

Studies on Courtship and Copulatory Behaviour in the Goldeneye (*Bucephala clangula* (L.)).

By HANS LIND.

(Med et dansk resumé: Hvinandens (*Bucephala clangula* (L.)) pardannelses- og parringsadfærd).

(Meddelelse fra Naturfredningsrådets reservatudvalg nr. 62).

Accidental observations of courting males of the Goldeneye (*Bucephala c. clangula*) made it evident to me that the courtship of this species is particularly suitable for a detailed analysis. In the first place, the males in the flocks that stay in the Danish waters in winter and in the spring very often show their courting display, so that it does not cause any difficulty to obtain a sufficiently large observation material. Secondly, this display includes a comparatively large number of different activities open to comparison and analysis, and thirdly, in its composition it shows some probably primitive features as compared with the courtship of the surface-feeding ducks.

The courtship of the Goldeneye has often been mentioned in the literature. The American form (*Bucephala clangula americana*) has been watched by TOWNSEND (1910), JOHNSGARD (1955), and BREWSTER (1911). The latter gives a rather thorough description of the various activities, but on the basis of less than two hours' observations. In Europe the behaviour of the Goldeneye has especially been studied by BERNHARDT (1940), and furthermore by MILLAIS (1913) and GUNN (1939), and as to the courtship, by BOASE (1924), v. HAARTMAN (1945), and HEINROTH (1911). However, the many different forms of display, some of which have a certain superficial similarity to one another, apparently have given rise to a considerable confusion in the descriptions. Since, furthermore, some actions and many details have not previously been mentioned, a description of all courtship activities is urgently needed. The same applies to the behaviour before, during and after the copulation.

The present work is mainly the result of investigations which I have been able to make at the sanctuary Tipperne (Ringkøbing Fjord, Western Jutland) in 1958 thanks to the courtesy of Naturfrednings-Dansk Ornithologisk Forenings Tidsskrift 53, 1959, Hefte 4.

rådet (Nature Conservancy Board) and to financial support from the Danish State Research Foundation. The Goldeneyes were watched every day for several hours from the end of March to the middle of April. A stationary telescope with a magnification of 35 and 56 times was used; it was placed in a conning-tower. The distance was 200–1000 metres. Normally there were 100–200 Goldeneyes within the observation distance.

Among the many different species of ducks in the Zoological Garden of Copenhagen there were during the winter 1956–57 for some time 4 males and 1 female of Goldeneyes, and during the following winter 2 males, but no female. I am much obliged to Dr. H. POULSEN for having given me an opportunity to study these birds, through which it was possible to provide a valuable supplement to my observations in the open. If an activity has only been observed in the Zoological Garden, this is expressly stated. Only in the Zoological Garden it was possible to determine the combination of movement and call, for which reason my statements concerning the calls are rather incomplete.

Description of the Courtship.

Courtship can be seen at any time of the day. It is mainly performed in flocks, several males gathering around one or (more rarely) two females. When the female lies quietly on the water, the males will slowly swim round her or lie still close to her. As a rule, however, the female swims off, the males following or accompanying her.

The head of the male as a rule is drawn almost down to the shoulders (fig. 1) but when he swims at high speed, the neck is stretched somewhat upwards, and due to the vigorous strokes the forepart of the body is raised somewhat out of the water. The quick forward swimming mostly takes place by stages of 1–3 metres; in this way the males can overtake the female. Only rarely a male chases another male. The males swimming beside and in front of the female often turn their heads quickly from side to side.

The courtship activities to be described below are only performed when the males are moving at moderate speed or lie still.

The female rarely flies up, but very frequently she dives, and the males immediately follow her. A male rarely dives without the female having done so first. The dives are of short duration, about 5 seconds. If the female changes the

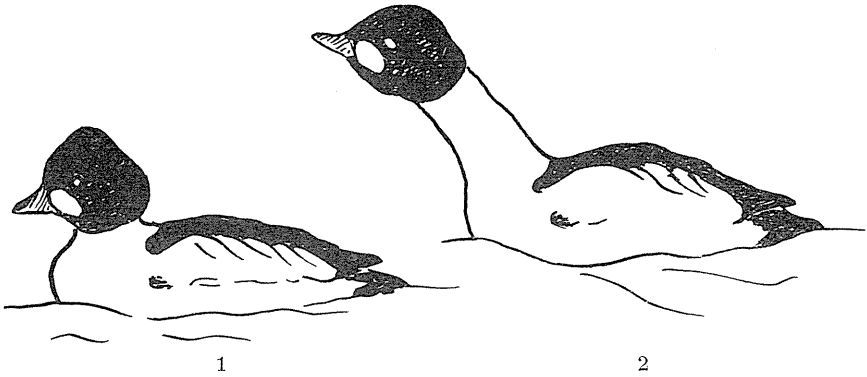


Fig. 1. The initial posture of the courtship activities.
Indledningsstilling for kurtiseringshandling.

Fig. 2. The Oblique Posture.
Skrå-posituren.

direction under the water and emerges in another place, the males at once head towards her. During the swimming the female also often changes direction. It seems that the female tries to escape from the males, which follow her without pursuing her. I have never seen a male attacking the female, but the female may make small attacks on the males.

Courtship occurs in other situations as well (p. 185), but in flocks as described above, we find the typical courtship, which consists of the following activities:

Head-shaking is the commonest. It follows immediately after most of the displays and after diving, but it also takes place isolatedly. The head is shaken laterally in a very quick movement, and the lengthened feathers are in a conspicuous way flung out from the head.

Head-bobbing: When the males after quick forward swimming have stopped and lie close around the female, they may several times in rapid succession stretch their necks vertically upwards and direct down to the starting position. This is rarely seen.

Oblique Posture I (fig. 2). The neck is stretched obliquely upwards and forwards at a jerk forming an angle of $45-60^\circ$ with the surface of the water. The bill points upwards at an angle of $15-30^\circ$. The feathers on the head are normally raised, but may be closely pressed to the head. When the bird is

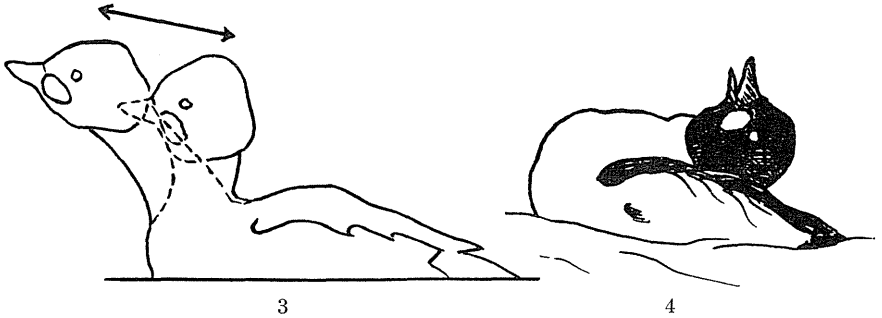


Fig. 3. Repeated stretching of the neck to the Oblique. The arrow indicates the movement.

Den gentagne halsstrækning til Skrå-positionen.

Fig. 4. The Snarl-throw.

Snerrekast.

swimming in this posture, it may often withdraw its head a little downwards and backwards, but not quite back to the starting position (fig. 3), and then stretch it into the Oblique again. The stretching is faster than the withdrawal. This movement may be repeated many times.

Fairly rarely the female may assume a similar posture as the male and make the same backward jerks with its neck, but less markedly.

Oblique Posture II: Now and then the neck is not stretched direct from the starting position to the Oblique, but is first stretched forwards and low over the water and then is raised obliquely upwards. The bill in some cases touches the water.

Both Oblique Postures are mostly assumed laterally to another bird. When a Goldeneye swims towards or in front of another, it will generally change direction when performing the Oblique. Often two males swim parallelly and close together with the Oblique jerks, and if one of them changes direction, often at an angle of 180° , the other immediately turns, too.

In many diving ducks a very conspicuous courtship activity occurs, in which the head is thrown backwards over the back in a greater or smaller movement. Such a backward *Head-throw* has also been described in the Goldeneye, but in this species there are two fundamentally different types, each with at any rate two different forms.

