DISPLAY BEHAVIOR OF BUFFLEHEAD, SCOTERS AND GOLDENEYES AT COPULATION

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THE displays which occur in connection with the mating act have been described in but a few species of birds, and in fewer still has any attempt been made to relate these to, or distinguish them from, the other courtship displays. In a recent study (Myres, M. T., 1957 MS. An introduction to the behaviour of the goldeneyes: *Bucephala islandica* and *B. clangula*. M.A. Thesis, University of British Columbia) it was shown that the pre- and post-copulatory displays of Barrow's Goldeneye were almost indistinguishable from those of the Common Goldeneye. This was in marked contrast to those courtship displays which have a primarily pair-forming and pair-maintaining function, which were remarkably different in the two species. It is therefore of considerable interest to make further comparisons in the displays connected with copulation between other species of sea ducks (tribe Mergini* of the family Anatidae). Such a comparison is presented here between the only other member of the genus *Bucephala* (*B. albeola*, the Bufflehead) and the two species of goldeneye already mentioned, and between two species of the genus *Melanitta* (*M. deglandi*, the White-winged Scoter, and *M. perspicillata*, the Surf Scoter) and the Bufflehead.

During the summer of 1957 I observed copulation of the Bufflehead on 12 occasions on Watson Lake, at 105 Mile, Cariboo Highway, in the Cariboo District of British Columbia. To my knowledge, the actions occurring at copulation have not been described previously for this species. On 103 Mile Lake, two miles away, I observed five instances of copulation in the White-winged Scoter. During the following winter, 1957–58, I saw copulation of the Surf Scoter on four occasions on salt water off Saltspring Island, B. C. The displays observed will be described for each species below, but a few remarks should be made regarding the manner of presentation.

Capitalized words are names allotted to distinct displays. In a few instances names are given to displays, described elsewhere, of other species. To prevent unintended homologization of displays between species, different names are employed wherever possible, except when it is believed that two displays are without any doubt homologous. It will become clear in the course of the discussion which displays, of the species described here, I believe to have had common origins. There may be instances where a name has been used, unavoidably, which is also used for a display in another species not discussed here. In such instances no homology should be understood, unless it has been clearly mentioned.

* Classification follows P. Scott, **Key to the Wildfowl of the World.** Severn Wildfowl Trust, Slimbridge, Gloucestershire, England. Revised, 1951.

In a few places it is stated that one display is more, or less, common than another. Because the number of separate copulations observed is only 21, and only one or two of these were recorded quantitatively by describing them onto magnetic tape, these assertions are not strictly objective. Rather they are subjective impressions received while watching the copulation sequence, in particular the course of the pre-copulatory display behavior.

Bufflehead

Copulation was observed 12 times between May 31 and June 16, 1957, as follows: May 31 (twice), June 1, 2, 3, 4 (three times), 5 (twice), 14 and 16. Most frequently the performance took place between 8:00 a.m. and midday, but on three of the 12 occasions it was seen in the evening. By June 16 many broods of downies were already on the lake, and I estimated that about half the broods subsequently present were there by that date. It is evident, for this and other reasons, that the females with whom males were seen to copulate were already well ahead with the incubation of their clutches by the first day in June.

The female assumes a flattened pose on the water (Prone-posture), but it is unusual for the female to assume this for more than a few moments before the male mounts (this is in contrast to the two goldeneyes where the female may remain in the Prone-posture for as long as 20 minutes).

The male swims around the female, or rests close by her on the water, performing the two main pre-copulatory displays. These are (1) a twitching of the water with his bill (Water-twitch), and (2) a preening movement over his back (Preen-dorsally):

1. The Water-twitch consists of dipping the bill to the water and then a slight sideways movement of the head, which is almost indistinguishable from a similar comfort movement. The movements may be distinctly separated by a pause, or by a Preen-dorsally, or they may be repeated one after the other in fairly quick succession.

