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THE SEXUAL BEHAVIOR AND SYSTEMATIC POSITION OF THE HOODED MERGANSER

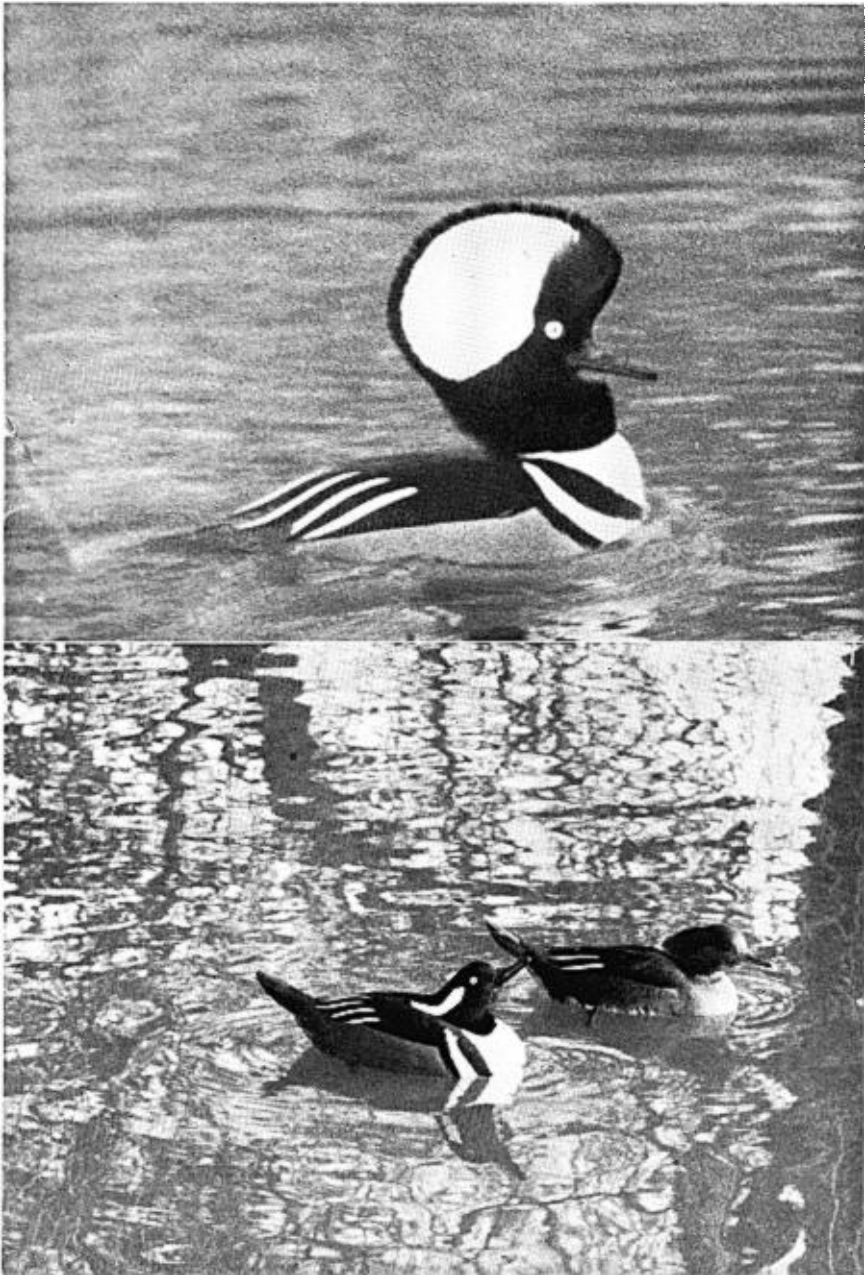
PAUL A. JOHNSGARD

IT has been over 15 years since Delacour and Mayr (1945) first urged that the mergansers (*Mergus*) and the goldeneye-Bufflehead group (*Bucephala*) be merged into a single tribe (Mergini) rather than being maintained in separate subfamilies (Aythyinae and Merginae). Their reasons for this change were several, and included such points as the similarities in the downy young, female color patterns, occurrence of wild hybrids between the two genera, and tracheal structure. Indeed, except for the shape of the bill in these two groups there is no good means of distinguishing the two subfamilies. As Delacour and Mayr pointed out, bill shape and structure is highly adaptive and should not be used for the erection of major taxonomic categories. However, these two subfamilies are still upheld in the fifth edition of the AOU Check-list.