In the *Snarl-throw I* (fig. 4) the head is thrown far backwards so that the nape touches the hindmost part of the back, the bill points vertically upwards and the forepart of the body is raised a little out of the water. Head and neck remain in this posture for 1–2 seconds, and with open bill the bird gives a faintly sounding, snarling call, “rrrrr-”. Only in the Zoological Garden it was possible to hear this sound, but it undoubtedly always accompanies the movement. Also v. HAARTMAN (1945) and perhaps HEINROTH (1911) mentions it. (The call of the Goldeneye which generally is mentioned in the literature, is the louder Kick-throw sound.) The movement is concluded by the head being thrown forward to the starting position, this being done very quickly. Immediately as the head stops in the final position, it is shaken very rapidly. This shaking seems to form an integral part of the Snarl-throw.

The termination often takes place differently from the way described above. Head and neck may be thrown right forward to the Oblique and be kept there for a moment, after which they are withdrawn with a head-shake. This performance must be considered a fixed combination of two activities, as the head-shake only follows after the Oblique. It is called *Snarl-throw II*. Now and then a bird performs Snarl-throw I with the final head-shake and immediately afterwards assumes the Oblique. In such a case it is not a question of one activity, but of two in rapid succession.

Kick-throw I is performed with very swift movements: the head is laid back over the shoulders (fig. 5a), thus not so far back as in the Snarl-throw, the bill pointing upwards. The bird then kicks backwards with both legs so that the water splashes up behind it. The foot is no doubt flung right out of the water (cf. photo in BERNHARDT 1940), but the movement is very swift and only the tarsus is seen immediately after the kick. As a consequence of the violent movement of the legs, the hind part of the body is raised out of the water and the forepart is lowered correspondingly. The tail is fanned and kept down against the surface of the water, neck and head are pressed forward, but the bill still points upwards (fig. 5b). As the body again assumes its usual position, the neck is rapidly stretched vertically upwards, and with a vertical and open

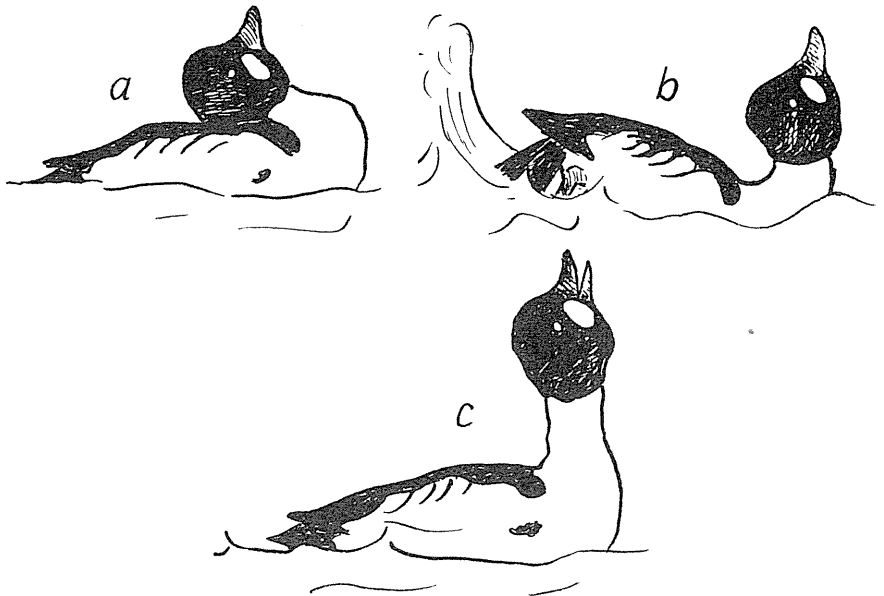


Fig. 5. Kick-throw I. a. The Head-throw. b. The Kick. c. The final stretching of the neck.

De tre faser i Spjætkast-I.

bill the bird utters a fairly loud call “rretsh-rrree” (BERNHARDT 1940: “Knirrlaut”) (fig. 5c), after which the head is withdrawn and shaken.

In *Kick-throw II* the introduction is performed more slowly and with other movements: the neck is fairly slowly raised vertically and the bill points upwards at an angle of about 75° (fig. 6a). In immediate continuation of this movement the head—the neck being stretched—is laid backwards (fig. 6b) nearly as far as in the Snarl-throw. The closed bill is vertical or points slightly backwards. Then the kick follows and the further procedure is as in Kick-throw I.

MILLAIS (1913) states that the kick is done alternately with both feet, and BREWSTER (1911) says that only one of the feet or perhaps both of them participate. TOWNSEND (1910) as well as BERNHARDT (1940) ascribe the kick to a simultaneous movement of both feet. In all those cases in which I had my attention directed towards the movements of the legs in the Kick-throw, both feet were used simultaneously.

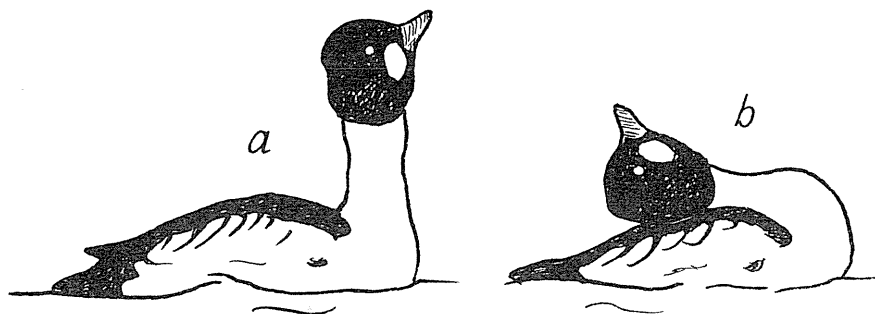


Fig. 6. The two first phases of Kick-throw II. a. The initial stretching of the neck. b. The Head-throw.

De to første faser i Spjætkast-II.

In the Zoological Garden I fairly often saw a third form of the Kick-throw, but never at Tipperne, even though I have watched many hundreds of kicks. The head was thrown backwards, the bill was vertical, then neck and head were stretched up vertically and only then the kick and the call followed.

Even though I have watched many Kick-throws very closely, I have never seen other forms than those mentioned. Nearly all descriptions of these activities in the literature, however, are different and differ from what I have seen. This is probably in part due to the fact that other forms of combinations may occur, but it may also be due to the fact that the watcher has not recognized more different fixed postures and activities. The four different Head-throws have a certain resemblance to one another, and the performance of these after each other and together with other activities in rapid succession, while other males are performing close by, will easily result in confusion in the description.

Only once I have seen a female making a movement reminding of the male's kick. From the Crouched Posture (see below) the head was bent to a vertical position (p. 185), and simultaneously she made a small kick with the feet so that the forepart of the body was pressed a little down into the water, but only little water splashed up. This was repeated three times.

Body-shaking occurs fairly often in the courtship. At the same time as the plumage is shaken, this being concluded by head-shaking, the body is raised quickly out of the water to an angle of 60–75°, after which it subsides.

The *Crouched Posture* is not restricted to the courtship. It is assumed by both the male and the female. In the commonest



Fig. 7. The Crouched Posture.
Dukket-positur.

performance (fig. 7) the body lies deep in the water, the neck is almost completely submerged, but the head projects obliquely out of the water at an angle of about 15° . The feathers are pressed close to the head, but the white spot on the cheek is the normal size and seems large in relation to the small head. The head may be turned from side to side at small jerks, but mostly is kept still in the same position. The tail is pressed down against the surface of the water. In other cases the head may be raised to about 45° or be kept horizontally in the surface of the water.

The posture is nearly always assumed when the bird is facing another and is often followed by diving and attack below water. A Goldeneye may swim towards another in the Crouched Posture, and the mere fact that it turns towards another in that posture is sufficient to make the other swim away. If one bird is facing another in the Crouched Posture and then dives, the other will immediately dive away. If a swimming Goldeneye is attacked from below, it escapes by "running" on the surface of the water with its neck stretched upwards, and then dives away. During brisk courtship chasing may now and then take place with the neck completely stretched forward (more than in the Crouched Posture) and with open bill, or at a swift run on the surface of the water with the forepart of the body raised.

The *Crouched-up-down Movement* (fig. 8): The bird lies still in the Crouched Posture, always with its head horizontally in the surface of the water, then head and neck are raised to the vertical position and the neck is stretched directly upwards. This is done at lightning speed. The vertical position of neck and head is maintained for a fraction of a second only; then neck and head are flung down directly into the Crouched Posture. During the whole performance the feathers are pressed close to the head. The bird lies with its head or side turned towards another bird. Like the Crouched Posture the Crouched-up-down Movement is very often followed by diving. The components in the Crouched-up-down are very closely con-

nected, and the Crouched Posture, which is part of the display, in contrast to the normal performance is invariable.

