

## REVERSE MOUNTING IN GREBES<sup>1</sup>

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**Abstract.** Reverse mounting (females mounting males) is common in many grebe species. Of 328 mountings observed and filmed in Silvery Grebes (*Podiceps occipitalis*), 27% were by the female. Similarly, for Hooded Grebes (*P. gallardoi*) observed during the same period, 15% of 95 mountings were reversed. For both species, reverse mounting was significantly more common early in the season. Reverse mounting in Silvery Grebes also was more frequently associated with pre- and postmounting courtship display activity at the nest than were copulations. We conclude that reverse mounting is not aberrant behavior in grebes, but constitutes a regular and integral part of their courtship behavior. Since reverse mounting also appears to occur in a wide diversity of other monomorphic bird species, we suggest that using mounting behavior to determine sex in these species may be unreliable.

**Key words:** Hooded Grebe; Silvery Grebe; Podiceps; reverse mounting; copulation.

### INTRODUCTION

Although reverse mounting has been reported for many bird species, most authors appear to regard the behavior as unusual or aberrant. The evidence from easily sexed, strongly dichromatic bird species generally lends support to this assumption (Morris 1954, 1955; Ficken 1963; Nolan 1978; Thompson and Lanyon 1979), but in grebes (Podicipedidae) and several other monochromatic species the behavior is sufficiently widespread to warrant re-examination of this assumption.

The prevalence of reverse mounting in grebes has become particularly evident in our research on the comparative courtship behavior of the colonial grebes. Because grebe pairs often engage in repeated mounting attempts (sometimes five or six copulations in a 15- to 20-min period), reversal in the roles of the sexes during such bouts is particularly conspicuous (see Storer 1969, 1971, 1976). Within colonies, sufficient sample sizes of both copulations and reverse mountings can be obtained to compare statistically the contexts and structural details of the two forms of mounting behavior.

Most authors describing copulation in grebes have used the neutral terms "passive bird" and "active bird," to avoid implying sex-specific behavior, but this practice ignores the possibility

that there may be important behavioral differences between reverse mounting and "normal" copulation sequences. In an analysis of filmed sequences of the Least Grebe (*Tachybaptus dominicus*), for example, Storer (1976) found significant differences related to whether or not the roles of male and female were reversed.

Several nonmutually exclusive hypotheses can be proposed to explain why reverse mounting occurs in grebes. Reverse mounting may (a) result in fertilization, (b) result from mistaking a partner's sex, (c) be an aberrant behavior, (d) play a role in courtship and pair formation, (e) indicate a reversal of dominance in the sexes (Storer 1976), or (f) stimulate the ovaries of the female to grow (Storer 1976).

The primary objectives of the fieldwork reported in this paper were to examine the contexts and behavioral details of reverse mounting in Silvery Grebes (*Podiceps occipitalis*) and Hooded Grebes (*P. gallardoi*), asking specifically the following questions: (1) Is reverse mounting aberrant behavior? (2) When in the pair-formation process do reverse mountings take place? (3) Does sperm transfer take place during reverse mounting? (4) Are there consistent differences in the platform displays of reverse mountings vs. copulation?

### METHODS

As part of a 3-year comparative study, we conducted fieldwork on Silvery and Hooded grebes on small (less than 2 km<sup>2</sup>) snow-melt lakes in the

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TABLE 1. Frequency of copulations (male on female: M/F), reverse mountings (F/M), and same sex mountings (M/M and F/F) in Silvery and Hooded grebes.

	Possible mountings			
	M/F	F/M	M/M	F/F
Silvery Grebe	239	88	1	0
Hooded Grebe	81	14	0	0

foothills of the Andes in southern Patagonia, Argentina (52°S, 72°E). Observations on reverse mounting and copulation were most intensive in the 1981–1982 season.

In November 1981, we observed a group of several hundred Silvery Grebes and 35 Hooded Grebes engaging in courtship activities on an unnamed staging lake, which we named Laguna Nevada. Unlike waterfowl (Anseriformes), grebes cannot mount in open water (McAllister and Storer 1963), and we observed Silvery Grebes using flat, partly submerged rocks on the far north end of the lake as copulation platforms. To obtain closer observation and films of this activity, we constructed platforms directly in front of our camp. These platforms consisted of three woven baskets placed in each corner of a floating triangular frame made of 3-m bamboo poles. The entire frame was then anchored in 1 m of water and protected from wave action by floating wave breaks.

These platforms were readily adopted by the grebes and over a 2-year period, we were able to film or observe more than 400 copulations or reverse mountings. Later in the season, mounting at nest platforms within breeding colonies was also observed from a floating blind. In Patagonia, both species were very tame and allowed the close observation distances necessary to sex the birds reliably.

