

## REVERSE MOUNTING DURING THE COURTSHIP OF THE EUROPEAN SHAG *PHALACROCORAX ARISTOTELIS*<sup>1</sup>

J. ORTEGA-RUANO<sup>2</sup> AND J. A. GRAVES

Department of Biology and Preclinical Medicine, University of St. Andrews,  
St. Andrews, Fife KY16 9TS, U.K.

**Abstract.** Reverse mounting (females mounting males) has been observed as a common occurrence in several species of Phalacrocoracidae. In a colony of individually marked European Shags (*Phalacrocorax aristotelis*) 25% of 261 focally observed mountings were reverse; 17 females (77%) and 16 males (73%) of 22 pairs were observed in reverse mountings. When courtship was divided into three periods before egg laying, we found significant differences in the frequency of reverse mountings and the frequency of pair and non-pair reverse mountings through the three periods. We conclude that reverse mounting is a normal part of courtship behavior in the shag and that it may have the same causes that have been proposed for reverse mounting in other species.

**Key words:** Shag; Phalacrocorax; reverse mounting; copulation; courtship.

### INTRODUCTION

In Phalacrocoracidae, reverse mountings have been recorded in the Great Cormorant, *Phalacrocorax carbo* (Portielje 1927; Kortlandt 1940, in press), Brandt's Cormorant, *P. penicillatus* (Williams 1942), European Shag, *P. aristotelis* (Snow 1963), and Cape Cormorant, *P. capensis*, (Berry 1976). Since the courtship displays of many of the Phalacrocoracidae are little known, it is probable that reverse mountings are more widespread than this indicates. It is not known whether or not insemination occurs during reverse mountings, nor have specific functions for this behavior been proposed.

Recently Nuechterlein and Storer (1989) have examined reverse mounting in the grebes. The widespread prevalence of reverse mounting in courtship in grebes convinced them that reverse mounting was not an aberrant behavior and that other explanations for this phenomenon would have to be found. Kortlandt (1940, in press, pers. comm.) also regarded reverse mounting as occurring often in the courtship behavior in Cormorants and as not aberrant.

Nuechterlein and Storer proposed five non-exclusive hypotheses for reverse mounting in addition to the proposal that it is an aberrant behavior: it may (a) result in fertilization, (b) result from mistaking a partner's sex, (c) play a role in courtship and pair formation, (d) indicate a re-

versal of dominance in the sexes, or (e) stimulate the ovaries of the female to grow.

They observed that reverse mountings were more common in the early period of courtship than later and that ejaculation never occurred in those reverse mountings where observation conditions were good enough for them to make a judgement. They concluded that reverse mounting is a regular and integral part of the courtship display of grebes (hypothesis c), but this conclusion does not exclude hypotheses d and e as well.

Here we present data on reverse mountings of the shag that support the conclusions of Nuechterlein and Storer. We examined the timing and behavioral context of reverse mountings, considering specifically: (1) When in the courtship period does reverse mounting occur and how frequent is it? (2) What is its relationship with mating strategy and copulation?

### METHODS

Observations were collected in the spring of 1984 from 51 individually color ringed shags forming 22 laying pairs on a subcolony on the Isle of May, Scotland, U.K. Three pairs at a time were focally observed, that is all courtship interactions between them were recorded, from a hide 12 m from the nearest nest for 6 hr a day for a total of 147 hr. An arbitrary division of the courtship period was made into an early period (up to 21 days before the first egg was laid) an intermediate period (from 20 days to 11 before the first egg) and a late period (from 10 days before until the first egg).

<sup>1</sup> Received 11 March 1991. Final acceptance 26 July 1991.

<sup>2</sup> Present address: Fac. Psicología, Universidad Autónoma, 28049 Madrid, Spain.