Delacour and Mayr described the general similarities in the sexual behavior of *Mergus* and *Bucephala*, but no one has yet had the opportunity of critically comparing the behavior of most species in the two groups. Myres (1957, 1959a, 1959b) reviewed well the behavior of the *Bucephala* species, but was not fortunate enough to compare directly copulatory behavior in this genus and *Mergus*. He has, however, provided detailed descriptions of courtship and copulation in the Common Goldeneye (*B. clangula*), Barrow's Goldeneye (*B. islandica*), and Bufflehead (*B. albeola*). The behavior of the Common Goldeneye has also recently been described by Dane et al. (1959) and Lind (1960). I have been able to observe closely courtship display in all three species of *Bucephala* and in four species of *Mergus*, including the Hooded Merganser (*M. cucullatus*), Smew (*M. albellus*), Red-breasted Merganser (*M. serrator*) and Common Merganser (*M. merganser*), both in the wild (Johnsgard, 1955) and under captive conditions at the Wildfowl Trust, Slimbridge, England. Here I also have observed copulatory behavior in the Common Goldeneye, Barrow's Goldeneye, Hooded Merganser, Smew, and Common Merganser, and have incomplete observations on the Red-breasted Merganser. Although a major summary of my observations on these species and the rest of the Anatidae will be published later, the following observations on the Hooded Merganser are of special interest and have a direct bearing on Delacour and Mayr's (1945) proposed classification.

OBSERVATIONS OF BEHAVIOR

Aside from the notes of Bagg and Eliot (1933), Harper (*in* Phillips, 1926) and Robb (1930), relatively little has been written on the courtship of the Hooded Merganser, and nothing has been noted regarding copulatory behavior. In the Anatidae, behavior associated with copulation is very conservative and



Hooded Merganser behavior.
(Above) Crest-raising by male. (Below) Precopulatory drinking by male.

thus is extremely useful in judging evolutionary relationships (Myres, 1959b, Johnsgard, 1960). The following behavioral patterns associated with courtship, or pair formation, have been observed by me:

Male Courtship. (1) Crest-raising (Front.). This is frequently performed, and may occur without other displays or in combination with them. Crest-raising also occurs in the Bufflehead and, in a less spectacular fashion, in the other species of *Bucephala* and *Mergus*.

(2) Head-shaking (Fig. 1). This is a rapid lateral shaking with crest raised, and is repeated three or four times before the Head-throw display. It serves the same function as does the "Introductory shake" of *Anas*, in that it draws attention to a male that is about to perform an elaborate display. Similar shaking movements occur in the Red-breasted Merganser and the Smew.

(3) Head-throw with Turning-the-back-of-the-head (Fig. 1). This is the most elaborate of the male courtship displays. It is directed to a particular female, to which the displaying male is usually parallel. The head is rapidly brought back to the back with crest erect and a call, a rolling frog-like *Crrrrroooooo* is uttered as the head is returned to the normal position and the crest is turned toward the courted female. I have never seen a kick accompany this display. Head-throws also occur in the Common and Barrow's Goldeneyes and in the Smew, but it is doubtful that these displays are all homologous, since Head-throw displays have clearly evolved independently in many genera of ducks (*Anas*, *Aythya*, *Clangula*, *Somateria*, etc.). Sometimes after several Head-shakes the male does not perform a Head-throw but only lifts his head, opens his bill, and utters a hollow *pop*. I know of no similar behavior in any other species.

