

COPULATION IN THE PIED-BILLED GREBE

NANCY M. McALLISTER AND ROBERT W. STORER

THE only published descriptions of "copulation" in the Pied-billed Grebe (*Podilymbus podiceps*) are those of Glover (1953) and Kilham (1954). Both authors describe a "forced copulation" on open water with both birds flapping their wings and the "female" sometimes diving away. This is entirely different from published accounts of copulation in other grebes (e.g., Simmons, 1955, for the Great Crested Grebe, *Podiceps cristatus*; Wobus, 1960, for the Red-necked Grebe, *P. grisegena*; Hosking, 1939, for the Horned Grebe, *P. auritus*; McAllister, 1958, for the Eared Grebe, *P. nigricollis*; Buddle, 1939, for the New Zealand Dabchick, *P. rufopectus*; and Hartley, 1937, for the Little Grebe, *P. ruficollis*). Our field data on the Red-necked Grebe and Storer's on the Horned and Eared Grebes are in agreement with the published accounts. Observations on the Western Grebe (*Aechmophorus occidentalis*) by Robert W. Nero and Fred Lahrman and by Storer, and on three South American species (*Podiceps occipitalis*, *P. chilensis*, and *P. major*) by Frank B. Gill and Storer indicate that the copulatory behavior of these four species follows the same general pattern as that in the six other species.

In the ten species, copulation takes place on a platform built by the birds, often the one used as a nest. Two soliciting postures: rearing (illustrated by Hosking and Newberry, 1946, Pl. 73; Buddle, 1939, Pl. 11, upper right-hand figure; Wobus, 1960, Fig. 2) and inviting (figured by these and several other authors) are employed by the "passive" bird prior to mounting by the "active" bird. The latter dismounts over the head of the "passive" bird and, in the case of most species, treads water in a "false bathing" posture (Simmons, 1955; and others). Observations on the Horned, Eared, Red-necked, and Western Grebes by Storer and on the Red-necked Grebe by McAllister indicate that the "active" and "passive" roles may be taken by birds of either sex (as reported for the Great Crested Grebe by Simmons, 1955). Reverse mounting appears to be more frequent in the early part of the breeding cycle than after the deposition of the first egg.

In view of the differences in the published descriptions of copulatory behavior between the Pied-billed Grebe and other species, it is of considerable interest to report in detail our independent observations on the platform behavior of the Pied-billed Grebe, which show that in most details it is similar to that of other grebes.

In May 1958, McAllister observed a nest of this species in Livingston County, Michigan. There was only one pair on the pond and therefore no territorial defense. The birds were observed for four hours each day, 21, 23, 25, and 29 April, during which no copulation calls were heard and no "forced

copulation" was attempted in open water. On 1 May the nest containing two fresh eggs was found. From 1 through 6 May, when the clutch was complete, daily observations were made from a blind 25 feet from the nest. On 4 May the nest was checked; on the other days, six to eight hours were spent in observation. A table of observations follows:

2 May	9:00	observer arrived
	9:30	female solicited
	9:40	copulation
	10:10	third egg laid
	12:10-1:20	observer out of blind but within hearing distance. No copulation call heard.
	2:30	copulation
	3:53	observer left
3 May	9:30	observer entered blind
	11:10	copulation
	11:40-1:45	observer out of blind but within hearing distance. No copulation call heard.
	2:20	fourth egg laid
	3:08	copulation
	3:50	observer left blind
4 May	2:30	four eggs present
5 May	9:30	five eggs present
	3:00	female solicited
	3:30	observer left blind
6 May	10:15	six eggs present
	3:05	observer left blind

Motion pictures were made of three of the four observed copulations at this nest. From these, Fig. 1 was traced. The only soliciting posture observed was inviting, simply the use of the passive copulatory posture on the nest. The second soliciting posture, rearing, was not observed at this nest. Only the female was seen in the inviting posture, and only infrequently. She adopted this posture immediately before copulation each time and only twice briefly otherwise. Neither inviting nor copulation was observed after the clutch was complete, although intensive observation was continued.