2. In the Preen-dorsally it is impossible to be certain that the wing has been lifted in any way on some occasions, and indeed it probably is not lifted on all occasions. The bill must then come into contact with the feathers of the back or the upper side of the folded wing. On other occasions the wing is seen to be only slightly raised, and on one occasion the long scapulars were seen to be lifted more than the carpal joint so that a tiny spot of white appeared (from the secondary feathers or coverts). More often, however, the movement of the wing was just the lifting of a black shape above the back. In the Preen-dorsally the head may be swung around through an arc on the side toward the female, or on the side away from her. It seems likely that the indefinite lifting of the wing, and the variability as to which wing is concerned, may be an indication that the display is not as ritualized as in the surface-feeding ducks in which the colored speculum is flashed during this display—presumably most often in the wing which faces the female. K. Lorenz (1941. *Jour. f. Ornithol.*, 89:194–294) states that in *Aix galericulata* this is invariably so in the Mock-preening display.

In the Bufflehead the Preen-dorsally is closely linked with the Water-twitch, and the latter generally occurs before the former, just as a bird performing

comfort-preening frequently dips his bill into the water in front of him. Undoubtedly the two displays originate from this comfort movement sequence. In the Bufflehead it was observed, however, that Water-twitching was more frequent than the Preen-dorsally (contrast White-winged Scoter).

The unritualized form of these displays is also indicated by the fact that in the goldeneyes the supposed homologues of these movements (Jabbing and Wing-preen) are very highly ritualized: the Jabbing or Water-flicking of the goldeneyes is a frenzied series of movements and the Wing-preen is brief and momentary. Also in the goldeneyes they occur in a fixed sequence leading into the motor pattern of mounting itself—the Wing-preen never occurs, in fact, except as a preliminary motion at the beginning of the Steaming movement which, in goldeneyes, brings the male onto the back of the female.

After a few moments, or a minute or two, of Water-twitch and Preen-dorsally display activity (the frequency of repetition is variable), the male suddenly moves toward the female and mounts. Generally he begins to move toward her from only a foot or so away, and the locomotory performance is not spectacular, but on one occasion it seemed that he made a slight rush over the water. On three occasions, out of eight in which the complete copulation sequence was observed, the wings were momentarily lifted off the back (Wing-flick) and snapped back into place about the time of intromission. This action has also been observed in goldeneyes and scoters. The tail is waggled from side to side during copulation.

On dismounting the male continues to hold onto the head of the female with his bill, and the male and female rotate around each other for one or two full turns (Rotations). On three occasions, out of the 12, it appeared that the female was almost turned over onto her back as the male pulled at her head during the Rotations, and one of her legs was seen thrashing above the water behind her.

As soon as he releases the female, the male almost at once begins to dip his head and the forepart of his body below the water, and to shimmer his wings in the water, as in normal comfort bathing (Bathing). The female also acts similarly, and then both birds stretch upward out of the water (Upward-stretch) and flap their wings (Wing-flap), in a fashion identical with the comfort movements. However, this was only seen to occur on four of the 12 occasions. Twice the male made a shallow plunge below the surface first, as if the movement were an exaggeration of the first dip of the Bathing behavior. On no less than six occasions the male dived deeply (Plunge) coming up from one to 15 feet away from the point of diving. On four of these last occasions the male performed the Upward-stretch and Wing-flap immediately on surfacing without prior Bathing, in another instance he performed Bathing, and in the sixth his actions were not recorded. On one of these six occasions the Upward-stretch and Wing-flap were followed by more Bathing. In two of the

12 instances the female, after she had performed some comfort movements at the end of copulation, performed a few of the neck-stretching and crouching movements which she generally performs when following a particular male away from a strange male or males (Following).

On two occasions the first attempt at mounting did not result in a successful ejaculation, because the male slipped off the back of the female and performed Water-twitching movements again before mounting again. In one of these cases three attempts were made to mount in succession, and in another case the male appeared to give three Water-twitching movements, followed by a single Preen-dorsally, while actually mounted on the back of the female. No Rotations were observed, nor did the male Plunge, after this but he did perform Bathing. The absence of the customary Rotations probably indicates failure to effect ejaculation, because in an unsuccessful copulation in *Bucephala islandica* the post-copulatory Rotations and Steaming displays were absent and the failure was followed by more pre-copulatory display actions, a successful copulation, and finally the normal post-copulatory displays (Myres, *op. cit.*).

