Ethology **84**, 232—238 (1990)

ISSN 0179-1613

*Laboratoire d'Ethologie, Université de Rennes, Rennes and Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire*

# Do Females Turn Males on and off in Barnacle Goose Social Display?

MARTINE HAUSBERGER & JEFFREY M. BLACK

HAUSBERGER, M. & BLACK, J. M. 1990: Do females turn males on and off in barnacle goose social display? Ethology **84**, 232—238.

## Abstract

Male barnacle goose *Branta leucopsis* display duration is longest when females respond with loud repetitious calls, intermediate when females follow silently and shortest when females call softly. We argue that these encouraging and discouraging vocalizations and the associated posturing is an influential behaviour used during the mate choice, pair maintenance and aggressive interaction processes.

Corresponding author: J. M. BLACK, Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire, GL2 7BT, U.K.

## Introduction

During the mate choice process in most animals it is assumed that discriminating individuals somehow show their attraction to the courting individual such that courtship is continued or curtailed. In other words, the chooser either encourages or discourages the displayer, perhaps by answering with vocalizations, performing displays or by simply presenting themselves or following (see examples in HALLIDAY 1978, 1983). Presumably both sexes make decisions on whether to persist in their relationship based on each others' performance in their social interactions.

In this paper we provide some information on the persistence time of male barnacle geese *Branta leucopsis* in social displays according to the females' participation. During the pairing process in geese mutual cooperation in social display, called triumph ceremonies, increases over a period of time, from days to months, in one or several trial liaisons with potential partners (BLACK & OWEN 1988; OWEN et al. 1988). We test the hypothesis that the males' persistence in social display is influenced by the females' responses. Once formed, a partnership can last for many years, yet each spring a peak in social display occurs. These

displays are thought to enhance the partners' relationship in such a way that enables them to compete with neighbours for essential resources prior to migration and breeding (FISCHER 1965; MCLANDRESS & RAVELING 1981; BLACK & OWEN 1988). The "supportive responses" of females in these displays are also thought to direct a male's behaviour in conflict situations (see RADESÄTER 1975; AKESSON & RAVELING 1982).

## Material and Methods

Opportunistic observations were made on individual pairs in the semi-captive free-flying barnacle goose flock at the Wildfowl and Wetlands Trust, Slimbridge. The flock consists of about 250 geese all of which are individually marked and their life histories are recorded [see BLACK & OWEN (1987) for more information on the flock]. Vocalizations and simultaneous commentaries of their behaviour were recorded with a Sony TCD5M cassette recorder and a Sennheiser MD421 microphone. Commentaries included identification of the bird, the mate, interacting neighbours and their behaviour/postures before, during and after each vocalization bout. Vocalizations were played into a Amiga 2000 microcomputer programmed to produce and measure sonogrammes. Calls were classified as soft calls (2 types), single loud calls, and alternating loud calls (duets). Female behaviour was classified according to her response to or involvement in the male's display. The duration of each display bout was measured and recorded according to five criteria for females' behaviour:

1) no response; no change in the female's current behaviour
2) follows the male but no vocal response
3) emits one or more soft calls
4) emits occasional (less than 5) loud calls
5) emits loud calls that alternate with the male's calls.

Additional data were obtained in Norway in May 1989 from wild birds to enable comparison with the semi-captive situation. The wild geese are unusually tame when they visit these highly protected Norwegian staging islands. The birds were therefore close enough (< 30 m) to identify the context and outcome of displays, and to record their calls using a Sennheiser 815T directional microphone.

## Results

A total of 259 triumph ceremonies of various intensities were recorded from 52 pairs in March and April 1989. Based on their life-history records 36 of the displaying partners were new pairs (not together in preceding breeding season) and 16 had been together between 1—8 years. We found no correlation in behaviour and vocalizations with the duration of attachment so the samples were lumped for other comparisons.

*Vocalization types:* In all cases it was the male who initiated the triumph ceremony by emitting loud calls. The loud calls given by males in triumph ceremonies are distinguishable from loud calls in other contexts by their repetitiveness (3 to 7 calls/s), with irregular intervals between successive calls (Fig. 1 a). Fig. 1 b, c show the occasional and repetitive alternating male/female loud calls. Two types of soft calls, similar in both females and males were identified (Fig. 1 d). Both were produced with the bill closed and could only be heard at a short distance.