Once the female rose on the nest and covered the eggs, then with the brood patch closed flopped down on them and invited. The other three times she invited without first standing. Inviting was similar to that in *Podiceps* spp. with the neck outstretched on a level with the belly and the bill pointed forward, making a straight line with the belly and neck. This position was held while the male swam around the nest and finally mounted. Then with the bill still pointing forward, she slowly retracted her neck, doubling it back over her shoulders until after a little more than a second the back of her head touched the male's breast. After approximately two seconds, during which she turned her head four or five times slowly from side to side and rubbed her crown

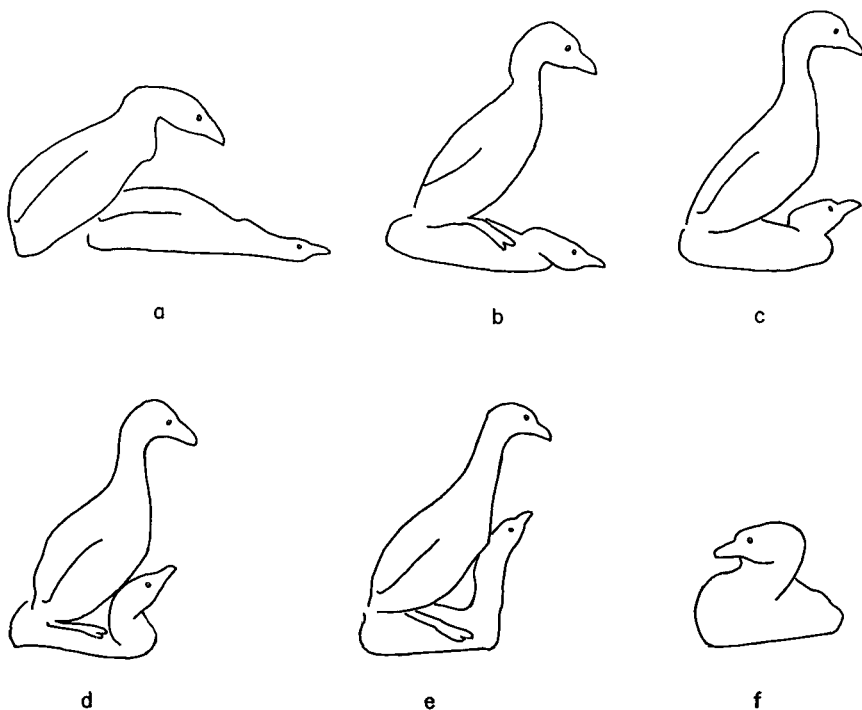


FIG. 1. Successive stages in copulation of Pied-billed Grebes (a. to e.). Postcopulatory posture of male on the water (f.). Traced from motion pictures by N. M. McAllister.

and nape against his breast, she raised her bill straight upward and stretched her neck upward still turning her head slowly and rubbing it against the male's breast.

Prior to mounting, the male stretched his neck upward and forward, then retracted it and jumped to the female's back with a single thrust of his feet. He landed with his neck partly arched and his body at an angle of about 45 degrees. He made several treading motions to establish his balance and his wings slipped free of his flank feathers but remained closed. After once regaining his balance, he did not move his feet. As the female began to draw her head back, the male stood more erect until the axis of his body was approximately 30 degrees from the vertical. His neck was extended and slightly arched, and his bill was tilted slightly downward of straight forward. He then called *quaa aaa aaa*, a short, wavering call, lower than in the other grebes, and not at all excited. There was no apparent movement associated with the call, and his bill was closed. After calling, the male began to retract his head and to lean forward, pushing the female's head down with his breast

until he flopped into the water over her shoulders, breast first with his neck doubled back on his shoulders. His tail dipped into the water leaving his white breast exposed for less than half a second. This posture was described for the Great Crested Grebe (Simmons, 1955:248), where it is associated with much rapid water treading. The male Pied-billed Grebe simply righted himself and swam off. He then brought a few loads of weeds to the nest and bathed in the usual way. The female shuffled her wings alternately on her back for a few seconds and then dived into the water and swam off.