(4) Pumping (Fig. 1). A frequent and silent display which appears to be aggressive in motivation is an upward and forward stretching of the neck which results in an elliptical movement of the head and bill, as if the bird were reaching for an invisible object. This is often repeated and is sometimes performed simultaneously in both sexes. None of the other *Mergus* species studied have such displays, but the Rotary Pumping of Barrow's Goldeneyes and the Bow-sprit Pumping of the Common Goldeneye (see Myres, 1959a) are similar in form and also appear to be hostile in motivation.

(5) Upward-stretch. This is a simple Head-shaking stretch with an erect crest. It is often done by displaying males and is clearly ritualized. Similar movements occur in all species of *Bucephala* and *Mergus* observed by me and likewise appear to be ritualized into displays.

(6) Upward-stretch with Wing-flapping. This is like the preceding display but the wings are also flapped several times. This display is found in all the species of *Bucephala* (especially the Bufflehead, in which it is certainly one of the major displays) and also in all the *Mergus* species observed by me.

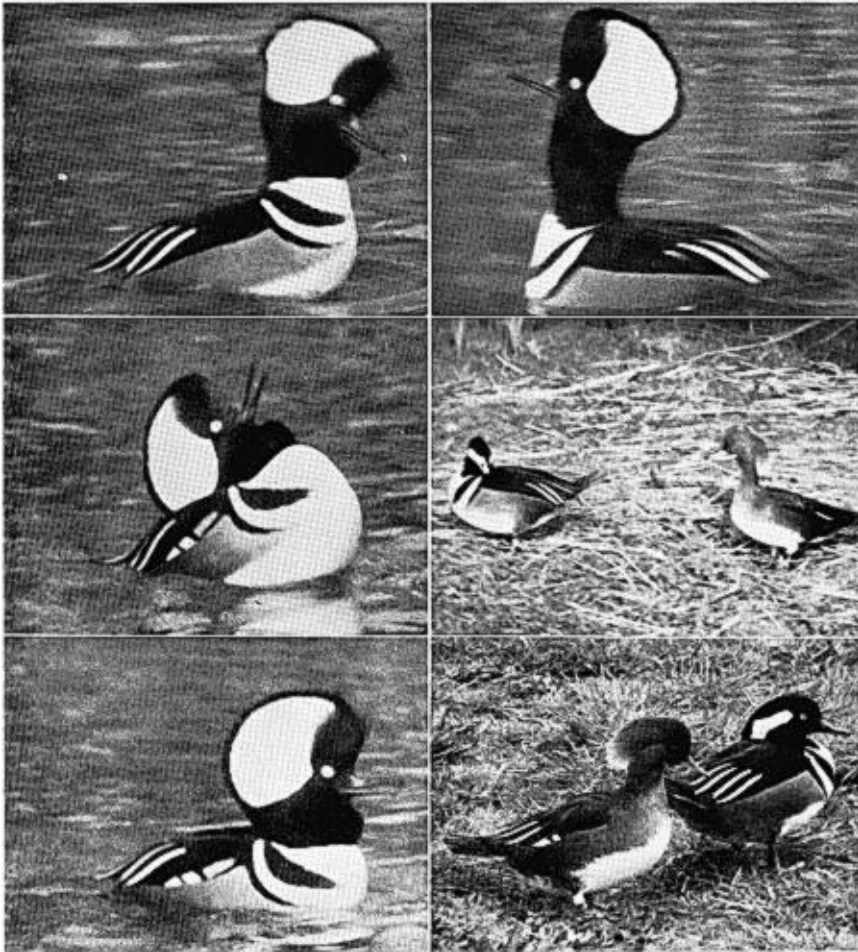


FIG. 1. Courtship displays of Hooded Merganser.

(Upper Left) Head-shaking.