Prior to mounting, all pairs in the sample were sexed visually using bill size, which is greater in males for most or all grebe species (Storer, unpubl. data). Only pairs that could be easily distinguished before making the behavioral observations were included in the sample. This sexing technique was verified for Silvery Grebes by R. W. Storer by measuring the bills of male and female specimens using dial calipers. Measurements taken included depth of the closed bill at the level of the posterior edge of the nostril and bill length from the anterior edge of the nostril to the tip, both to the nearest 0.1 mm. For both measures, bills of males were highly significantly

larger than female bills ( $t = 6.0$ ,  $df = 28$ ,  $P < 0.001$  for bill length;  $t = 3.9$ ,  $df = 28$ ,  $P < 0.001$  for bill depth). When both measures were used in combination, there was almost no overlap between male and female bill measurements. Although too few museum specimens exist for a similar statistical analysis of bill size for the rarer Hooded Grebe, a similar bill dimorphism was evident.

Most mounting activities were observed from 4 to 10 m distance using either binoculars or a 15–60× spotting scope. We also obtained films of the behavior from within a distance of 5 m using a 16-mm Beaulieu camera and the floating blind. For each mounting, we noted the sequence of platform displays that occurred and whether the active and passive birds were male or female. Display terminology used in this paper is that of Storer (1969).

In late November, the courting flocks of grebes on Laguna Nevada dispersed to other small lakes in the area for breeding. In December 1981, Nuechterlein set up platforms on Laguna Blanchillo, where over 100 Silvery Grebes and 30 Hooded Grebes eventually nested. Most birds on this lake arrived already paired, so these observations and those at the nesting colony provided us with a late-season sample that could be compared to that from Laguna Nevada.

## RESULTS

We observed 328 mounting attempts in Silvery Grebes and 95 in Hooded Grebes. All attempts involved a male and female except for one case in Silvery Grebes where a male attempted to mount another male (Table 1). This case also was unusual in that the passive male neither Reared nor Invited.

Reverse mounting was common in both species, accounting for 27% of the mountings in Silvery Grebes and 15% in Hooded Grebes (Table 1). This was particularly evident early in the season on the temporary platforms, where 40% of 185 mounting attempts by Silvery Grebes were by females. Later, in the egg-laying period, reverse mounting was significantly less frequent (9.8% of 142 attempts, Table 2). A similar tally of reverse mountings vs. copulations in Hooded Grebes showed that pairs just beginning to build their nesting platforms (first day) engaged in significantly more reverse mountings than did pairs with well-formed cupped nests during the same 3-day period (33% vs. 5%, Table 2).

TABLE 2. Frequency of copulation vs. reverse mounting by: (A) Silvery Grebes on platforms during the pair-formation period (26–27 November, Laguna Nevada) vs. at nests during egg laying (11–12 December, Laguna Blanchillo); and (B) Hooded Grebes during early and late stages of nest building.

	Copulations	Reverse mountings	
A. Silvery Grebe			
Platforms	111	74	$G^2 = 40.4, df = 1, P < 0.001$
Nests	128	14	
B. Hooded Grebe			
On new nesting platforms	22	11	$G^2 = 13.4, df = 1, P < 0.001$
On cupped nests	59	3	

A behavioral analysis of copulation and reverse-mounting sequences in Silvery Grebes indicates many significant differences (Table 3). In contrast to copulatory sequences, ejaculation never occurred in reverse mountings, although sample size for this behavior was somewhat limited ( $n = 21$ ) owing to the necessity for close observations of birds that were facing directly away from the observer. Tail thrusting by the female, however, occurred in 29% of 72 reverse mounts, and the cloaca of the male often was everted during reverse mounts (Table 3B).

Whether male or female, the passive bird of opposite-sex mountings always Invited mounting by holding its head low over the water with crest flattened. There were differences, however, in two displays that frequently preceded this invitation to mount. In reverse-mounting se-

quences males were significantly more likely to Rear and Wing-quiver (Table 3A) prior to Inviting the female to mount. Postmounting display activity, particularly Head-flicking and Habit-preening, also was more frequent when females mounted males (Table 3C).

DISCUSSION

On the basis of our data from the Silvery, Hooded, and other grebes, we can reject several of the proposed hypotheses. If fertilization were involved, we would predict that reverse mounting would be most frequent during the egg-laying period and that ejaculation would occur. Instead, data from studies of the Silvery Grebe show that the frequency of reverse mounting is much greater during early pair formation than during or immediately preceding egg laying. Furthermore,

TABLE 3. Comparison of behavior occurring (A) before, (B) during, and (C) after copulations vs. reverse mountings in Silvery Grebes. Behaviors are listed in sequence, with those of the passive (mounted) bird denoted by \*. Postmounting displays often were given by both birds, but only those of the active bird were tallied.