Subsequent to McAllister's observations, Storer observed copulation by two pairs of Pied-billed Grebes. The first pair was on a pothole approximately two miles south of Fort Qu'Appelle, Saskatchewan. On 26 May 1959, the nest was under construction. At about 8:35 AM, the male deposited two loads of nest material and then hopped onto the nest to arrange the new material. When the female swam up and moved about on the water near the nest, the male assumed a rearing posture, his throat and crown feathers flattened and his neck with a decided crook in it. While in this posture, he shook his closed wings, then sat down and began to arrange the nest material. Two days later there was one egg in the nest. At 11:20 AM on 28 May, the female hopped onto the nest, removed the material covering the egg, and sat down. Presently she invited, but the male, who was swimming about near the nest did not mount. At 11:32, the male again appeared near the nest and the female invited. This time the male gave a soft version of the *cuk-cuk-cuk-cow-cow-cow* call and mounted. During copulation the female stroked the male's breast with the top of her head as described above. The male dismounted over the female's head, remaining only momentarily in front of her before swimming off to feed. Copulation was also observed at this nest at about 3 PM the same day and between 9:20 and 9:25 the following day (29 May). In both instances, the sequence of events was similar to that observed previously, except that it was noted that after dismounting, the male turned toward the female and remained for a short time in the false bathing posture.

The second pair of grebes was building a nest on Jemmerson Slough, two miles west of the town of Spirit Lake, Dickinson County, Iowa. In the course of approximately seven hours spent watching this pair on 24 April 1960, Storer observed rearing by the male (six times, three times with wing shaking) and by the female (twice, neither time with wing shaking). Only the female was observed inviting (three times), and twice this was followed by copulation, which in most details was similar to that of the two pairs already mentioned. The postcopulatory display of this pair, however, was somewhat different: The male tread water rapidly with his *side* toward the female and after he subsided into the swimming position, he turned to face the female and a bout of intense head-shaking followed. The head shakes were very

rapid, much more so than those of other species which we have observed. In the case of one of the copulations, the birds were facing $\frac{3}{4}$ away from the observer, and it was noted that the female raised her head to stroke the male's breast as cloacal contact was made.

To date, we have not observed inviting by the male, wing-shaking by the female during rearing, or reverse mounting; but in view of our observations on other species, it is highly likely that all these occur. It is interesting that there seems to be more variability in the details of copulatory behavior in grebes than in ducks. With the stronger and longer-maintained pair bond, perhaps there need be less stress on precision of innate copulatory and post-copulatory postures in the grebes.

From these descriptions it is clear that the normal copulatory behavior of the Pied-billed Grebe is essentially similar to that of other grebes. How then, can we interpret the observations of Glover (1953) and Kilham (1954)? In our many hours of watching Pied-billed Grebes, we have only once observed behavior comparable to that described by these authors. On 16 May 1960, Storer was watching grebes at the north end of Cawes Lake, two miles south and three miles east of Ellerslie, Alberta. At 12:30 PM, a small Pied-bill, probably a female, was found foraging along the northwestern edge of the lake. At about 2:15 the bird moved across the north end of the lake, still foraging, and by 2:30 had worked down the east side to where a second, somewhat larger bird (possibly a male) had been feeding. Without any preliminaries, the larger bird grabbed the smaller one by the back of the head or nape, and the smaller bird struggled forward without diving until it escaped. The larger bird again grabbed the smaller one by the nape and they continued to move forward with their heads and part of the larger bird's body above water. After several seconds, the smaller bird escaped, moved away, and resumed foraging. There was no indication that the birds were paired; no calls were heard in the more than two hours during which the birds were within earshot. (Paired Pied-bills call to each other at frequent intervals when separated.)

A similar encounter between two Horned Grebes was filmed by Storer in Saskatchewan in 1959, however, in this instance both birds dived and came up, the uppermost still holding the other bird by the nape. Simmons (1955: 139) has recorded similar behavior in his discussion of aggressive behavior of the Great Crested Grebe.