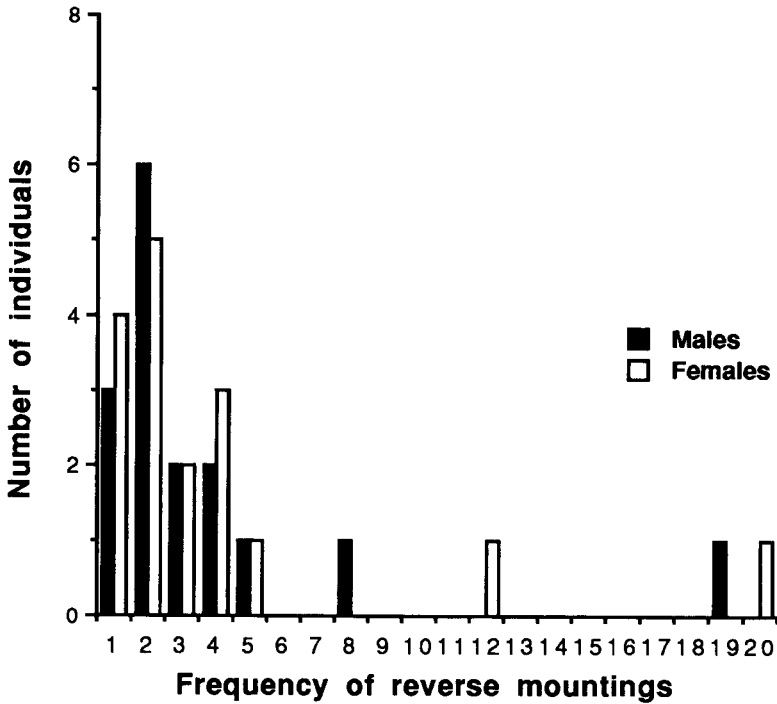


FIGURE 1. Frequency of occurrence of reverse mountings by individuals.

Birds were sexed using size and vocalization criteria. Males are larger (Cramp and Simmons 1977), and females are mute except for a hiss and the soft throat clicks. The male is quite noisy.

Behavioral categories were recorded on a portable computer. A courtship sequence was defined as a sequence of any of the social displays of the shag (Snow 1963). A bout of behavior was considered concluded if either partner left the area or if the pair ceased interacting for more than one minute. We use the following categories described by Snow (1963): *Dart Gape* (males only), *Driven Away* (attack by male on female), *Mounting*, and *Copulation*.

*Mounting (both sexes)*. When one bird is in a sitting position and the other hops onto its back with both feet. This position is necessary for copulation, but copulation may or may not follow. To indicate the sex of the upper bird we refer to mounting by males as reverse mounting. This latter term is not neutral but is common in the literature and we have retained it (see Nuechterlein and Storer 1989, Bowen et al. 1991).

*Copulation*. After mounting, when the upper bird is the male, he grips the back of the female's neck with his beak while uttering the "ark" call, depresses his tail, and makes thrusting tail movements. The female holds her head down with the

beak in the nest material, if there is any, near her breast and holds her tail up and to the side while rhythmically opening and closing the cloacal aperture.

When the female is the upper bird, the male assumes the same position as the female in the above description. She does not grip the back of the male's neck, and is mute, but does depress the tail and make thrusting tail movements.

Cloacal contact could be observed when the birds were facing more or less directly away from the observer. When the male was the upper bird, occasionally the sperm secretion could be seen either in the female cloaca or next to it. It usually was not possible to determine whether or not cloacal contact took place when the female was the upper bird, but it was observed on some occasions. No sperm secretion was observed.

## RESULTS

Of 22 pairs for which we have focal data, 17 females (77%) and 16 males (73%) were observed in reverse mountings at some point in the season. Figure 1 shows the frequency of occurrence of reverse mountings by individuals. A total of 261 mountings was recorded for the three periods where both the identity of the pairs and the laying date of the female were known. Of these 65 (25%)

TABLE 1. The frequency and percentage of reverse and normal mounts in the three periods of courtship prior to egg laying.

	Early	Intermediate	Late
Reverse mounting <i>n</i> (%)	23 (28.3)	30 (34.5)	12 (12.9)
Mounting by males <i>n</i> (%)	58 (71.7)	57 (65.5)	81 (87.1)

were reverse mountings. In addition we recorded six reverse mountings where either the identity of the female or her laying date, if any, was not known.

Reverse mountings were not equally represented in the three periods of courtship (Table 1) ( $\chi^2 = 11.96$ ,  $df = 2$ ,  $P = 0.0025$ ).

