made only a single long bow when they arrived at the colony. This also suggests that it is important to study the bowing displays of collared pratincoles in contexts different from that considered here.

RESUMEN.—*Algunas especies monógamas realizan exhibiciones sexuales posteriormente a la formación de las parejas en las que participan tanto el macho como la hembra. Algunas de las características de la exhibición sociosexual de la canastera común Glareola pratincola fueron analizadas con especial atención en el número de arqueos realizados para tratar de obtener información acerca de su posible función. Las exhibiciones fueron observadas al comienzo del período reproductor; los machos parecieron ser los emisores de la señal y, aunque realizaron un único arqueo en la mayoría de los casos, se registraron mayores valores con una frecuencia menor. Estos resultados indican que la teoría de la manipulación debería ser considerada para estudiar la función de este comportamiento.*

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BIBLIOGRAPHY

- BUTLER, R. G. and JANES-BUTLER, S. 1982. Territoriality and behavioral correlates of reproductive success of Great Black-backed Gulls. *Auk*, 99: 58-66.
- CRAMP, S. and SIMMONS, K. E. L. (Eds.) 1983. *The Birds of the Western Palearctic. Volume III*. Oxford University Press. Oxford.
- DALE, J., LANK, D. B. and REEVE, H. K. 2001. Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *American Naturalist*, 158: 75-86.
- DAVIS, E. S. 1997. The Down-Up display of the mallard: one display, two orientations. *Animal Behaviour*, 53: 1025-1034.
- DAWKINS, R. and KREBS, J. R. 1978. Animal signals: information or manipulation? In, J. R. Krebs and N. B. Davies (Eds.): *Behavioural Ecology. An Evolutionary Approach*, pp. 282-309. Blackwell Scientific. Oxford.
- DE LOPE, F. and MØLLER, A. P. 1993. Female reproductive effort depends on the degree of ornamentation of their mates. *Evolution*, 47: 1152-1160.
- DOLZ, J. C., DIES, I. and BELLIURE, J. 1989. Las colonias de canastera (*Glareola pratincola*, Linn 1766) en la Comunidad Valenciana. *Medi Natural*, 1: 69-80.
- ENQUIST, M. and ARAK, A. 1998. Neural representation and the evolution of signal form. In, R. Dukas (Ed.): *Cognitive Ecology. The Evolutionary Ecology of Information Processing and Decision Making*, pp. 21-87. University of Chicago Press. Chicago.
- FORSTMEIER, W. 2004. Female resistance to male seduction in zebra finches. *Animal Behaviour*, 68: 1005-1015.
- HALL, M. L. 2004. A review of hypotheses for the functions of avian duetting. *Behavioral Ecology and Sociobiology*, 55: 415-430.
- HAYMAN, P. 1986. *Shorebirds*. Helm. London.
- JOHNSON, K. P. 2000. The evolution of courtship display repertoire size in the dabbling ducks

- (Anatini). *Journal of Evolutionary Biology*, 13: 634-644.
- JOHNSTONE, R. A. 1998. Game theory and communication. In, L. A. Dugatkin and H. K. Reeve (Eds.): *Game theory and animal behaviour*, pp. 94-117. Oxford University Press. Oxford.
- KINKEL SOUTHERN, L. 1981. Sex-related differences in territorial aggression by Ring-billed Gulls. *Auk*, 98: 179-181.
- KLOMP, H. 1970. The determination of clutch size in birds. A review. *Ardea*, 58: 1-124.
- KREBS, J. R. and DAWKINS, R. 1984. Animal signals: mind-reading and manipulation. In, J. R. Krebs and N. B. Davies (Eds.): *Behavioural Ecology. An Evolutionary Approach*, pp. 380-402. Sinauer. Sunderland.
- LEVIN, R. N. 1996. Song behaviour and reproductive strategies in a duetting wren, *Thryothorus nigricapillus*. II. Playback experiments. *Animal Behaviour*, 52: 1107-1117.
- MARTIN, P. and BATESON, P. 1986. *Measuring Behaviour*. Cambridge University Press. Cambridge.
- MORENO, J., SOLER, M., MØLLER, A. P. and LINDEN, M. 1994. The function of stone carrying in the black wheatear, *Oenanthe leucura*. *Animal Behaviour*, 47: 1297-1309.
- MORENO, J., BUSTAMANTE, J. and VIÑUELA, J. 1995. Nest maintenance and stone theft in the chinstrap penguin (*Pygoscelis antarctica*). 1. Sex roles and effects on fitness. *Polar Biology*, 15: 533-540.
- NEGRO, J. J. and GRANDE, J. M. 2001. Territorial signalling: a new hypothesis to explain frequent copulation in raptorial birds. *Animal Behaviour*, 62: 803-809.
- PRATER, A. J. 1997. *Guide to the identification and ageing of Holartic waders*. BTO. Norfolk.
- REDONDO, T. 1994. Comunicación: teoría y evolución de las señales. In, J. Carranza (Ed.): *Etología: introducción a la Ciencia del Comportamiento*, pp. 255-297. Servicio de Publicaciones de la Universidad de Extremadura. Cáceres.
- TORRES, R. and VELANDO, A. 2003. A dynamic trait affects continuous pair assessment in the blue-footed booby, *Sula nebouxii*. *Behavioral Ecology and Sociobiology*, 55: 65-72.
- VAN DE KAM, J., ENS, B., PIERSMA, T. and ZWARTS, L. 2004. *Shorebirds. An illustrated behavioural ecology*. KNNV Publishers. Utrecht.
- VIÑUELA, J., AMAT, J. A. and FERRER, M. 1995. Nest defence of nesting chinstrap penguins (*Pygoscelis antarctica*) against intruders. *Ethology*, 99: 323-331.
- WACHTMEISTER, C.-A. 2001. Display in monogamous pairs: a review of empirical data and evolutionary explanations. *Animal Behaviour*, 61: 861-868.
- WACHTMEISTER, C.-A. and ENQUIST, M. 1999. The evolution of female coyness: trading time for information. *Ethology*, 105: 983-992.
- WACHTMEISTER, C.-A. and ENQUIST, M. 2000. The evolution of courtship rituals in monogamous species. *Behavioral Ecology*, 11: 405-410.
- ZAR, J. H. 1999. *Biostatistical analysis. Fourth edition*. Prentice Hall. New Jersey.

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