Now and then bathing movements (head-neck-dipping) of short duration are seen, always subsequent to intensive chases and presumably provoked by them (LIND, in press). Flapping with the wings is almost exclusively seen after the performance of bathing movements and after chases, and cannot be considered as courtship activity. MILLAIS (1913) states that the tail at times may be raised during the courtship; I have only seen this at rest, sleeping, and preening.

Activities of the courted female. During courtship the female as a rule swims with the neck stretched upwards and with the head raised a little above the horizontal position (fig. 9), but she may also assume the normal swimming position.

Now and then she performs an "inciting" display oriented towards two males successively: she will swim behind a male (often the mate) in the Courtship Posture mentioned above, then she will stretch her neck aside and often a little backwards low over the water as in the Crouched Posture in the direction of a male that follows them and again, with a relatively slow movement, move neck-head forward and upwards to the initial position; or she may turn her neck forward, still in the Crouched Posture, and when the head points towards the male in front of her, she, in a slow movement, will raise her head to the vertical position without raising her neck, which at times may be completely immersed in the water (fig. 10). The head then is shaken while at the same time head and neck assume the normal position. The upward bending of the head may vary between 45° and 90° above the water. The turning of the neck towards the males may be accompanied by a turn of the body. Fairly often the female may perform the upward bending of the head from the Crouched Posture towards a male (e. g. the mate) without any preceding movement towards another male. v. HAARTMAN (1945) mentions a call originating from the female.

Courtship situations. The typical and most elaborate display occurs in the flocks, but also under other circumstances the males may perform courtship activities, thus a male who is swimming alone in the direction of or away from a displaying

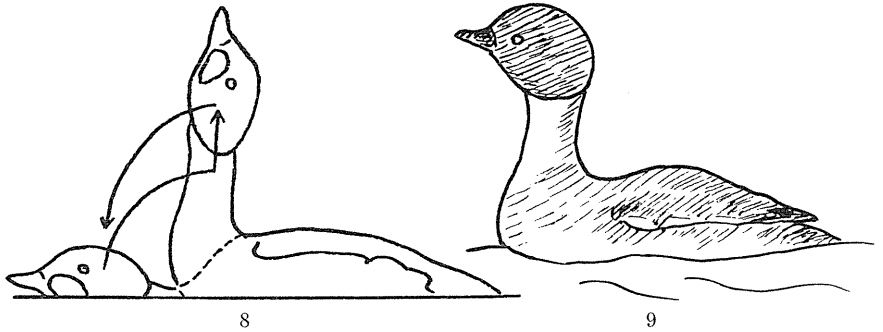


Fig. 8. The Crouched-up-down Movement. The arrows indicate the movement from the initial posture to the stretching of the neck and back.

Dukket-op-ned-posituren, pilene angiver bevægelsen.

Fig. 9. The Courtship Posture of the female.

Hun-positur i kurtiseringsspillet.

flock, or who is staying near by, and a male who is staying with or is swimming towards a pair. The male in the pair also makes courtship display. A single male may court a female with which it has not been paired (to judge from its behaviour before and after the courtship), or it may perform some displays belonging to the pre-copulatory behaviour. Finally a solitary male may perform Kick-throw I.

The frequency of one action in relation to the others varies from situation to situation. Even in the courtship flock one may have a greater tendency towards performing some definite actions than others. Thus the female often swims behind one definite male, at any rate for some time, and the other males come up behind them or beside them. Now and then the female may perform her inciting display near him. I have termed this male the leading male (occasionally he is apparently the mate of the female, but he need not be so). He is obviously in another situation than the other males and his behaviour also differs to some degree.

Partly in order to establish the variation of the behaviour of the males as being dependent on the situation, partly in order to provide a basis for a determination of the motivation of the courtship activities, a quantitative determination of them in a number of common situations was made. In each case one definite male was constantly watched, and all activities performed by it were recorded. In the flocks a male could

as a rule be followed for a short time only because of the divings. Enumerations were not made in flocks consisting of less than 6 males.

The results are grouped in Table I. The variation in behaviour from one situation to the other is evident and will be discussed below. Only a few remarks about some of the situations will be made here.

Situation A: When the flock is swimming fast forward, especially Snarl-throws I and II are seen, and to a certain degree Oblique Posture I as well. The first posture assumed by a male when he enters a flock is often Oblique Posture I. There is a tendency for males staying near the female to swim in Oblique Posture I and Snarl-throw II, and males swimming somewhat farther away mostly perform Snarl-throw I. Kick-throws I and II and the Crouched-up-down mostly are performed by males on the fringe of the flock, especially when the flock is stationary. Oblique Posture II is especially performed by males passing close to the female.

Situation C: The Kick-throws can be performed while the male is still as far as 20-30 metres from the flock, whereas Oblique Posture II is not assumed until he is less than one metre from the others.

Situation D: When a male is swimming away from the flock, a female may follow him, but I have never seen them to stay together. As a rule the male returns to the flock alone.

Situation E and F: When the strange male is 2-3 metres away from the pair, he generally changes swimming direction so that he does not head directly towards the others, or he stops completely. The male of the pair swims towards him. The female may also react to the strange male, rarely with Oblique Posture I, more frequently with the inciting display or only the Crouched Posture; the strange male falls back before her.

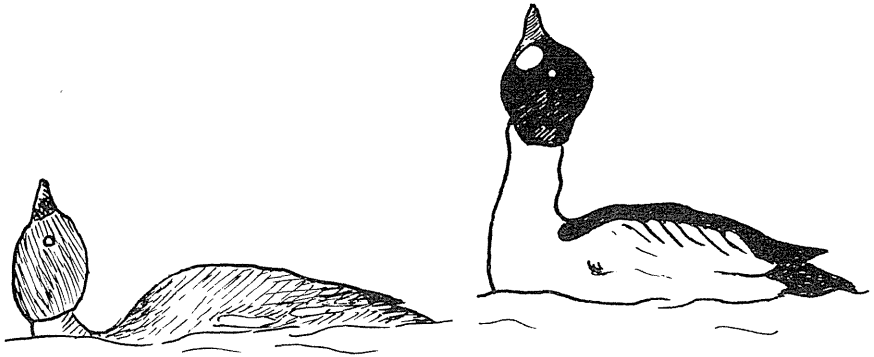
Situation H: The female shows no reaction to the male.

Table I includes quantitative determinations of the behaviour in another two situations, viz. prior to the copulation and prior to the flying-up.

Description of the behaviour before, during, and after copulation.

In March-April copulations can be watched at any time of the day, perhaps least in the evening. I have watched 16 complete matings and furthermore 28 cases in which the copulation or the introduction to it was interrupted.

Mostly the female takes the initiative, assuming the *Copulation Posture*. She lowers her head and stretches it for-



10

11

Fig. 10. The second part of the Inciting-display.
Anden del af Ophidsehandlingen.

Fig. 11. Vertical Drinking.
Lodret Drikke-positur.

ward in the surface of the water, then keeping it immovable in that posture. She lies deep in the water, exactly as in the Crouched Posture. If the male does not respond, or if his introductory display takes too long, the female may now and then raise her head and lower it again, or she may bend her head upwards. If the male swims away, the female may follow him in the Copulation Posture.

The male reacts to the posture of the female with an introductory ceremony, which may take several minutes. He will swim around the female at a distance of generally 30–60 cm, performing very definite activities:

Vertical Drinking: The bill is thrust into the water, after which the neck and head are stretched vertically upwards with a jerk (fig. 11). He maintains this posture for a moment (less than a second). The upward movement is not performed so fast as in the Crouched-up-down and Oblique Posture II. In the normal drinking movement the bill is only raised to 45–60°, in some cases perhaps to 90°, but then without stretching of the neck (it is often difficult to decide whether the drinking is normal). Only in the Zoological Garden the Goldeneyes would drink with complete stretching of the neck; but there most courtship activities could apparently be performed without any external cause. Repeated Vertical Drinking is no doubt identical with the “mehrmaligem Durchstrecken des

Halses", which by BERNHARDT (1940) is stated to occur as pre-copulatory display.

The *Wing-display* (GUNN 1939) is apparently performed exactly as the stretching of wing and leg. The bird holds head and neck, with feathers pressed close to the head, a little forward, while turning his body a little on one side, and stretching wing and leg on the opposite side backwards. The tip of the wing touches the water behind the bird, and the foot with spread toes is generally seen above the wing, but may also be held behind it.