Of the 23 reverse mountings that occurred in the early stage of courtship, before the pair bond was established, only six (26%) were in sequences that contained the male advertisement behavior Dart Gape; none of these included Copulation. Table 2 presents the frequency of copulation following reverse mounting and mounting by males. Copulation occurred in the same sequence with reverse mounting 23% of the time. There was no significant difference between the three periods in the frequency of copulation with reverse mounting ( $\chi^2 = 2.14$ ,  $df = 2$ ,  $P > 0.05$ ), but the frequency of copulation following mounting by males did change as the season progressed ( $\chi^2 = 9.68$ ,  $df = 2$ ,  $P < 0.01$ ). Mounting by the male was never seen in the same sequence as either Dart Gape or Driven Away.

Seven females (32%) copulated with more than one male, but only one female, termed the pair female, was ever seen to incubate the eggs in a nest. Eleven (16.9%) of the reverse mountings were by a non-pair female. There was a significant difference in the frequency of pair and non-pair reverse mountings in the three periods ( $\chi^2 = 24.18$ ,  $df = 2$ ,  $P < 0.001$ ). All of the non-pair reverse mountings were by three females and all occurred in the early period.

## DISCUSSION

The frequency of reverse mounting in shags (25%) is similar to that in the Silvery Grebe (*Podiceps occipitalis*) and the Hooded Grebe (*P. gallardoi*),

27% and 15% respectively (Nuechterlein & Storer, 1989). In the Groove-billed Ani (*Crotophaga sulcirostris*) Bowen et al. (1991) found that 55% of the observed mountings were reverse, but most occurred in the pre-breeding period when only reverse mountings were recorded. We agree with Nuechterlein and Storer and with Bowen et al. that reverse mounting is too widespread and frequent to be dismissed as an abnormal or aberrant behavior. Since reverse mountings are widespread and frequent among shags, we also agree that they appear to play a role in courtship and pair formation (hypothesis c).

We can offer no comment on stimulation of the ovaries that Nuechterlein and Storer also suggested as a possible function of reverse mounting in grebes (hypothesis e). They also suggested that a possible hypothesis (b) would be that reverse mountings result from mistaking a partner's sex. Presumably if adopting the postures normally made by the other sex were the result of making a mistake, the mistake would have to be its own sex rather than the partner's. This is a most unlikely hypothesis for two reasons: first it is far too widespread with 73% of males and 77% of females observed in reverse mountings, and second, were it the case, some same sex mountings would be expected and none were observed. Moreover, no evidence of a mistake in any other behaviors was found; all males showed behaviors that are exclusively male and frequently in the same courtship sequence with reversed mounting.

The absence of an operational definition of dominance between the sexes inhibits evaluation of hypothesis d, that reverse mountings indicate a reversal of dominance in the sexes. Certainly, in those reverse mountings that occurred early in the season, the male was the territory holder

TABLE 2. Co-occurrence of mountings with copulation in the three periods. The total occurrence of mountings in each period is given after the /.

	Early	Intermediate	Late	Total
Reverse mounting	3/23	9/30	3/12	15/65
Mounting by males	23/58	36/57	52/81	111/196

and the female approached the territory only hesitantly, although reverse mountings did occur.

Hypothesis a, the relationship of reverse mountings to fertilization is more problematical in shags. It was difficult to see whether cloacal contact was made in any copulation attempt. However, unlike Nuechterlein and Storer, we could not see whether ejaculation occurred in reverse mountings. Failure to observe sperm secretion is not compelling since we seldom saw it even in the mountings by males.

Both Nuechterlein and Storer and Bowen et al. found that reverse mountings were more frequent in the pre-breeding period than during the egg laying period. A similar pattern can be observed in Table 1 with reverse mountings less frequent and mountings by males more frequent in the late period. While there is a significant difference in the frequency of mounting by males followed by copulation in the three periods, there is no significant difference in the frequency of reverse mountings followed by copulation. This suggests that fertilization is unlikely to be a primary role of reverse mounting. Unfortunately, nothing is known about sperm storage or competition in Pelecaniforms, but it can be assumed that any copulations near egg laying would more likely achieve fertilization than earlier ones (Birkhead 1987, Birkhead et al. 1987).