Behavior <sup>1</sup>	Copulation		Reverse mounting		More frequent in:	Significance <sup>2</sup>
	Did	Did not	Did	Did not		
A. Before						
Rear*	15	113	20	47	Reverse mounting	$P < 0.005$
Wing-quiver*	3	13	13	4	Reverse mounting	$P < 0.005$
Invite*	141	0	75	0	—	ns
B. During						
Evert cloaca*	52	1	6	8	Copulation	$P < 0.001$
Tail-thrust	132	9	51	21	Copulation	$P < 0.001$
Ejaculation	23	18	0	21	Copulation	$P < 0.001$
C. After						
Patter	160	2	72	0	—	ns
Head-flick	3	111	12	42	Reverse mounting	$P < 0.001$
Face partner	41	63	24	31	—	ns
Head-turn	121	32	50	24	Reverse mounting?	$P < 0.06$
Habit-preen	6	108	17	37	Reverse mounting	$P < 0.001$

<sup>1</sup> Display terminology from Storer (1969).

<sup>2</sup> Significance levels are for G-tests ( $df = 1$  in all cases) of the null hypothesis that behavioral frequencies for copulatory mounting vs. reverse mounting are not different.

we did not observe ejaculation in any reverse mountings. Likewise, in the case of the Horned Grebe (Storer 1969), reverse mounting was most frequently observed on early platforms that were not used for egg laying, and cine films of both Horned and Least grebes also showed no cloacal contact (Storer 1976).

If reverse mounting were aberrant behavior, it should be rare. However, 27% of 328 mountings by Silvery Grebes and 15% of 95 mountings by Hooded Grebes were by the female. Reverse mounting is also common in at least Horned (*Podiceps auritus*) (Storer 1969), Great Crested (*P. cristatus*) (Selous 1901), Least (Storer 1976), Eared (*P. nigricollis*), and Western grebes (*Aechmophorus occidentalis*) (Nuechterlein, unpubl. data), and it has been reported by Storer (1976) in Red-necked (*P. grisegena*) and Pied-billed grebes (*Podilymbus podiceps*), and in the New Zealand Dabchick (*Poliiocephalus rufopectus*). This suggests that far from being aberrant behavior, it is of regular occurrence in many, if not all, grebe species.

If reverse mounting were a matter of mistaking the sex of the partner, one would predict that mounting by birds of the same sex also would be common. However, of 327 mountings by Silvery Grebes, including 88 reverse mountings, only one was by a bird of the same sex as the bird mounted (both males). We know of no other records of same-sex mountings in grebes.

If reverse mounting has been incorporated as part of courtship, we can make three predictions: (1) that reverse mounting would be most frequent early in the season during pair formation, (2) that some functional details of the movements involved in copulatory mounting may show signs of becoming cursory or ritualized, and (3) that reverse mounting in birds would be most common in monogamous, monomorphic species, in which male and female commonly engage in other reciprocal or mutual courtship displays.

The first of these predictions is supported by our data from the Silvery Grebe (Table 2), and Storer (1969) reported that reverse mounting in at least the Horned Grebe occurs "early in the season." Field studies presently underway show a similar bias towards early season reverse mounting in Eared Grebes (G. Nuechterlein and D. Buitron, unpubl. data).

In the Silvery Grebe, Inviting invariably preceded both copulation and reverse mounting, but other pre- and postmounting displays varied sig-

nificantly in frequency. In reverse-mounting sequences, Inviting was more frequently preceded by Rearing and Wing-quivering, and mounting was followed more frequently by Head-flicking and Habit-preening. All of these are ritualized displays commonly used in courtship sequences during early pair formation. In contrast, the functional copulatory movements of everting the cloaca, tail-thrusting, and ejaculation were all significantly less frequent during reverse mounting (Table 3).

Finally, all grebes that have been studied are monogamous, monochromatic, and engage in mutual or reciprocal displays. In the Least Grebe (Storer 1976), reverse mounting differs from copulation in the lack of cloacal contact, the less regular alternation of postcopulatory displays, and a difference in the reaction time between postcopulatory displays. We conclude that reverse mounting is a regular and integral part of the "courtship" behavior of grebes. Whether dominance reversal or stimulation of the ovaries or both are involved cannot be determined from our data.