(Center Left) Head-throw.

(Lower Left) Turning-the-back-of-the-head
after the Head-throw.

(Upper Right) Pumping.

(Center Right) Male with crest depressed
and directed toward female, who is per-
forming "Bobbing" movements.

(Lower Right) Low-intensity "Bobbing" by
female.

(7) Drinking (Front.). Ritualized drinking with a depressed crest occurs as a courtship (and precopulatory) display in the Hooded Merganser, the Smew, and to a lesser degree in the other mergansers. In *Bucephala* it is primarily a precopulatory display. In the Hooded Merganser it may be distinguished from normal drinking in that the bill is raised almost to the vertical and the crest is strongly depressed.

(8) Tail-cocking. This display occurs in the Hooded Merganser in association with the following display, which appears to be related to pair-bond maintenance. The male usually swims ahead of the female with his tail cocked at about a 45-degree angle. Similar displays occur in the Smew and in the Common and Red-breasted Mergansers, but I have not seen it in males of *Bucephala*.

(9) Crest-depressed and directed toward female (Fig. 1). This is similar to the Turning-of-the-back-of-the-head display in male *Anas* (Lorenz, 1951-53) and is distinct from the usual head profile of a resting or frightened bird in that the forehead feathers are raised and the crest itself is strongly depressed. A very similar display occurs in the Smew (but in this species the color pattern produced is a black "V" against a white head rather than a white "V" against a black head).

(10) Tertial-lifting. This is a slight and often-repeated lifting of the ornamental tertials while performing displays (8) and (9). I have not observed it in any other species, and am uncertain whether the movement actually has a signal function.

Female Courtship. (1) "Bobbing" (Fig. 1). This is the term used by Hollom (1937) for a display in the female Smew that is obviously homologous to this movement of the Hooded Merganser. It is clearly an especially intensive form of inciting (see Lorenz, 1951-53), in which the female's head moves in a jerky, upward bobbing fashion, with the bill pointed downward, as a hoarse *Cack* is uttered. It is rather rare in the Hooded Merganser, but is very frequent in the Smew. I have also observed this type of inciting in the Red-breasted Merganser, but in the Common Merganser inciting takes a form more like the inciting of pochards (*Aythya*) and dabbling ducks (*Anas*), in that the "bobbing" component is not so conspicuous. Inciting in goldeneyes ("Jiving" of Myres, 1957, 1959a) has a markedly different form, but the equivalent behavior of Buffleheads ("Following") is more like the typical *Mergus* type of inciting. The male response in all these species is the same, namely to swim ahead of the inciting female while directing the back of his head toward her.

(2) Pumping. This is identical to Pumping in the male and is usually performed in response to male Pumping in the same way that female goldeneyes respond to Rotary and Bowsprit Pumping by males.