GUNN (*l. c.*) has described this action as a particular display in the Goldeneye, but it does not appear clearly that it only occurs prior to copulation. BERNHARDT (1940) denies the significance of the action as display, but undoubtedly mistakes it for the wing-flapping occasionally occurring in the courtship.

Vertical Drinking and the Wing-display are performed several times at short intervals, alternating with one another and now and then with swift rubbing movements with the bill on the chest and with head-shaking.

As conclusion of the pre-copulatory display the male shows some activities which always follow quickly after each other and always in the same succession: the *Mock-preening Complex*. The bird lies laterally to or facing the female; 3-13 times he thrusts the bill and a small part of the head into the water and shakes it convulsively so that the water is splashed up (fig. 12a). At each shaking movement he moves backwards in the water, up to one metre during a bout of bill-dipping. The movements of the head in the water apparently have the same effect as the propeller of a ship. After the last bill-dipping the head is quickly moved backwards and the bill is put into the feathers on the back, where it is kept for only a fraction of a second. The wings are lifted a little from the back and as the head again is moved forward, the bill glides along the scapulars (or perhaps some of the secondaries), lifting them a little (fig. 12b). In direct continuation of this movement the neck is stretched upwards and a little forward at a jerk and the bill is tipped up in continuation of the neck. At the same moment the male rushes towards the female, often so quickly that the forepart of the body is raised out of the water (fig. 12c).

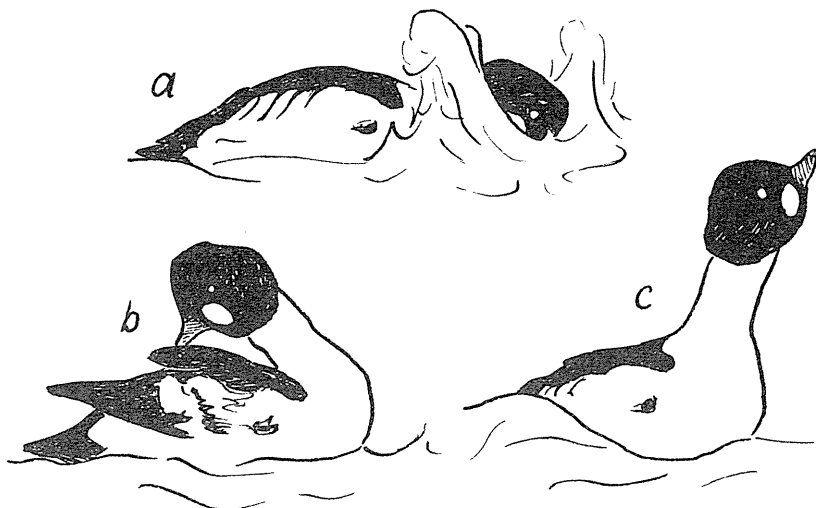


Fig. 12. The Mock-preening Complex. a. The Bill-dipping and -shaking. b. The Mock-preening. c. The final stretching of the neck.
De tre faser i Falsk-pilnings-komplekset.

The bill is fairly soon moved downwards to the horizontal position. The only variable in this sequence of activities is the number of bill-dippings.

Bouts of bill-dipping may occur together with Vertical Drinking and Wing Display, which are probably cases of an interrupted Mock-preening Complex. I have not seen interruptions at other stages of this display. The Mock-preening Complex is always followed immediately by an attempt to mount the female. Inversely, such an attempt never takes place without the preceding Mock-preening.

The copulation. As the male reaches the female, he bends down his bill. With retracted neck he immediately mounts her and catches her neck with his bill. Then he 1-6 times at short intervals makes a series of whirring movements with the wings, which are only a little held off the body. His tail may be raised and fanned. Then the copulation takes place. If the male does not succeed in taking hold of the nape of the female, the copulatory behaviour is immediately interrupted, the female gliding away under the male. As a rule the female then retains the Copulation Posture, and the male, who remains in the place, may again begin the introductory activities.

The presence of a strange male especially seems to have a disturbing effect on the female, who may chase him. The mate as a rule is passive. He continues the copulatory behaviour or swims away. The stranger performs courtship activities, especially the Kick-throw and may even show pre-copulatory behaviour.

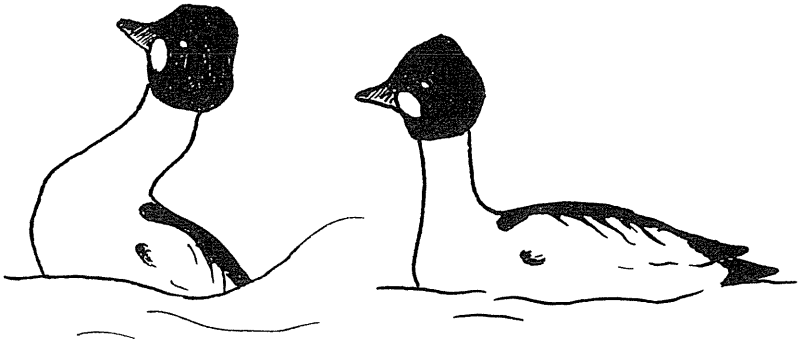
After copulation the male glides down to one side, and keeping his hold on the nape of the female, he pulls it upwards with the neck stretched and the head bent down. During this procedure the male turns his body away from the female, while she as a rule remains completely passive. The male lets go his hold and rushes off on the water away from the female, assuming the *Post-copulatory Posture* (fig. 13). The forepart of his body is raised and the hind part disappears completely in the water, which rises about the bird. The neck is stretched and curves back in sigmoid form. The bill points upwards at an angle of about 30°. After a few seconds he starts making some very swift turns of the head, more swiftly than in the courtship. When he has got 4–5 metres away from the female, he swims more slowly, and gradually the body assumes its normal position. In all cases observed the posture was the same. I have not seen that the neck could be retracted as pictured by MILLAIS (1913), nor directed forward as in the photo in BERNHARDT's paper (1940). Finally the male dives and/or makes a few bathing movements with subsequent wing-flapping. The female also bathes for a short while and with low intensity. In one case the male flew up followed by the female, and in another the male performed Kick-throw I and then bathing movements and diving.

The described termination of the copulatory behaviour only occurs when the copulation has been complete.

Introduction to the flying-up and the diving-away.

This will be described for the sake of the discussion of the activities mentioned above.

Prior to the flying-up the male Goldeneye turns in the direction of the wind and stretches his neck vertically upwards. The feathers are pressed slightly to the head and the bill is horizontal (fig. 14). At short intervals the head is shaken quickly. In between he may, like



13

14

Fig. 13. The Post-copulatory Posture.
Efter-parringsposituren.

Fig. 14. Attitude prior to flying-up.
Stillingen der går forud for opflyvning.

other ducks, stretch wing and leg (as in the Wing-display) and wings and neck, and shake his body. The relative frequency of these movements is indicated in Table I. While some birds in a flock slightly scared up behave as just described, it may happen that one performs Kick-throw I. This was seen particularly frequently in the Zoological Garden in the winter of 1957-58 when there were only two males.

In cases of disturbance, but also without apparent connexion with it, the Goldeneye may with neck and head make some movements which I have not seen in any other duck. With feathers pressed close to head and neck, the neck is held erect, the bill pointing upwards at an angle of about 15° . At short intervals the neck is jerked backwards so that the bill points upwards at an angle of about 45° , but without the nape touching the back, and then forward again without any stop in the hindmost position (fig. 15). The movement is accompanied by head-shaking when the neck is held vertically, and perhaps by a call. If a gradual relaxation does not occur, the *Head-jerking*, as the movement is to be termed here, is nearly always followed by diving, and is undoubtedly an exaggerated and ritualized intention movement to diving. Immediately prior to e. g. diving for feeding the head is often with a quick movement jerked a little upwards and backwards, and it is no doubt this movement which has been ritualized. In all diving the feathers are pressed close to the head. In two cases the neck was retracted more and more during Head-jerking, then the Crouched Posture was assumed, after which the bird dived. It appears that Head-jerking may introduce not only escape-diving, but aggressive diving as well.

Discussion of the ritualized behaviour patterns.

On the basis of an analysis of the ritualized activities it is to a certain extent possible to determine their origin. As pointed out by TINBERGEN (1952), many, perhaps all, forms of display are derived from displacement activities and intention movements. In the case of some activities this determination is very easy, as they are made almost exactly as their "examples" (TINBERGEN, *l. c.*), and the problem is first of all whether they are ritualized at all, *i. e.* whether they have got a signal function. As to other behaviour patterns, it is difficult, perhaps impossible, to determine their origin, as during the evolution they have changed considerably; some may be the evolutionary result of a combination of several different activities.