*Display duration:* The females' influence on male behaviour was tested in three ways 1) comparison of multiple bouts in one pair, 2) comparison of one bout for all pairs and 3) comparison of the means for all pairs (Table 1).

In display bouts from the most frequently observed pair (V4/XI), the female responded with loud calls 3 times, soft calls 5 times, followed silently 3 times and did not respond at all 22 times. The duration of the male's display was longer if the female followed (Mann-Whitney U test, $z = 2.14$, $p < 0.016$) or produced loud calls (occasional and alternating loud calls lumped, $z = 2.84$, $p < 0.0023$) compared to no response. The longest duration was observed when she produced loud calls; significantly longer than following ($U = 0$, $p < 0.05$) and soft calls

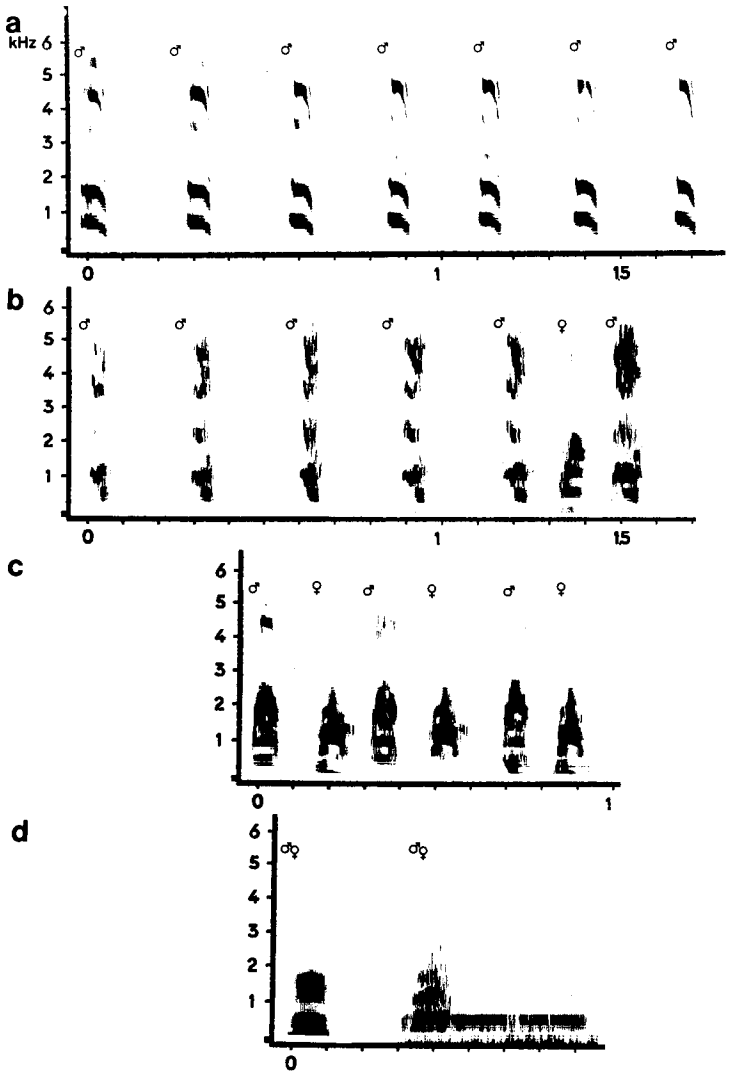


*Fig. 1:* Sonogrammes recorded during barnacle goose social displays: a) male repetitive loud calls, b) male repetitive loud calls with occasional female response call, c) male and female repetitive and alternating loud calls, d) soft calls; types 1 and 2 (male and female soft calls are similar). x-axis: time in s