Precopulatory and Postcopulatory Behavior. In *Bucephala* as well as *Mergus*

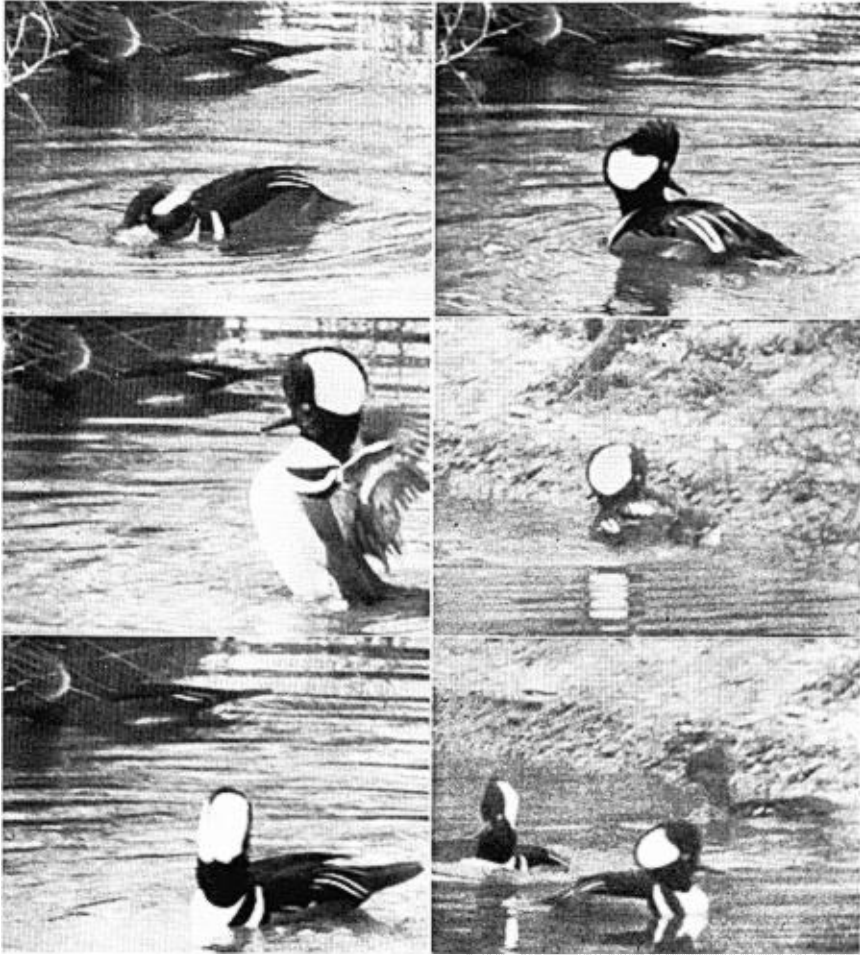


FIG. 2. Copulatory behavior of Hooded Merganser.

(Upper Left) Water-twitching.

(Center Left) Wing-flapping.

(Lower Left) Preening-behind-the-wing.

(Upper Right) "Tacking" toward female.

(Center Right) Postcopulatory "Rotations."

(Lower Right) Postcopulatory "Steaming."

the female solicits copulation while stretched out prone and stationary on the water after both birds have performed display drinking. Before mounting, males of all species perform repeatedly numerous displays which usually include ritualized drinking, stretching, or preening movements. These have been described by Myres (1957, 1959a, 1959b) for the Bufflehead and the two goldeneyes, and by Dane et al. (1959) and Lind (1960) for the Common Goldeneye. Copulatory behavior in the Common Merganser has been described by Christoleit (1927), and Hollom (1937) and Lebreton (1958) have described the corresponding behavior of the Smew. Adams (1947) and Myres (1959a) have provided incomplete descriptions of copulation in the Red-breasted Merganser.

I have seen several sequences of copulatory behavior in the Hooded Merganser which may be summarized as follows: The male swims near the female, frequently performing drinking movements with a depressed crest. The female responds by drinking, and each time lifts her head high and forward, with her crest depressed. After several such mutual drinking displays the female assumes the prone posture, with her head held just over the water and her tail flat on the water surface (as in *Bucephala* and the Common Merganser). The male immediately begins to make rather jerky forward and backward head movements which are less exaggerated than, but otherwise almost exactly like, the "Pouting" behavior of Smeews (see Hollom, 1937). (In Smeews "Pouting" is a courtship rather than a precopulatory display.) The male frequently makes drinking movements and also occasionally performs an Upward-stretch. Suddenly the male begins to dip his bill and part of his head (Fig. 2) rapidly and repeatedly in the water while shaking the bill (as in the *Bucephala* "Water-twitch" display described by Myres, 1959a). After several such shakes (6, 7, and 8 have been counted on three different occasions) the male suddenly stops (at this point a male goldeneye would Preen-behind-the-wing once and "Steam" to the female), performs an Upward-stretch with or without Wing-flapping (three flaps counted on one occasion) (Fig. 2), then settles back in the water and immediately Preens-behind-the-wing (Fig. 2) on the side toward the female (exactly as would a goldeneye), and starts swimming in rapid, jerky, Pouting movements toward the female. He does not Steam directly to the female as a goldeneye would, but rather "Tacks" in a zig-zag course toward her (Fig. 2), alternately presenting (seven times in about 5 feet in one instance) the two sides of his crest to her view, the crest being fully raised and presented to the female's full view with each Tacking movement. In five cases I have seen, this sequence of "Water-twitching—Upward-stretch—Preen-behind-the-wing—Tacking-toward-female" was identical every time, but I am not certain how many times Wing-flapping accompanied the Upward-stretch. As soon as the male reaches the female he attempts to mount her, but in only two times observed by me was he successful.