If the origin of the activities can be established, we may in this way learn about the motivation which originally determined the activities of the birds in the situation in question. Especially ritualized intention movements, but also to some extent the ritualized displacements, may give information about the original motivation. (The term displacement activity is used here about irrelevant activities which appear in situations in which one or more drives apparently have been thwarted or are in conflict, following the definition given by TINBERGEN (*l. c.*). See further p. 201).

However, the tendency or tendencies that originally determined an activity, need not determine this activity after ritualization has taken place (cf. LORENZ 1951). Therefore it is necessary to try to obtain a determination of the motivation of the ritualized activities.

In various species of birds it has been established that a sexual, aggressive, and escape tendency determines the courtship (TINBERGEN 1952, HINDE 1953, 1955, MOYNIHAN 1955). In these species the courtship often is directly connected with the copulation. In the case of the most ducks courtship and pre-copulatory behaviour are not identical. This does not, however, necessarily mean any qualitative difference in the causation of the courtship among ducks and other birds. It is no doubt simply connected with the fact that pair-formation (and courtship) among the ducks takes place in flocks and

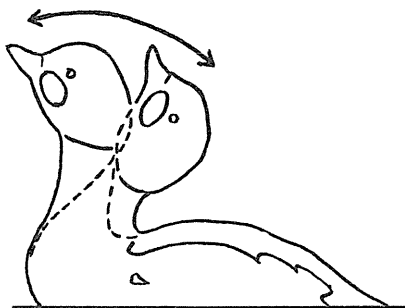


Fig. 15. Foremost and hindmost position in the Head-jerking. The arrow indicates the movement.

Forreste og bageste stilling i den ritualiserede bevægelse, der kan indlede dykning.

copulatory behaviour in pairs. Even though the tendencies of the male are the same in the two cases, the behaviour may be different because of quantitative differences in the various stimuli and perhaps because of ritualization. There may, however, be reason to discuss in some detail the motivation in the courtship of ducks (see further p. 207).

It must be supposed that the courtship originally arose in a situation corresponding to the present one, males gathered near a female. In such a situation there must in the males be partly an aggressive tendency, partly an escape tendency; this is clearly confirmed by the fact that in the present courtship attack and escape behaviour occurs in ritualized as well as unritualized form. Furthermore there must be a sexual tendency present, that which has attracted the males to the female. Indeed, there does not occur any sexual (*i. e.* copulatory) behaviour in the present courtship in contrast to attack and escape behaviour, but, as mentioned below and p. 207, this is fully understandable. It is characteristic of ducks that the courtship starts already in the autumn, which seems immediately to tell against the influence of the sexual tendency. Copulations, however, also may occur frequently in the autumn and winter, e. g. in the case of the Mallard (*Anas platyrhynchos*), which shows that the sexual tendency is present in these seasons. That there is a difference in time between the start of courtship and copulations (cf. WEIDMANN 1956) is in agreement with the fact that only a comparatively faint sexual

tendency is contributory in the courtship (p. 197). The occurrence of courtship activities in the post-copulatory behaviour of some ducks (cf. LIND 1958) also points towards the presence of the sexual tendency during the courtship. Furthermore, there occasionally in the courtship of the Goldeneye (especially in Sit. H, Table I) occur activities characteristic of the sexually dominated pre-copulatory display. It shows firstly, that a female evokes the sexual tendency in a strange male, and secondly, that this tendency will become strong and dominant during courtship only when no other males are present¹).

In the present courtship the males receive the same stimuli as originally produced the three tendencies in them, originating from the presence of other males and the female. There is no reason to suppose that these stimuli should not also now evoke the same tendencies, and to a much higher degree than now and then expressed in the unritualized attack and escape behaviour. The courtship performances must be the result of the three co-operative tendencies. The incessant variation in their mutual strengths has been expressed in ever varying activities, some of which must have been retained at the ritualization. The disconnected variation is characteristic of a ritualized course of activities in the case in question due to "typical compromise and intensity" (MORRIS 1957). Each of the ritualized activities must correspond to a definite combination of the three courtship tendencies. In the present Goldeneye courtship we also see a variation in behaviour dependent on the place of the bird in relation to the other males and the female, i. e. the ritualized courtship activities vary with the stimuli that will give rise to variation in the strengths of the attack, escape, and sexual tendencies.

Towards the immediate interdependence of various tendencies also points the disorderly mixture of the courtship activities of the Goldeneye. It does not seem possible to explain it as variation in the strength of one tendency, but rather as interplay of two or three.

¹) The pre-copulatory display of the *Aythya nyroca* male (always?) consists in typical courtship activities, and prior to copulation the *Aythya fuligula* male may first perform courtship activities (incl. a head-throw as in *A. nyroca*) and then the typical pre-copulatory display. In these species the participation of the sexual drive in the causation of the courtship activities is obvious.

When the three tendencies together determine the courtship, it might be expected that now and then, in situations which seem irrelevant for courtship performances, these would still appear, as the three tendencies "happen" to be present at the same time. Actually this is what happens, examples having been mentioned in the case of the Red-crested Pochard (*Netta rufina*) (LIND 1958). As to the Goldeneye, it may be mentioned that the paired male performs courtship activities when a strange male joins the pair. See also p. 201 and 207, and, with regard to the behaviour of the female, p. 204.

The problem now is that of determining the relative importance of the three tendencies in each ritualized activity. MOYNIHAN (1955, 1958) could determine the relation between attack and escape tendencies in the hostile behaviour of different gulls, but as to the courtship of the ducks a corresponding determination is more difficult because of the simultaneous co-operation of not two, but three tendencies, and of the high degree of ritualization. Therefore it should be emphasized that it can be made with great uncertainty, only.

In the case of the Red-crested Pochard (LIND 1958) it proved possible to make a very rough determination of the relation between the three tendencies on the basis of an analysis of the activities and their orientation. In the Goldeneye there is a resource more, viz. the variation in behaviour from one courtship situation to another. Through this we are informed not only of the original motivation, but of the present motivation as well. In each of these situations (cf. Table I) it must be supposed that there is a definite relation between the three tendencies (of course with some variation), as will be discussed below. If an activity tends towards particularly occurring in a situation in which it must be supposed that, for instance, the aggressiveness is greater than the sexual tendency, the motivation of this activity is probably to a greater extent aggressive than sexual.

Situation A: The strongest tendency in the males must be one of mutual aggression as in males of other species in the corresponding situation, e. g. in the Carolina Duck (*Lampronessa sponsa*) (LORENZ 1952), the Goosander (*Mergus merganser*), and the Shelduck (*Tadorna tadorna*). The escape tendency must necessarily also be present as a

consequence of the mutual aggressiveness. As the males not only react to one another but to the female as well (follow her without showing aggressive behaviour towards her), their behaviour must to some degree be sexually motivated. When the males do not swim fast, but only keep together around the female, the sexual motivation is possibly relatively greater. As unambiguous aggressive and escape behaviour is regularly seen, but never copulations or attempts at copulation, the sexual tendency, as in most other courtship situations, must be considerably slighter than the two others.

Situation B: As compared with A the escape tendency must be greater, as the male is followed by the female as well as the other males.

Situation C: As it must be assumed that the sexual tendency leads the male to the female and thus to the courtship flock, this tendency, although it is rather weak, must be predominant in relation to the weak aggressive and escape tendencies, which are due to the presence of the other males with the female. The nearer the male approaches to the flock, the greater importance the aggressive and escape tendencies will get.

Situation D: As the male does not show any escape behaviour, his behaviour must no doubt first of all be due to a decrease in the sexual tendency which attaches it to the flock. When he withdraws from the other males, the attack and escape tendencies will immediately decrease. This means that the sexual tendency, although weak, will become of relatively greater importance. That it continues to be present appears from the fact that the male often returns to the flock again. (The strength of the sexual tendency will vary rather slowly, as, in contrast to the attack and escape tendencies, it is mainly due to internal stimuli).

Situations E-F: The behaviour of the mated male will first of all be determined by the presence of the strange male and to a smaller degree to that of the female. The attack and escape motivation must be great, but also a sexual tendency will be present (it assists in connecting the mates, is increased periodically, and then manifests itself in copulation). The behaviour of the strange male, on the other hand, will be equally determined by the presence of the male and that of the female, and besides the attack and escape motivation a considerable sexual motivation will also be present.