White-winged Scoter

Copulation was observed on five occasions: May 31 (once), June 2 (twice in succession), June 3 and 5 (once each). At this period many of the pairs (of which there were about 15 present on 103 Mile lake), were not, apparently, incubating their eggs. They may also have been nonbreeding birds.

The female assumes the Prone-posture from a position in which the head is elevated and forward, as in the "alarm" posture of this species. However, the Prone-posture is assumed only just before the male mounts. On three of the five occasions on which copulation was observed the female suddenly stretched her neck rigidly upward at an angle of 45 degrees forward as soon as the male caught hold of her head feathers on mounting. The same posture was observed when the female reappeared above the water after copulation.

Three displays were observed in the male prior to copulation: (1) False-drinking, (2) Water-twitch, and (3) a Preen-behind-the-wing display (which is presumably the homologue of Preen-dorsally in Buffleheads). It should be mentioned here that during the winter of 1957–58 courtship behavior of this species was watched on a number of occasions. The main elements were the same as in the pre-copulatory behavior (namely the three displays mentioned above). This is the *only* species, of the ones reviewed here, in which this equivalence has been found. In the goldeneyes, Bufflehead and Surf Scoter the courtship displays of the pair-forming and pair-maintaining series differ quite markedly from the pre-copulatory displays.

1. False-drinking was performed by the male alone, or mutually by both male and female when it may be repeated a number of times. The display consists of dipping the bill to the water in front of the bird and a sudden elastic elongation of the neck forward and upward at an angle of about 75–80 degrees, until it is fully stretched and the head and neck appear to be larger than the rest of the body. The neck relaxes and shortens, more slowly, immediately afterward. In the final stages of the pre-copulatory behavior, the False-drinking display may sometimes be less common than it is in the courtship behavior, this

was not consistently the case.

2. The Water-twitch was a dipping of the bill to the water, but with only a slight shake of the head. Generally the head was immediately lifted and swung round to the side, through 170 degrees, to the middle of the back and the Preen-behind-the-wing took place. The Preen-behind-the-wing was sometimes more common than the Water-twitch (contrast Bufflehead), but whenever the Water-twitch occurred it appeared always to be followed by a Preen-behind-the-wing.

3. The Preen-behind-the-wing takes three forms: (a) the scapulars and secondaries are lifted and held up for some movements which also exposes the white speculum, distinctive of this scoter. The preening movement may take place with the wing on the side toward the female, or on the side away from her. It often occurs when the male is some distance from the female; (b) the bill is thrust along the side of the body, or into the shoulder feathers, and the pink bill is then clearly visible against the black body plumage as the preening movement is made; and (c) the back feathers are nibbled. The white iris and white feathers around the eye are also most striking in both (b) and (c).

Eventually the male mounts the female, but there is a considerable period between the time the male covers the female and the Wing-flick. This movement was observed to occur once (or twice) in all five of the copulations observed. It was a vigorous movement, and made a sound as the wings beat the water. Upon dismounting, on two occasions the male was just holding on to the head of the female, but only a fraction of a circle (perhaps 20–30 degrees) was rotated. There was no post-copulatory display (contrast Surf Scoter), except that the male (upon slipping back into the water) flicked the tips of the primaries to rearrange the wings. The male was then in a hunched posture and drifted or swam slowly away from the female. The female also rearranged her wings.

Surf Scoter

Copulation was observed on four occasions in midwinter on the sea off Saltspring Island, B. C.: December 29, 1957 (once), January 3, 1958 (twice in midafternoon) and January 5, 1958 (once in the afternoon). On all occasions there is no evidence to indicate that the birds involved were permanently paired. It would appear, by comparison with copulations of the White-winged Scoter observed on the breeding grounds, that the complete copulation display sequence was observed, despite the time of year.

The Prone-posture resembles that of the goldeneye. The female lies flat with the neck below the water, and the bill curved upward. The longest time this was held was about two minutes in one of the copulations.

The displays involved were extremely similar to those observed at copulation of the White-winged Scoter. The main pre-copulatory displays were the Water-twitch and the Preen-behind-the-wing, though these were not described in detail, while False-drinking was also observed.