The extent to which reverse mounting in other birds is functionally similar to that in the grebes is unclear. Reverse mounting in at least two non-passerines species appears to occur in different contexts from that in grebes. In the Hamerkop (*Scopus umbretta*), "repeated false mounting is performed, apparently largely indiscriminantly among groups of up to 8-10 birds near the nest" (Brown et al. 1982); and in the Acorn Woodpecker (*Melanerpes formicivorus*), pre-roosting mounting has been reported by MacRoberts and MacRoberts (1976). The latter is apparently neither age- nor sex-related, and its function is unknown, although it may be related to reducing aggressiveness prior to group roosting in holes where birds may be crowded together.

The difficulty of determining the sex of monomorphic birds is an important obstacle for researchers studying their behavior. A common method used by ornithologists is to color-mark individual birds, then "sex" them by noting which bird mounts during "copulation." The researcher thereby avoids the disturbance and difficulties associated with live-capture and laparotomy techniques. Applications of this procedure, however, entails an important implicit assumption: that in birds, males mount females and not vice versa.

This assumption may not be valid, not only

TABLE 4. Preliminary list of species in which reverse mounting has been reliably observed. Relative degree of sexual dichromatism is indicated (M = monochromatic, M' = nearly monochromatic, D = dichromatic).

Grebes, Podicipedidae (many species)	M	This paper
Wedge-tailed Shearwater, <i>Puffinus pacificus</i>	M	Shallenberger 1973
Red-footed Booby, <i>Sula sula</i>	M	Verner 1961
Peruvian Booby, <i>Sula variegata</i>	M	Nelson 1978
Northern Gannet, <i>Sula bassana</i>	M	Nelson 1965
Great Cormorant, <i>Phalacrocorax carbo</i>	M	Kortlandt 1942
Brandt's Cormorant, <i>Phalacrocorax penicillatus</i>	M	B. Boekelheide, pers. comm.
Shag, <i>Phalacrocorax aristotelis</i>	M	E. Cullen in Nelson 1965
Cattle Egret, <i>Egretta ibis</i>	M	Skead 1966, Blaker 1969, Lancaster 1970
Hamerkop, <i>Scopus umbretta</i>	M	Brown et al. 1982
Hadada Ibis, <i>Bostrychia hagedash</i>	M	D. S. DeCoursey, pers. comm.
Moorhen, <i>Gallinula chloropus</i>	M	Huxley 1914, Howard 1940, Anderson 1975
Piping Plover, <i>Charadrius melodus</i>	M	S. Haig, pers. comm.
Southern Brown Skua, <i>Catharacta skua</i>	M	P. F. Jenkins, pers. comm.
Pigeon Guillemot, <i>Cephus columba</i>	M	Storer 1945
Rock Dove, <i>Columba livia</i>	M	Huxley 1914, N. Burley, pers. comm.
Pied Barbet, <i>Tricholaema leucomelan</i>	M	Curio 1978
Red-headed Woodpecker, <i>Melanerpes erythrocephalus</i>	M	Brackbill 1969
Acorn Woodpecker, <i>Melanerpes formicivorus</i>	M'	MacRoberts and MacRoberts 1976
Lewis' Woodpecker, <i>Melanerpes lewis</i>	M	Bock 1970
Red-bellied Woodpecker, <i>Melanerpes carolinus</i>	M'	Kilham 1958, 1961; Hauser 1959
Northwestern Crow, <i>Corvus caurinus</i>	M	James 1983
Rook, <i>Corvus frugilegus</i>	M	Coombs 1978
European Starling, <i>Sturnus vulgaris</i>	M	Glick 1954
Prairie Warbler, <i>Dendroica discolor</i>	D	Nolan 1978
Painted Bunting, <i>Passerina ciris</i>	D <sup>1</sup>	Thompson and Lanyon 1979
American Redstart, <i>Setophaga ruticilla</i>	D	Ficken 1963
Zebra Finch, <i>Poephila guttata</i>	D	Morris 1954

<sup>1</sup> Reported case involved a young male in subadult plumage.

for grebes, but for many other monochromatic bird species. In recent years, the increased focus on marking and observing known individuals has provided documented instances of reverse mounting for a wide diversity of species, particularly early in pair formation (Table 4). Our research and review suggest that reverse mounting in many species may be more common than frequently supposed, and that observations of mounting behavior should not be used indiscriminately as prima facie evidence for sex determination.

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not been previously published. Although this table undoubtedly provides a woefully incomplete picture of the extent of reverse mounting in birds, we hope it may stimulate others to make the critical observations necessary to document this behavior in other species.

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