Situation G: The motivational state of the male will be the same as in Situation C, perhaps with a somewhat slighter attack-escape motivation, as there is only one male near the female.

Situation H: In contrast to the case of the above-mentioned situations there are no other males that can increase the aggressiveness and the escape tendency in relation to the sexual motivation, which attracts the male to the female. On the other hand, the female will evoke both of these tendencies in the male, and to a somewhat higher degree than before copulation because of lack of mutual habituation.

As mentioned above, the pre-copulatory behaviour is probably due to an interplay of the same three tendencies as those determining the courtship. The difference between courtship and pre-copulatory behaviour must be due to a difference between the relative and in part also the absolute strengths of the three tendencies. The pre-copulatory behaviour in contrast to the courtship activities must be determined by a strong sexual tendency, partly because of internal, partly because of external stimuli (the Copulation Posture of the female). Furthermore, the attack and escape tendencies must be weak, and weak in relation to the sexual tendency, as only the close contact with the female (and not as in the courtship with other males as well) will evoke these tendencies in the male, and as copulation only takes place between the mates in a pair, the male is even accustomed to the female.

In what follows the origin and motivation of the ritualized activities are to be discussed on the lines indicated above. This discussion should be compared with the descriptions.

Oblique I is undoubtedly a ritualized intention movement forward, as shown very clearly in the repeated performance. In *Oblique II* this intention movement is combined with a drinking movement, which has been changed somewhat at the ritualization. As compared with a normal drinking movement the dipping is performed very rapidly and incompletely, and the forward movement, which is characteristic of the stretching of the neck, manifests itself already in this introductory movement.

The drinking movement is a very common displacement in ducks ("Antrinken", HEINROTH 1910) and is performed in situations in which it must be assumed that a simultaneous attacking and fleeing tendency plays a part, viz. when two or more ducks meet. This "Antrinken" is further ritualized in the *Oblique II*, indicating that attack and escape motivation is present. The forward directed intention movement is most probably aggressive; it is common in birds that the aggressive movement in intraspecific encounters is reorientated (cf. the orientation of the *Oblique*, p. 180). This means that *Oblique I* is more aggressive than *Oblique II*. However, the interrupted movement in the repeated performance of *Oblique I* shows a

conflict. Probably the importance of the aggressive tendency is only little stronger than that of the escape tendency. It appears from Table I that Oblique I is much more frequent than Oblique II, but in three situations (C, G, H) in which the sexual motivation plays a relatively greater part than in the others, the Oblique I only occurs rarely or not at all, and Oblique II is more frequent than it there. Thus the sexual tendency seems to play a greater part in Oblique II than in Oblique I. The same appears from a comparison of their occurrence in Situations E and F. The special occurrence of Oblique II in Situation C (cf. p. 187) shows the placement of this posture in a motivational respect between the sexually and little aggressively marked Kick-throw (p. 200) and the other courtship activities.

The origin of the *Snarl-throw* is difficult to determine. However, there can hardly be any doubt that one of the components in this activity is an intention to dive. This intention movement is just characterized by a throwing back of head-neck when the diving tendency is thwarted (p. 192). In the courtship such a thwarting is very probable.

The Goldeneye dives in three cases: when feeding, in escape behaviour, and as an introduction to an attack. The following arguments point towards the intention to dive in the Snarl-throw originally being connected with an aggressive tendency: (1) The Snarl-throw is performed when the bird is lateral to or facing other Goldeneyes, and particularly frequently when the males are swimming rapidly side by side, thus under circumstances which in birds often show reorientated aggression. (2) Particularly in the Zoological Garden a Snarl-throw was often followed immediately by the Crouched Posture

It also appears from Table I that the motivation of the Snarl-throw I is mainly aggressive. It occurs with greatest frequency in Situation A, in which the mutual aggressiveness between the males must be assumed to play a great part, and furthermore fairly frequently in B, E, and F. As compared with Oblique Posture I the escape tendency is possibly fairly inconsiderable; in the Snarl-throw there is thus no visible escape component. Furthermore the degree of activation is certainly greater in the Snarl-throw.

Snarl-throw I especially occurs when the males are swimming rapidly side by side. When the speed is increased no courtship activity takes place. Possibly the great aggressiveness between the males has been ritualized in the speedy forward swimming by stages, corresponding to a similar behaviour in the Mandarin Duck (*Aix galericulata*) (LORENZ 1952) and the Red-crested Pochard (LIND 1958).

In *Snarl-throw II* Oblique Posture I is combined with Snarl-throw I. This combination is not surprising, as both activities mainly are of an aggressive character. It might be expected that the relation between the strengths of the attack and escape tendencies in Snarl-throw II would be between that which characterizes each of the components of the activity. This is corroborated by the information in Table I at a comparison of the frequencies of the three activities in Situations A and B and in Situations E and F.

The backward movement of the head in the *Kick-throw* is no doubt of the same origin as that in the Snarl-throw, as is confirmed by the fact that in the Kick-throw there are further signs of checked diving. As a rule the Goldeneye dives without much effort, gliding directly into the water, but now and then the diving is introduced by a distinct stretching of the neck (ritualized in the Head-jerking and further in the Head-throw), after which the legs, when shoving off, splash a little water backwards, the hind part of the body is raised a little with lowered and fanned tail, and the forepart of the body simultaneously is pressed into the water. All these characteristics are found in the Kick-throw in more or less exaggerated form. Especially the splashing of water is highly exaggerated. The final stretching of the neck is performed as in Vertical Drinking, the two movements no doubt being of the same origin, in the Kick-throw only further ritualized by combination with the utterance of a call and the intention to dive. The introductory stretching of the neck in Kick-throw II reminds very much of that accompanying the Head-jerking and indicates an originally greater checking of the diving tendency in Kick-throw II than in I.

The two forms of the Kick-throw, as clearly appears from Table I, are to a higher degree determined by the sexual

tendency than the activities mentioned so far (especially frequent occurrence in Situations C, D, G, and H, and more frequent in F than in E).

Two facts suggest that in the Kick-throw there is a diving tendency marked by escape, in contrast to the Snarl-throw, which is marked by aggressiveness. (1) In contrast to aggressive diving, escape diving is very often performed with a slight leap and splashing of water. (2) The Kick-throw is rather often performed with the back turned towards other Goldeneyes, as never in the case of the Snarl-throw.

The causal difference between the two forms of the Kick-throw is uncertain. Table I gives a slight indication of a comparatively greater importance of the attack and escape tendencies in Kick-throw II (Situations D and H as compared with C and G). The same is suggested by the succession of the two forms performed by a male who approaches a flock (the attack and escape tendencies presumably become of increasing importance): in seven cases both forms were performed, and in six of these first one or more performances of Kick-throw I and then one or more of Kick-throw II. Only once the succession was the reverse.

Kick-throw I is the only courtship activity occurring together with the comfort-displacements in the behaviour introductory to flying-up (Table I). The cause of this seems evident. There is much to suggest that a displacement activity is activated through its own "centre" and not by a "sparking-over" in the nervous system, i. e. the activity which is most strongly activated after the dominant tendencies have been thwarted, is performed as a displacement (see e. g. BAGGERMAN *et al.* 1956, LIND, in press¹). Amongst other things for this reason displacements will often be forms of low intensity. In the Kick-throw, as compared with the other courtship activities, the three courtship tendencies, in the first place, are rather weak, secondly, the most important of them, the sexual tendency, is to a less degree dependent on external stimuli than the other two, and thirdly, the tendency towards escape is more pronounced than the aggressive tendency. Out of all courtship activities the Kick-throw therefore will stand the best chance of being activated when the tendency towards flying-up is thwarted. Furthermore, the Kick-throw may apparently go off in vacuum, which may be explained in a similar way (weak sexual tendency due to internal stimuli, combined with weak attack-escape

¹) In a recent paper by J. J. A. VAN IERSEL and A. C. ANGELA BOL (*Behaviour* **13**, 1958, p. 1-88) this is called the "disinhibition hypothesis".

tendency due to external stimuli; such stimuli, *e. g.* due to the presence of other Goldeneyes at some distance, are easily overlooked by the observer). V. HAARTMAN (1945) mentions that solitary males may perform courtship activities (it is not indicated which), and interprets them as vacuum activities.