*Table 1:* Mean duration (± SD) of male display according to female responses using data from three sources 1) the pair with most display sequences, 2) display duration for one randomly chosen sequence from each pair and 3) overall mean of recorded sequences. Sample sizes in parentheses

| Male display data | Type of female response | | | | |
|---|---|---|---|---|---|
| | none | follows | soft | loud | alt. loud |
| 1) V4—XI | 6.0 ± 5.1 | 9.7 ± 2.5 | 5.4 ± 3.0 | 29.0 ± 6.0 | 38.0 ± 0.0 |
| | (22) | (3) | (5) | (2) | (1) |
| 2) Mean (1/pair) | 8.2 ± 7.1 | 10.7 ± 7.4 | 4.2 ± 1.4 | 22.9 ± 10.7 | 18.1 ± 10.0 |
| | (39) | (15) | (13) | (10) | (28) |
| 3) Overall mean | 7.3 ± 5.8 | 10.0 ± 6.8 | 5.9 ± 4.1 | 18.0 ± 12.8 | 17.9 ± 9.1 |
| % of all | 57.6 | 8.2 | 7.8 | 7.8 | 18.6 |
| observations | (155) | (22) | (21) | (21) | (40) |

($U = 0$, $p < 0.018$). No significant differences were found between soft calls and no response but the trend was in the direction of shorter durations with soft calls ($U = 2$, $p < 0.07$).

When considering the different pairs Wilcoxon matched pair tests were used, taking the first clear sound recording of each category per pair. The duration of male display was longer when the female produced loud calls compared to no response ($n = 22$, $T = 9$, $p < 0.005$), soft calls ($n = 10$, $T = 0$, $p < 0.005$) or following ($n = 10$, $T = 9$, $p < 0.025$). Display duration was also longer when the female followed compared to no response ($n = 13$, $T = 15$, $p < 0.025$) or soft calls ($n = 7$, $T = 2$, $p < 0.02$) but shorter after soft calls compared to no response ($n = 11$, $T = 7$, $p < 0.01$). Soft calls seem to have an inhibiting effect; in 21 observations the male stopped displaying 18 times within 5 s following the production of soft calls by the female; males never stopped displaying within 5 s when females gave other responses ($n = 93$). No difference was found according to whether the female produced occasional or alternating loud calls.

Table 1 also lists overall means of 259 display bouts. Although statistical tests are invalid due to the skew in sample size the means indicate the same trends as discussed above. In addition, the durations of male displays in wild geese were in the order expected from the previous analysis; loud call bouts were significantly longer than in no response situations (Mann-Whitney $U = 0$, $n1 = 2$, $n2 = 7$, $p = 0.028$, one-tailed test).

*Triumph ceremonies and other behaviour:* 141 (54 %) of the observed triumph ceremonies took part without interaction between neighbours. The other displays occurred after ($n = 69$), during ($n = 45$) or before ($n = 4$) conflict situations. Usually only the male (96 %, $n = 118$) performed the aggressive act, while the female gave either no vocalization (74 %), emitted soft calls (4 %) or loud calls (15 %). Females gave a similar number of vocalizations during aggressive and non-aggressive situations. This was tested in two pairs (V4/XI, binomial test $p = 0.22$; PD/4K, $p = 0.29$).

In the instances when a female produced soft calls the male immediately stopped (within a few s) calling and behaving aggressively. In all five cases when

neighbouring pairs encountered each other the pair that gave alternating loud calls beat the pair in which both partners were silent.

## Discussion

We have shown that the duration of male barnacle goose social display corresponds with the female's reaction. Displays are longest when the female produces loud calls. After soft calls males stop displaying and performing agonistic behaviours almost immediately. Loud calls are accompanied by a characteristic erect posture, neck waving and wing flicking, whereas soft calls are usually produced when the female resumes or continues to feed, a head-down posture. The influence of female action on male behaviour has also been noted in mallards *Anas platyrhynchos* (WEIDMANN & DARLEY 1971). Similarly, kittiwake *Rissa tridactyla* (DANIELS et al. 1984) and whooper swan *Cygnus cygnus* (BLACK 1988) partners respond to each others' pre-flight intention signals (or lack of them) thus synchronizing or inhibiting departure.

Barnacle goose pairs are capable of performing a synchronized duet during the triumph ceremony (Fig. 1c) which is not unlike many if not all goose and swan species (pers. obs.; JOHNSGARD 1965). The postulated functions for the triumph ceremony include enforcing or redirecting male aggressive behaviour, enhancing partnerships and aiding in food acquisition (see Introduction). Soft calls have been labeled "contact calls", inferring that they function in maintaining proximity between partners (COLLIAS & JAHN 1959).