In each case the male remained mounted for ten seconds or more, and performed on each occasion a single Flick-of-the-wings while mounted (as in goldeneyes). After the male successfully completed treading, he slipped off to one side but retained hold of the female's nape for several seconds, during which the two birds "Rotated" slightly (Fig. 2). In neither case was a complete circle rotated, as usually occurs in goldeneyes (see Myres, 1957; Dane et al., 1959). The male then released the female and "Steamed" directly away from her with crest erect (Fig. 2). In one case the male "Plunged" under the water (as often occurs in Buffleheads after copulation) when he was about 5 feet away from the female. In the other case the male swam about 25 feet away from the female in a straight line, exactly as would a male goldeneye except that no lateral head-turning ("Ticking") was observed. The male then began to bathe. The female started bathing as soon as it was released by the male in both instances.

By comparison, the typical *Mergus* precopulatory behavior consists of the male performing repeated drinking movements, together with Upward-stretches (with or without Wing-flapping) and Preening-dorsally, all of which occur independently. I have not observed any Water-twitching in any of the other species of *Mergus*, and have only observed a Preening-behind-the-wing once in the Smew, but it was not linked to any other behavior and may not have actually been a true display. In *Bucephala* (and the Hooded Merganser) however, the Preen-behind-the-wing is completely ritualized, occurring only once and being firmly linked to the preceding Water-twitching (or "Jabbing") and the following Steaming to the female. Male Smews and Common Mergansers lack such a spectacular approach to the female, but rather repeatedly approach and retreat, until they finally are successful in mounting or the female comes out of the prone posture. During treading I have observed that the Smew repeatedly Flicks-the-wings (five times in one case), but this display (which probably has auditory rather than visual function) did not occur in any of the three Common Merganser copulations I have observed. Neither the Smew nor the Common Merganser exhibits postcopulatory Rotations. Male Smews and Common Mergansers swim away from the female after copulation while Turning-the-back-of-the-head to her.

DISCUSSION

Both in courtship and in copulatory behavior most species of *Mergus* and *Bucephala* share certain patterns and differ in others. However, the Hooded Merganser bridges some of these differences in its courtship, and especially in its copulatory behavior. Precopulatory displays of the Hooded Merganser that are typical of *Bucephala* are the repeated Water-twitching and the subsequent Preen-behind-the-wing. In its linkage of these two displays into a rigid sequence just before approaching the female the Hooded Merganser is more similar to the goldeneyes than is the Bufflehead! Typical *Mergus* precopulatory patterns