Our observations of copulation in the Pied-billed Grebe have been limited to nests on small bodies of water on which only two or three birds were found, situations in which little or no territorial defense or other aggressive behavior was observed. Glover studied a large, complex marsh containing at least 44 territories of the species, and he stated that territorial defense was

common. Having so many individual grebes under observation and so much conflict, it would not be surprising to mistake aggressive behavior for copulation. This type of behavior is frequent in strongly territorial grebes such as the Great Crested and Horned. Glover's reports that this kind of activity continued throughout the nesting cycle and in gradually decreasing intensity until 5 August strengthens our interpretation of this behavior as aggressive. In our observations, copulation on the nest stopped when the clutch was complete.

Observers familiar with the mating habits of waterfowl too frequently fail to realize that members of the family Anatidae are the only birds which are known with certainty to copulate on the water, a habit made possible by their intromittent organ. The phallus of waterfowl is generally considered a hold-over from a condition common to all ancestral birds (Witschi, 1961:125). Among living birds, only the ratite birds, tinamous, and cracids have similarly well-developed ones. The lack of an intromittent organ in all other swimming birds is strong evidence that copulation on the water is an impossibility for them.

There is additional evidence that the behavior reported by Glover and Kilham and observed by Storer in Alberta is aggressive in nature. In diving birds such as grebes, loons, penguins, and alcids, the species-specific patterns and conspicuous colors are found largely on the head. These areas are focal points during display and quite naturally, for attack as well. (In limited tests by McAllister with paper models, one captive adult Pied-bill pecked the model vigorously and always on the head.) Sexual dimorphism in grebes is slight, the males being somewhat larger, larger billed, and in those species with ornate head plumes, longer crested. Sexual recognition is probably slow in these birds and may occur only after the initial stages of pair formation have taken place. On the basis of Storer's observations on several species, soliciting appears to be initiated early in the season by the male, and mounting by the female often follows. Elaborate, "self-exhausting" displays (in the sense of Huxley, 1914) appear to function as outlets for sexual drives in grebes prior to nest building. In birds with this sort of behavior, "forced copulation" seems an extremely unlikely action. "Forced copulation" is rare among birds. The best known example is in ducks in which the sexes are very different in color and pattern and in which the pair bond is broken at the onset of incubation, forced copulation most frequently taking place after a female has lost her first set of eggs.

The recent report (Southern, 1961) of "copulation" on the water by Common Loons (*Gavia immer*) is subject to the same criticisms as the reports of Glover and Kilham for the Pied-billed Grebe. Two other species of loons (*G. arctica*, Zedlitz, 1913:183; and *G. stellata*, Huxley, 1923:260-261) are

known to copulate on land or on nest platforms, and like grebes, all loons lack an intromittent organ. These birds are strongly territorial and lack sexual dimorphism. We predict that when the courtship of the Common Loon has been adequately studied, it will be found that copulation regularly takes place on land and the behavior reported by Southern will prove to be aggressive rather than sexual.

In conclusion, copulation of Pied-billed Grebes, like that of other grebes as far as is known, takes place on the nest or a nest-like platform. It may be preceded by two soliciting displays, rearing (with or without wing shaking) and inviting, and may be followed by "escape bathing" and rapid head-shaking. During copulation, the "passive" bird strokes the breast of the "active" bird with the back of its head, a behaviorism shared by the Little Grebe of the Old World but by no other species so far studied. Observations of "forced copulation" on the water by grebes and loons are best explained as purely aggressive behavior.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF BRITISH COLUMBIA, VANCOUVER,
BRITISH COLUMBIA, CANADA, AND MUSEUM OF ZOOLOGY, THE UNIVERSITY OF
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Mr. Hamilton, whose ornithological interest is field migration, has been an active member of the Wilson Ornithological Society since 1948. He also enjoys being a "bird watcher chauffeur" for Mrs. Hamilton and Connie Hagar. Also, he is a Charter Member of the Texas Ornithological Society and a member of the AOU.