The male mounted the female slowly, as in the White-winged Scoter, and in every case the wings were eventually flicked, but the movement was a single Wing-flick, not a double one. Upon dismounting, however, there was

a display not observed in the White-winged Scoter. This display (Chest-lifting) was seen on all four occasions as follows:

As soon as the male slipped back into the water he threw his head back until it was over the middle of his back, which developed a 45 degree slope, and he thrust out his chest. Chest-lifting greatly resembles a display which is seen in a courting party. It is a sudden and brief movement. After Chest-lifting, no other movements by the male were observed. In one case the female did some unidentified movements afterwards, and then did the Upward-stretch and Wing-flap.

There were unusual features about two of the copulations observed: (a) the third copulation occurred only a few minutes after the second, though it is not certain that the same male was involved in each case. The time was around 3:00 p.m. It was very mild, and drizzling at the time. A small party of Surf Scoters broke up, leaving two females and a male. The two females were tilting their bills upward repeatedly without lifting their heads, as in the Chin-lifting of Lesser Scaup (*Aythya affinis*). The male, between them, was performing the display in which he lifts the head and makes a scooping movement across the chest. The male also performed Water-twitches and Preens-behind-the-wing. Then he did some violent dipping, of the Bathing sequence, and one of the females assumed the Prone-posture. The male mounted her and copulation proceeded although the other female was almost touching them. (b) In the fourth and last copulation, the male mounted the female from in front, over her head. She quickly swung around beneath him, but there was (as usual) a considerable pause before he seized her head feathers.

Discussion

The displays occurring in the copulation sequence of the two genera *Bucephala* and *Melanitta* are listed and compared in Table 1. The pre-copulatory displays of the male Bufflehead consist of twitching the water with the bill, and making a preening-type movement in the dorsal region between the wings. Similar displays occur in the two scoters studied. In the two goldeneyes, by contrast, the predominant pre-copulatory displays of the male are stretching the wing and leg, and flipping water into the air with the bill. As I was more familiar with the goldeneyes I was not at first sensitive to the fact that Water-twitches and Preening-dorsally were indicative of copulation behavior in the Bufflehead.

It seems to be significant that in Buffleheads the Water-twitch movement may be more frequent than the dorsal preening movement, whereas in the White-winged Scoter the preening movement is the more frequent pre-copulatory display. Whenever the Water-twitch did occur in the scoter it was generally followed immediately by a Preen-behind-the-wing. The twitching of the water with the bill before preening is, of course, a normal part of a comfort movement sequence in diving ducks, and it is most interesting that *M. deglandi* and *B. albeola* have diverged in the relative frequency with which they use these two movements in display. I find that Lorenz (*op. cit.*) also noted instances of variously ritualized linkages of two displays of the general courtship sequence

in some other ducks. In the Wood Duck (*Aix sponsa*) and the Mandarin Duck (*Aix galericulata*) of the tribe Cairinini, for example, the Mock-preening display never occurs without the preceding "drinking" movement. In the Wood Duck "drinking" may occur at lower intensity by itself, but in the Mandarin Duck the two displays are absolutely linked. In the Gadwall (*Anas strepera*) Lorenz found, furthermore, that the two displays are equally firmly linked, but in the reverse order (Mock-preening is followed by "drinking").

TABLE 1

DISTRIBUTION OF MALE COPULATORY DISPLAYS IN *MELANITTA* AND *BUCEPHALA*[1]

M. perspicillata	M. deglandi	B. albeola	B. islandica B. clangula
Pre-copulatory			
False-drinking	False-drinking	———	**Water-flip**[2]
———	———	———	**Wing- and Leg-stretch**
Water-twitch	Water-twitch	**Water-twitch**	Note[2]
Preen-behind-wing	**Preen-behind-wing**	Preen-dorsally[2]	Note[2]
Mounting			
———	———	———	Water-flick (and Jabbing)[3]
———	———	———	Wing-preen[2]
———	———	———	Steaming
Single Wing-flick	Double Wing-flick	Wing-flick(?)	Wing-flick
Post-copulatory			
———	———	Rotations	Rotations
Chest-lifting	———	———	Steaming
———	———	Plunge or Bathing	Bathing
?	Rearrangement-of-wings[3]	Upward-stretch and Wing-flap[3]	Upward-stretch and Wing-flap[3]

[1] The displays in boldface are the most frequent displays in each species.
[2] It should not be taken as certain that any of these displays are homologous until analytical ethological work has been conducted, but in the discussion it has been assumed that Water-twitch, Water-flick and Jabbing may be the same; that False-drinking and Water-flip are the same; and that Preen-behind-the-wing, Preen-dorsally and Wing-preen are the same.
[3] Generally this is followed by a Tail-wag, but this was not specifically noted in these displays, though it probably occurred. The Rearrangement-of-wings of **M. deglandi** may represent the settling of the wings after the Wing-flap which generally coincides with the Tail-wag.