TABLE 1
COMPARISON OF PRESUMABLY HOMOLOGOUS BEHAVIOR PATTERNS IN *MERCUS*
AND *BUCEPHALA*

	Buffle-head	Common Goldeneye	Barrow's Golden-eye	Hooded Merganser	Smew	Red-breasted Merganser	Common Merganser
MALE COURTSHIP							
Upward-stretch	x	x	x	x	x	x	x
Wing-flapping	X	x	x	x	x	x	x
Crest-raising	X	x	x	X	x	x	x
Head-throw	-	X	x	x	x	-	-
Tail-cocking	-	-	-	x	x	x	x
FEMALE COURTSHIP							
Inciting	x ¹	x ²	x ²	x ³	x ³	x ³	x
COPULATORY BEHAVIOR							
Drinking by ♂	?	x	x	x	x	x	x
Drinking by ♀	?	x	x	x	x	x	x
Female prone	x	x	x	x	x	x	x
Upward-stretch (♂)	-	-	-	x	x	x	x
Preen-dorsally (♂)	x	-	-	-	x	x	x
Water-twitch (♂)	x	X	X	x	-	-	?
Preen-behind-wing (♂)	-	X	X	X	?	-	-
Steaming to ♀	-	X	X	x ⁴	-	-	-
Flick-of-wings (♂)	x	x	x	x	x	?	-
Steaming from ♀	-	x	x	x	-	-	-

x the behavior pattern was observed

X the behavior pattern was exceptionally well developed

- the behavior pattern is apparently absent

¹ "Following" of Myres

² "Jiving" of Myres

³ "Bobbing" of Hollom

⁴ "Tacking"

include the Smew-like Pouting and the Upward-stretch and Wing-flapping. Behavioral patterns it shares with both genera include mutual drinking and the female prone posture. In its approach to the female by Tacking, the male Hooded Merganser is intermediate between the direct and rapid Steaming approach of the goldeneyes and the repeated approach-retreat behavior of the typical mergansers. This "compromise behavior" of Tacking immediately calls to mind the "Zig-zag Dance" (Tinbergen, 1951) of the male Three-spined Stickleback (*Gasterosteus aculeatus*) and the pivoting approach of the male to the female in the Zebra Finch (*Poephila guttata*) described by Morris (1954).

The Hooded Merganser also has a single Flick-of-the-wings during treading which occurs in all *Bucephala* species but which I have only otherwise observed in the Smew among the *Mergus* species. Postcopulatory Rotations are also

present, and this behavior is typical of all *Bucephala* species but of neither of the two species of *Mergus* observed by me. Enough evidence is at hand, therefore, to point out the fact that *Bucephala* and *Mergus* share so many complex behavioral patterns in their courtship and copulatory displays that an extremely close evolutionary relationship exists between them (see Table 1). Thus the continued subfamilial separation of these groups that is still adhered to by the AOU Checklist is untenable. Additional evidence for the Hooded Merganser's close relationship to *Bucephala* is provided by the structure of the male's trachea (see Beard, 1951; Johnsgard, 1961). The downy young possess unstreaked cheeks as are typical of *Bucephala* and Smew downy young, rather than the streaked cheeks typical of the other *Mergus* species. The egg-white proteins of the Hooded Merganser exhibit an electrophoretic pattern practically identical to those of the Red-breasted Merganser and *Bucephala* (see Sibley, 1960). The Hooded Merganser is perhaps more closely related to *Bucephala* than is the Smew, which possesses a more *Bucephala*-like bill, which points out the fallacy of regarding bill shape and specialization as a major index to evolutionary relationships.

SUMMARY

The courtship and copulatory behavior patterns of the Hooded Merganser are described, and probable homologies are pointed out with other *Mergus* species and with *Bucephala*. In some of its courtship displays ("Tail-cocking," female "Bobbing") and precopulatory behavior ("Pouting," "Upward-stretch") the Hooded Merganser exhibits typical *Mergus* elements, whereas in others ("Water-twitch" linked to Preen-behind-the-wing, postcopulatory Rotations) it clearly shows affinities with *Bucephala*, and in fact is even more like the goldeneyes in some respects than is the Bufflehead. In still other aspects of display it is intermediate between the typical species of the two genera ("Tacking" toward the female rather than the *Bucephala* "Steaming," or the approach-retreat behavior typical of *Mergus*). The Hooded Merganser thus provides an almost perfect connecting link between *Bucephala* and *Mergus*, and it is concluded that these two groups are no more than generically distinct.

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