The *Crouched Posture* is a threat posture, which is found in a similar form in other ducks. It is mostly followed by an aggressive dive, and this connexion undoubtedly has had a developmental influence on the Crouched Posture (body and neck deep in the water, the tail pressed downwards). As a threat posture the Crouched Posture is ambivalent (attack-escape); the varying lifting of the head is no doubt due to variation in the relative strength of the escape component, the horizontal position of the head indicating insignificant influence. This has not, however, been investigated in detail.

Strangely enough the purely hostile behaviour is fairly rare in Situation A. In E, on the other hand, it is rather frequent, as might be expected. Perhaps the purely hostile behaviour can only manifest itself when the sexual tendency becomes very weak (it must be supposed to be so fairly frequently in Situation E), and when the aggression momentarily becomes very strong.

One component in the *Crouched-up-down Movement* is the strongly aggressive variant of the Crouched Posture. The other component is probably a drinking movement. This is indicated by some similarity to Vertical Drinking and a great similarity to a ritualized drinking movement in the Goosander. Furthermore, the movement is introduced as in the case of normal drinking by the head being bent upwards, and only then follows the extreme stretching of the neck.

The Crouched component especially shows aggressive, but also escape motivation, as also indicated by the drinking component ("Antrinken"), although the attack and escape tendency here should be in equilibrium.

A comparison between the frequency of the Crouched-up-down in Situation E and F (Table I) shows that the sexual tendency probably also plays a part. It seems as if the causation of Oblique Posture II and the Crouched-up-down is the same, a combination of aggressive and escape tendency, the

former a little stronger than the latter, and some sexual tendency. However, it seems evident that there must be a difference.

The explanation perhaps is to be found in the above-mentioned fact that the courtship in spite of the ritualization is still dependent on "the external situation", in this case the distance from the courted individual. If two Goldeneyes are close to one another, an attack will be made by forward swimming and pecking with the bill, but if they are farther away from one another, it mostly takes place like this: Crouched Posture—diving—attacking from below. Intention movements for these two ways of attack seem to be components of respectively Oblique Posture II and the Crouched-up-down. The distance from the other individual thus would seem to determine which of the two activities is performed. Observations show that there is such a "difference in distance" between the two activities; cf. p. 187. Furthermore, the two males in Situation E-F are often 2-3 metres from each other, and the Crouched-up-down is only performed in such cases.

The *Head-bobbing* undoubtedly shows intention movements of escape; cf. the stretching of the neck in the introduction to the flying-up. No doubt it only appears by intense thwarting as in the courtship. Head-bobbing is possibly ritualized, but perhaps not as a special courtship activity.

The *head-shaking* that follows the performance of the courtship activities is undoubtedly a normal comfort movement. The isolated head-shaking (only such are included in Table I), on the other hand, is without doubt a displacement. In the courtship it has probably no releasing function, but the frequent occurrence immediately before flying-up (Table I) seems to show that in this situation it may be so (the form is unchanged).

In many ducks the *Body-shaking* is ritualized in the courtship, e. g. in the Sheldduck, the Mallard (LORENZ 1952) and the Goosander, but in the case of the Goldeneye it is rather uncertain. It is performed as the normal shaking movement, and the frequency is not higher than might be expected for an unritualized displacement of the comfort type. There is, however, a suggestion of slight ritualization, as it now and

then is performed by several males in rapid succession; but this is rare.

Most of the behaviour of the female is characterized by escape, as she swims or dives away from the males. Also the *Courtship Posture* of the female is undoubtedly mainly due to escape motivation, as the positions of head and neck partly remind of those assumed by a Goldeneye that is chased by another, partly about that accompanied by head-jerking and preceding diving. The way in which the posture is retained for prolonged periods, suggests ritualization.

The *Inciting* shows great similarity to a corresponding behaviour in other ducks (e.g. LORENZ 1951, 1952). It consists of a threat part (the Crouched Posture, mainly aggressive) orientated towards a strange male and a second part orientated towards (mostly) the mate. This second part is obviously determined mainly by escape motivation. It is either the Courtship Posture (see above) or the extreme upward bending of the head. The origin of this movement is without doubt the Crouched Posture characterized by escape. Transitional forms between the normal and the exaggerated form can be seen. In the Red-crested Pochard the slightly ritualized inciting display also includes a distinct escape component (LIND 1958). The sexual tendency also is determinative of the Inciting, as the female not only evades the strange male, but moves towards the mate (or another male).

As only the latter part of the Inciting is concluded by head-shaking, the two parts at the ritualization seem to have been combined into one activity (cf. p. 179). The latter part, however, may occur independently of the threat part. The Inciting causally and probably functionally as well corresponds to the courtship activities of the male. The upward bend of the head which the female may perform in the Copulation Posture (p. 188) perhaps is part of the Inciting. It is performed when the sexual tendency is being weaker, and probably the relation between the three tendencies reaches the same stage as during the courtship.

The similarity between the *Copulation Posture* of the female and the Crouched Position perhaps is only superficial, but the possibility cannot be rejected that the Copulation Posture is

ambivalent, consisting of a position advantageous to the copulation determined by sexual motivation and of the Crouched Posture determined by attack and escape motivation.

Vertical Drinking is undoubtedly a further ritualized "An-trinken", and like that determined by attack-escape motivation in conflict, but furthermore by a considerable sexual tendency, as appears from the frequent occurrence in the introduction to the mating.

The *Wing-display* is also in origin a displacement activity. The frequent occurrence in the pre-copulatory display shows that it is ritualized. It has not been possible to determine any difference in motivation between Vertical Drinking and the Wing-display.

The shaking of the head and the rubbing of the breast in the pre-copulatory display are presumably unritualized displacements (cf. the frequency shown in Table I).

The introductory bill-dipping in the *Mock-preening Complex* is probably an exaggerated performance of the bill-dipping that accompanies normal preening. The subsequent backward stretching of neck-head is a displacement preening movement corresponding to the "Mock-preening" in other ducks. Many ducks (e.g. LORENZ 1952) put the bill behind the raised wing, whereas the Goldeneye only puts it into the mantle feathers, and the same applies to the Red-crested Pochard in the pre-copulatory display. In the latter species it is accidental whether some feathers are lifted by the bill when it is moved forward again, but in the Goldeneye it has become an integral part of the Mock-preening.

It is difficult to determine the origin of the extreme stretching of the neck that concludes the Mock-preening Complex. It does not seem probable that it should be an exaggerated form of an intention movement to the mounting of the female, as it follows immediately in the normal form, i.e. as among other ducks. The stretching of the neck and the position of the bill, on the other hand, has a resemblance to a drinking movement, which in other ducks (e.g. LORENZ *l.c.*) may be linked to a Mock-preening movement. It is not surprising that the introductory bill-dipping in the drinking movement has disappeared at the ritualization, as there has been a develop-

ment in the same direction in Oblique Posture II. The stretching of the neck shows a considerable similarity to that found in the Oblique Postures. This is no doubt due to the fact that in the Mock-preening Complex as well a forward intention movement is included, but in this case determined by the sexual, not the aggressive, tendency. As the Mock-preening Complex always immediately precedes the copulation, there can be no doubt that it is strongly sexually motivated, but the origin in displacements shows that the inhibiting influence from the attack-escape tendency still asserts itself.

The *copulation* differs from the ordinary type in ducks by the whirring movements of the wings, which originally may have served the male to keep his balance, but the present stereotyped performance suggests ritualization. Possibly a certain aggressiveness was originally admixed in the sexual behaviour, *viz.* pecking in the direction of the female's head. The male's hold on the female's nape now seems to be necessary for the copulation, either by having a stimulating effect on the female, or by keeping her head above the water.

The *post-copulatory behaviour* of the male shows a distinct conflict situation. At the same time as the position of the body and perhaps the stretching of the neck show intention to swimming away, he still holds on to the female with his bill. This reminds much of the behaviour of the Mallard in the same situation (LORENZ 1952). The subsequent behaviour is greatly characterized by escape, as only the escape tendency can be responsible for (1) the swift swimming away from the female, (2) the turning of the head, which at any rate in some cases is real head-flagging ("Hinterkopf-zudrehen", LORENZ 1941), (3) the final dive or flying-up. In the Red-crested Pochard and perhaps in the Mallard as well the corresponding behaviour is mainly of an aggressive character (LIND 1958). The Post-copulatory Posture, however, is not determined by the escape tendency alone. The bending of the neck shows that the motivation (sexual or perhaps aggressive) which determines the male's hold on the female's nape, is present to begin with. A sexual tendency rapidly decreasing in force must at any rate play a role. The position of the body is due partly to the conflict between the tendencies and partly to the quick strokes in

swimming, but there is no doubt that by ritualization it has been highly exaggerated. Only once a courtship activity was observed; as might be expected, it was the Kick-throw, which especially is determined by the sexual and the escape tendencies. The reason why courtship activities do not regularly occur in the post-copulatory behaviour (cf. p. 195), is probably that no courtship activity is determined by so comparatively great an escape tendency as that found in the male after the copulation.