Other clues on the role reverse mountings play in courtship and pair formation come from their behavioral context. In the shag, reverse mounting with copulatory movements by the female evidently requires familiarity with the partner. Dart Gape is one of the advertisement displays of the male shag which holds a territory and is used to attract females new to him (Snow 1963). While reverse mounts as a response to Dart Gape do occur, they are not common. Usually the female sits beside the male rather than on his back. Only six (23%) of the sequences that contained reverse mounting also contained Dart Gape and none of these contained Copulation. Failure to realize that the mounts seen following the Dart Gape were reverse mounts has led to difficulties in the past. Witherby et al. (1940) and Armstrong (1942) systematically misidentified the sexes in the displays of the shag. This confusion is understandable since the female mounts the male, and also the male assumes a female-like copulatory posture as the female comes to him. Portielje (1927) made the same mistake with Great

Cormorants for the same reasons (Kortlandt, pers. comm.).

Males that mated with more than one female usually did so only early in the season and only briefly (Graves et al., in press), so that the requisite familiarity between the partners may not have been reached. This may explain the finding that reverse mountings with a non-pair male only occurred in the early period. Kortlandt (1940) also found that reverse mountings were more frequent in pairs of Great Cormorants that had been together for some time.

Our observations show that reverse mounting is common and shown by most pairs. The finding that most reverse mountings occurred in the birds that remained paired and the differences in reverse mounting and mounting by males as the season progresses suggest that reverse mountings play a role in courtship and pair formation in the shag.

#### ACKNOWLEDGMENTS

We are grateful to Drs. J. R. Alvarez Collado and J. M. Garcia de la Vega for helpful comments on the problem of reverse mounting in birds, to Dr. A. Kortlandt for sending us a manuscript of his unfinished book on cormorants and for comments on this manuscript and to Prof. P.J.B. Slater and two anonymous referees for improving the manuscript. We are grateful to the Nature Conservancy Council for permission to carry out our studies on the Isle of May Nature Reserve. The observations reported here are part of the study of the courtship and reproductive success of the shag supported by Natural Environment Research Council grant GR3/7249.

#### LITERATURE CITED

- ARMSTRONG, E. A. 1942. Bird display: an introduction to the study of bird psychology. Cambridge Univ. Press, Cambridge, England.
- BERRY, H. H. 1976. Physiological and behavioural ecology of the Cape Cormorant *Phalacrocorax capensis*. Madoqua 9:5-55.
- BIRKHEAD, T. R. 1987. Behavioural aspects of sperm competition in birds. Adv. Stud. Behav. 18:35-72.
- BIRKHEAD, T. R., L. ATKIN, AND A. P. MØLLER. 1987. Copulation behaviour of birds. Behaviour 101: 101-133.
- BOWEN, B. S., R. R. KOFORD, AND S. L. VEHCAMP. 1991. Seasonal pattern of reverse mounting in the Groove-billed Ani (*Crotophaga sulcirostris*). Condor 93:159-163.
- CRAMP, S., AND K.E.L. SIMMONS. 1977. Handbook of the birds of Europe, the Middle East and North Africa, Vol. 1. Oxford Univ. Press, Oxford, England.

- GRAVES, J. A., R. T. HAY, M. SCALLAN, AND S. ROWE. In press. Extra-pair paternity in the shag *Phalacrocorax aristotelis* as determined by DNA fingerprinting. *J. Zool.*
- KORTLANDT, A. 1940. Eine Übersicht der angeborenen Verhaltensweisen des Mittel-Europäischen Kormorans *Phalacrocorax carbo sinensis* Shaw & Nodd, ihre Funktion, ontogenetische Entwicklung und phylogenetische Herkunft. *Arch. Neerl. Zool.* 4:401-442.
- KORTLANDT, A. In press. Patterns of pair-formation and nest-building in the European cormorant. *Ardea*.
- NUECHTERLEIN, G. L., AND R. W. STORER. 1989. Reverse mounting in grebes. *Condor* 91:341-346.
- PORTIELJE, A.J.F. 1928. Zur Ethologie bezw. Psychologie von *Phalacrocorax carbo subcormoranus* (Brehm). *Ardea* 17:112-149.
- SNOW, B. K. 1963. The behaviour of the Shag. *Br. Birds*, 56:77-103; 164-186.
- WILLIAMS, L. 1942. Display and sexual behaviour of the Brandt Cormorant. *Condor* 3:85-104.
- WITHERBY, H. F., F.C.R. JOURDAIN, N. F. TICEHURST, AND B. W. TUCKER. 1940. The handbook of British birds, Vol IV. H. F. & G. Witherby Ltd, London.