We suggest that these goose vocalizations and displays signal different meanings depending on who is perceiving the call; e.g. signalling social status to opponents and signalling continued association to partners.

1) *Signalling social status to opponents:* During conflict, mutual calling (with associated postures) may signal social status to opponents which then decide about their chances in an encounter. In geese, which are highly gregarious, social rank is ordered according to the number of members in social units; large families, small families, pairs and singles (BOYD 1953; RAVELING 1970). Most encounters in goose flocks involve nearest neighbours and consist of threats by dominant birds and quick retreats by subordinates, the whole episode lasting only a few s. Encounters are won with minimal efforts such that threat intensity is less when encountering smaller units compared to larger or equal sized units. This implies that relative fighting potential is being assessed by opponents (BLACK & OWEN 1989). If geese are assessing opponents by a kind of call quality then we would expect the largest groups to be the most frequent or coordinated callers or perhaps the "noisiest" before and/or during an encounter. This assumes that neighbours monitor other units' vocal interactions; triumph ceremonies are infrequent (about 2/min in a flock of 1000, BLACK & OWEN 1988) yet perhaps conspicuous enough to be assessed by other flock members. Especially when equally matched units get involved in grappling wing-beating battles vocalizations may play a role. During fights family members gather around, emit loud repetitious calls and toss their heads towards the opponents. In this study we provide a little evidence for this idea by showing that in the five cases of pair-pair

diads the pair that gave loud alternating calls won the encounter and the losers were silent. However, other factors such as age were not accounted for. In at least two other animals the call type has been linked with fighting ability: pitch of croaking in toads (DAVIES & HALLIDAY 1978) and roaring tempo in deer (CLUTTON-BROCK & ALBON 1979).

Similarly soft calls may facilitate segregation between immediate neighbours. These calls are the most frequently emitted vocalization by pairs during foraging flock situations (unpubl. data). If soft calls actually do subdue aggressive behaviour, as our data indicates, then perhaps they also inhibit aggression in nearest neighbours. Manipulating nearest neighbour behaviour in this way may keep feeding bout interruptions to a minimum, thus enhancing feeding performance in those that give the calls.

2) *Signalling continued association to a partner:* OWEN et al. (1988) provided evidence that pairs that remain together year after year produce significantly more offspring than those that change mates; each change of mate reduced the potential lifetime production by 15 %. Triumph ceremony duets may express both partners' reliability in their relationship. For example, by alternating her calls with the male's a female may indicate her willingness to continue her affiliation with that male. This willingness is what LAMPRECHT (1984) called pair-bond strength. Differences in the "quality" of her calls (intensity or synchronization) may reflect differences in her bond strength. This can occur in neutral situations, before, during and after conflict situations and indeed during the pairing process. The "louder" she gives calls the more reliable she is as a resource for the male and the more he is willing to stay with and/or fight for her. In this case both members are choosing to continue in the partnership based on the other's performance. In this sense the "pair-bond" is a dynamic two-sided and continuous process.

The female may also answer with soft calls, thus stopping the male's advances. A soft call may also signal the female's willingness to continue her association. Only this time she does so without interrupting her feeding bout. Females in established pairs presumably answer their partners' advances with soft calls more frequently than females in new pairs because of their accumulated experience of the males' reliability as a resource. Whether or not females tend to use soft calls or a no response behaviour to inhibit advancing males during the pairing process has yet to be investigated.

Adequate evidence for this theory is yet to surface but FISCHER (1965) working on greylag geese *Anser anser* described how females from pairs with the most frequent triumph ceremonies tend to follow their partners more. LAMPRECHT et al. (1985) suggested that when parents answer each other's calls, when their goslings are lost, it frees the partner from mate-monitoring so the search can continue, signalling cooperation to a partner. Perhaps pairs that coordinate their behaviours with vocalizations during feeding bouts and aggressive encounters are able to acquire more and better food to enable success in breeding. TEUNISSEN et al. (1985) showed that female brent geese *Branta bernicla* feeding performance was positively correlated with their partners' aggressiveness and DITTAMI (1981) found a correlation between triumph ceremony frequency and reproductive success in individual semi-captive bar-headed geese *Anser indicus*.

## Acknowledgements

We thank S. CHOUDHURY, M. OWEN, E. C. REES for commenting on an earlier version of the paper and are particularly grateful to J. LAMPRECHT for his insight which substantially improved the manuscript. The British Council provided a travel grant for this project.