Preen-dorsally, or Preen-behind-the-wing, may well be homologous with the Mock-preening movements found in the general courtship displays of *Aix* and *Anas*, in which a colored speculum has been evolved, which emphasizes this ("morphological reinforcement"), and other movements (Lorenz, *op. cit.*; Tinbergen, N., 1952. *Quart. Rev. Biol.* 27: 24 and 27). In *Anas discors, A. cyanoptera, A. querquedula* and *A. clypeata* there is a further development. The secondary coverts are pale blue, and Lorenz (*op. cit.*) states that in *A. querquedula* the preening movement takes place on the outside (instead of the inside) of the wing, and that the bill is actually directed at these coverts

rather than the speculum. In only one of the three scoters are the secondaries differentiated and at variance in color from the rest of the black plumage of the wing. But display-preening is not absent in the two scoters studied merely because of this. Instead of plumage differentiation we find that the scoters have brightly colored bills (bright pink; white, orange and black; pale yellow or orange). It seems certain that the colored bill must be an alternative method of emphasizing the display movement. It really matters very little, so far as producing additional sign stimulation is concerned, whether this is done by preening *specula* (or *coverts*) which are colored, or by a *bill* (colored) preening a uniformly dull wing.

The Water-twitch of the Bufflehead is probably homologous with the Jabbing display of *B. clangula* or the Water-flicking behavior of *B. islandica* (Myres, *op. cit.*) which also occur in the pre-copulatory sequences. Jabbing in *B. clangula* immediately precedes the momentary Wing-preen display before mounting. But the Water-twitching movement of *B. albeola* was never a group of frenzied Jabbings as it is in *B. clangula*. The Wing-preen display of the goldeneyes is very rapid and, as a display, occurs only in the pre-coition sequence: in *B. clangula* it is a single momentary movement just as the pre-coition Steaming posture is assumed. In the Bufflehead and White-winged Scoter the movement is not unusually rapid, and so appears less ritualized. No False-drinking, Wing- or Leg-stretching, or Steaming movements were observed in the pre-copulatory behavior of the Bufflehead. But False-drinking (comparable to Water-flip of the goldeneyes) occurs in the pre-copulatory display of the White-winged Scoter, though rather less frequently than the Preen-behind-the-wing or the Water-twitch.

The post-copulatory displays are also interesting. Rotations do not occur in the White-winged or Surf Scoters at all. In the two goldeneyes they do not appear to differ at all from the Rotatory movements of Buffleheads. It is not clear to me yet which of the two sexes is providing the propulsive thrust, and which the drag, which results in circling of both birds over one spot.

The pre-and post-copulatory Steaming displays of the two goldeneyes appear to be completely absent from *B. albeola* and the two scoters. In the Bufflehead a deep dive (Plunge) occurs on some occasions, which would appear to be an exaggeration of the preliminary plunges or dips which accompany Bathing. Bathing always occurs after copulation in the two goldeneyes, as well as in the Bufflehead, but in the latter species was omitted when the Plunge occurred. The Plunge was followed directly by the Upward-stretch and Wing-flap. Bathing and even the Upward-stretch and Wing-flap were absent in the post-copulatory sequence of the two scoters, and the only comfort action was a flicking of the tips of the primaries (Rearrangement-of-wings), which is possibly homologous with the final motions of closing the wings after the Wing-flap which completes the sequence in *Bucephala*. The only way in

which the Surf Scoter differs in copulatory behavior, qualitatively, from the White-winged Scoter is in having a distinct post-copulatory display (Chest-lifting).