## Literature Cited

AKESSON, T. R. & RAVELING, D. G. 1982: Behaviors associated with seasonal reproduction and long-term monogamy in Canada geese. Condor **84,** 188—189.

BOYD, H. 1953: On encounters in wild white-fronted geese in winter flocks. Behaviour **5,** 85—129.

BLACK, J. M. 1988: Preflight signalling in swans; a mechanism for group cohesion and flock formation. Ethology **79,** 143—157.

— — & OWEN, M. 1987: Determinants of social rank in goose flocks: acquisition of social rank in young geese. Behaviour **102,** 129—146.

— — & — — 1988: Variation in the pairbond and agonistic behaviours in barnacle geese on the wintering grounds. In: Waterfowl in Winter. (WELLER, M., ed.) Univ. of Minnesota Press, Minneapolis, pp. 39—57.

— — & — — 1989: Agonistic behaviour in goose flocks; assessment, investment and reproductive success. Anim. Behav. **37,** 199—209.

COLLIAS, N. E. & JAHN, L. R. 1959: Social behavior and breeding success in Canada geese *Branta canadensis* confined under semi-natural conditions. Auk **76,** 478—509.

CLUTTON-BROCK, T. H. & ALBON, S. D. 1979: The roaring of red deer and the evolution of honest advertisement. Behaviour **69,** 145—170.

DANIELS, D., HEATH, J. & RAWSON, W. 1984: A declaration of intent in the kittiwake gull. Anim. Behav. **32,** 1151—1156.

DAVIES, N. B. & HALLIDAY, T. R. 1978: Deep croaks and fighting assessment in toads *Bufo bufo.* Nature **274,** 683—685.

DITTAMI, J. PH. 1981: Seasonal changes in the behaviour and plasma titres of various hormones in bar-headed geese, *Anser indicus.* Z. Tierpsychol. **55,** 289—324.

FISCHER, H. 1965: Das Triumphgeschrei der Graugans (*Anser anser*). Z. Tierpsychol. **22,** 247—304.

HALLIDAY, T. R. 1978: Sexual selection and mate choice. In: Behavioural Ecology: An Evolutionary Approach. (KREBS, J. R. & DAVIES, N. B., eds.) Blackwell Sci. Publ., Oxford, pp. 180—213.

— — 1983: The study of mate choice. In: Mate Choice. (BATESON, P., ed.) Cambridge Univ. Press, Cambridge, pp. 3—32.

JOHNSGARD, P. 1965: Handbook of Waterfowl Behaviour. Cornell Univ. Press, Ithaca.

LAMPRECHT, J. 1984: Measuring the strength of social bonds: experiments with hand-reared goslings (*Anser indicus*). Behaviour **91,** 115—127.

— —, KAISER, A., PETERS, A. & KIRCHGESSNER, C. 1985: Distance call duets in bar-headed geese (*Anser indicus*): co-operation through visual relief of the partner? Z. Tierpsychol. **70,** 211—218.

MCLANDRESS, M. R. & RAVELING, D. G. 1981: Hyperphagia and social behavior of Canada geese prior to spring migration. Wilson Bull. **93,** 310—324.

OWEN, M., BLACK, J. M. & LIBER, H. 1988: The duration of the pair bond and the timing of its formation in barnacle geese. In: Wildfowl in Winter. (WELLER, M., ed.) Univ. of Minnesota Press, Minneapolis, pp. 23—38.

RADESÄTER, T. 1975: Interactions between male and female during the triumph ceremony in the Canada goose (*Branta canadensis* L.). Z. Tierpsychol. **39,** 189—205.

RAVELING, D. G. 1970: Dominance relationships and agonistic behavior of Canada geese in winter. Behaviour **37,** 291—319.

TEUNISSEN, W., SPANNS, B. & DRENT, R. 1985: Breeding success in brent in relation to individual feeding opportunities during spring in the Wadden Sea. Ardea **73,** 109—119.

WEIDMANN, U. & DARLEY, J. 1971: The role of the female in the social display of mallards. Anim. Behav. **19,** 287—298.

*Received: October 27, 1989*

*Accepted: December 20, 1989 (W. Wickler)*