Whereas in the goldeneyes the female may be in the Prone-posture for a considerable time (as long as 20 minutes), in the Bufflehead and Surf Scoter the Prone-posture is assumed only a short while before the male mounts, and in the White-winged Scoter was observed only immediately prior to mounting, or as the male trod the female. There may be a correlation between the duration of soliciting by the female and the number and variety of displays in the male, e.g., the most are found in the long-soliciting goldeneyes, and the fewest in the White-winged Scoter. In the Bufflehead there were a few suggestions that, while mounted, the wings of the male were flicked. In goldeneyes the Wing-flick is a regular accompaniment of intromission. In all five instances of copulation in the White-winged Scoter a double Wing-flick was noted, and in all four instances a single Wing-flick was seen in the Surf Scoter.

A major theoretical interest of the pre- and post-copulatory behavior of the ducks under discussion is that the displays involved are generally confined to the moments just before, and just after, the act of mating. They are generally confined to this moment in the reproductive cycle, and are rare in the more frequently described courtship behavior. Thus the Head-bobbing of the Bufflehead, which is the most well-known display of the male of that species, is absent completely from the copulation sequence. This rule applies fairly well also in the two goldeneyes. The Headthrow of *B. clangula* and Rotary-pumping of *B. islandica*, which are respectively the most frequently observed displays of these species, occur infrequently in the pre-copulatory behavior. In *B. islandica* it is possible to watch the Rotary-pumping display give way as the time for coitus approaches, to Water-flips and the Wing- and Leg-stretching displays indicative, in the male, of copulation.

Ethologists are asked to realize the importance of the displays associated with copulation. These displays prove to be, in ducks, more conservative than the general courtship displays with pair-forming and pair-maintaining function. The copulation sequence may thus be of considerable importance in studies of the taxonomic relationships of species and genera. Thus, taking all displays into account, it is very hard to place the Bufflehead in the family tree, but considering only the displays of the copulation sequence it appears to be intermediate between the scoters and the goldeneyes. A much clearer picture will be established when descriptions of coitus are available for the other ducks comprising the tribe Mergini.

Another interest of the displays occurring at copulation lies in the light they may throw on the *successive* evolution of courtship displays within a differentiating stock of animals. In the present case the developmental status of the Jabbing and Wing-preen displays of the Common Goldeneye, on the one hand,

and the Mock-preening of *Anas* and *Aix* on the other, appears uncertain. The Water-twitch and Preen-dorsally, or Preen-behind-the-wing, displays appear less ritualized than either, but the direction in which evolution may have proceeded in regard to these displays is not yet clear. A comparative review of the evolution of courtship *versus* the copulation displays is planned.

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SUMMARY

The copulation of *Bucephala albeola* was observed 12 times, of *Melanitta deglandi* five times, and of *M. perspicillata* four times. The displays and actions employed are compared with those occurring at copulation in the two goldeneyes (*Bucephala* spp.). The Wing- and Leg-stretch display of the latter was completely absent from *B. albeola* and *M. deglandi*, in which the Water-twitch and the Preen-behind-the-wing predominated. Both these movements occur in association, however, in the normal comfort-preening sequence of ducks, and in similar (? non-homologous) Mock-preening displays in the general courtship displays of members of both the Anatini and Cairinini. In the copulation behavior of goldeneyes they occur only in a momentary form just immediately prior to the exaggerated Steaming display which constitutes the approach to the female at mounting in these species. The post-copulatory Rotations, alone of all the displays, take exactly the same form in all three species of *Bucephala*. Rotations were not observed in scoters and the only difference between the two scoters in the displays occurring at copulation was in the existence of a Chest-lifting display after coitus in the Surf Scoter. The post-copulatory Steaming of the goldeneyes is replaced in *B. albeola* by a Plunge movement on some occasions. This may be an exaggerated prelude to the bathing that occurs after coitus. Scoters lack Steaming displays and the White-winged Scoter merely rearranges the wings after dismounting.

Ethologists, it is suggested, should pay more attention to the comparative aspects of copulation displays, since they are probably conservative. Taken with other differences in display between *B. albeola* and the goldeneyes, the possibility exists that *B. albeola* should not be placed in the same genus as the goldeneyes. The evolution of morphological reinforcement of the sign stimulatory effects of motor patterns of display is discussed in reference to the speculum of ducks in general, and to the colored bills of scoters in particular.

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