In contrast to the courtship the pre-copulatory behaviour of the male exclusively consists of displacement activities, ritualized and unritualized; only in the very last activity performed an intention movement is included. There is reason to consider this fact more closely. As stated above, it must be assumed that the sexual tendency in the pre-copulatory behaviour is strong and dominant, which involves that the aggressive and escape tendencies have no chance of being expressed directly, not by intention movements either. Obviously sexual behaviour can only take place when the male is in contact with the female. Until then the sexual tendency, in spite of its dominant role, can only manifest itself in a movement towards the female, first inhibited, therefore as a circling course round the female, later directed towards the female in an intention movement ambivalent with the final drinking movement in the Mock-preening Complex, and at last as a forward swimming directly towards the female. Therefore, it is understandable that the sexual tendency does not in the courtship manifest itself in sexual behaviour, either. The only behaviour in the courtship which can be ascribed to the sexual tendency, is the search for the female. Possibly it influences the orientation of some of the courtship activities, and perhaps it partly determines the turns of the head.

As mentioned above, the ritualized activities in the courtship and the pre-copulatory behaviour must be determined by a combination of attack, escape, and sexual motivation. The motivation of the displacements is completely changed. They were probably originally determined by their "normal" motivation (cf. p. 201), but now they are determined by the motivation in the conflict situation, which originally gave rise to the

activization of them. The motivation of the intention movements has only in part been changed. They were originally determined by an attack and/or escape tendency, now probably by all the three tendencies present.

The pair-formation function of the originally purely hostile behaviour patterns (including displacements) has developed parallelly to the connexion with the sexual motivation.

As mentioned above with reference to the Kick-throw, and as also seems to appear from the deviating descriptions in the literature, there may be some variation in the combination of the components of the ritualized activities. The ritualization involves that a minor change in the strength of one of the three courtship tendencies does not apply to the form of the activity (cf. p. 195). This is indicated directly by the complex origin of *e.g.* the Kick-throw and the Crouched-up-down, as an original sequence of activities corresponding to a change in motivation during the evolution is concentrated into one act. Only in case of a greater change there will suddenly appear quite a different act. Apparently there may be ritualized transitional forms, thus Snarl-throw II between Snarl-throw I and Oblique Posture I. Probably an "accidental" mixed form or another variation of the activity may appear when the motivation ratio is being shifted from that which determines one activity to that which determines another. Even though the courtship of the Goldeneye includes several highly ritualized activities, the variations in form as well as occurrence seem to indicate a generally less pronounced ritualization of the courtship patterns than is the case *e.g.* in the surface-feeding ducks.

In two cases pre-copulatory behaviour (including the Mock-preening Complex) was observed to occur alternating with courtship activities: (1) In a male coming to a pair that showed pre-copulatory behaviour (p. 191). (2) One of the two males in the Zoological Garden (in 1958) would now and then show typical pre-copulatory behaviour towards the other male, these behaviour patterns then alternating with Kick-throw, Crouched-up-down, and Oblique Postures; this presumably does not happen under natural conditions. In both cases a comparatively strong attack-escape tendency (as in the courtship) met with a comparatively strong sexual tendency (as

in the pre-copulatory ceremony). In (1) the sexual tendency was increased because of the behaviour of the pair, no doubt especially the behaviour of the female, and in (2) it was increased by accumulation (no female in the pond). The conditions of a mixture of the activities thus were present. The courtship performances are especially such as are marked by a rather strong sexual tendency. In Situation H (Table I) a similar mixture takes place.

The occurrence of threat-posture, attacking and fleeing behaviour in the courtship is undoubtedly due to the fact that the motivation ratio becomes another than the one characterizing the courtship activities as a whole. The copulation is an analogical case (cf. LIND 1958).

Table II includes the determinations of the origin and motivation of the activities in question. These determinations are not, of course, accurate, but may contribute to an attempt at obtaining a closer understanding of the complicated behaviour of the ducks, especially the Goldeneye, in the early state of the reproductive cycle. In the table each component of an activity (displacement and intention movement or perhaps a complete action) is indicated by a cross. The relative importance of each motivation component is indicated by a rough number increasing from 0 to 10. Thus the degree of activation has not been considered. The activities have been divided into the following groups: I. Accompanying activities in the courtship. II. The courtship activities proper of the male. III. Activities of the male before, during, and after the copulation. IV. Behaviour patterns of the female.

The function of the ritualized activities has only been touched on in what precedes. Therefore some remarks should finally be made on this problem.

Probably the intensely coloured feet function as releasers in the Kick-throw, as assumed by TOWNSEND (1910), just as the very splashing of water may be of importance.

If the colour of the foot acts as a releaser in the Kick-throw, it is natural to assume that the same is the case in the Wing-display, in which it is displayed still more distinctly and often is held above the wing so that it can be seen by the female. This assumption is supported by the fact that the sexual motivation is of fairly great importance in both foot-displays, even though similarity in causation need not involve similarity in

TABLE I. The relative frequency of the activities of the Goldeneye male (exclusive of the Mock-preening Complex), and *Den relative hyppighed af de handlinger, hvinandhannen udfører i 8 kurtiseringssituationer (A-*

Situation		Number of individuals observed <i>Antal iagttagne individer</i>	Number of activities recorded <i>Antal registrerede handlinger</i>	Number of records in <i>Antal registreringer i</i>				
				Kick-throw I <i>Spjætkast-I</i>	Kick-throw II <i>Spjætkast-II</i>	Snaul-throw I <i>Snerrekast-I</i>	Snaul-throw II <i>Snerrekast-II</i>	Oblique Pos. I <i>Skrå-pos.:I</i>
In the court-ship flock <i>I kurtiserings flokken</i>	A. ♂ following der følger	80	418	9,3	6,1	41,9	14,1	7,4
	B. ♂ leading der fører	12	107	10,3	49,5	31,8
C.	♂ swimming towards the flock der svømmer med flokken	23	66	48,5	33,3	1,5
D.	♂ swimming away from the flock der svømmer bort fra flokken	12	24	70,8	25,0
♂ + pair ♂ + par	E. The mated ♂ Den parrede ♂	25	108	0,9	1,8	19,4	25,9	32,4
	F. The strange ♂ Den fremmede ♂	33	113	15,9	3,6	10,6	8,0	22,1
G.	♂ swimming towards a pair der svømmer mod et par	9	20	50,0	35,0	5,0
H.	♂ by unmated ♀ hos uparret ♀	13	30	33,3	10,0	3,3
Introduction to copulation <i>Indledning til parring</i>		22	213
Introduction to flying-up <i>Indledning til opflyvning</i>		24	93	4,3

function. GUNN (1939) assumes, perhaps justly, that the colours on the upper side of the stretched-out-wing are releasers in this display (therefore the term Wing-display). It is adduced in support of this assumption that the male in most cases stretches wing-leg of the side turned away from the female. As the bird under the activity tips over towards the opposite,

in 8 courtship situations (A–H), in the pre-copulatory behaviour in the behaviour introducing the flying-up.

H), i før-parringsspillet (undtagen Falsk-pilnings-komplekset) og i indledningen til opflyvning.

percentages of the total number of activities recorded in each situation.
procent af det samlede antal handlinger, der er registreret i hver situation.

Oblique Pos. II <i>Skrå-pos. II</i>	Crouched-up-down <i>Dukket-op-ned-pos.</i>	Body-shaking <i>Krop-ryst</i>	Crouched Pos. and chasing <i>Dukket-pos. og jagning</i>	Head-shaking <i>Hovedryst</i>	Vertical Drinking <i>Lodret-drik</i>	Wing-display and wing-stretching <i>Vinge-pos. og -strækning</i>	Rubbing the breast <i>Gnidning af brystflæene</i>	Bout of Bill-dipping <i>Næbdypnings-udbrud</i>	Stretching of neck and wings <i>Strækning af hals og vinger</i>
5,3	2,6	4,1	1,2	7,7	0,2
0,9	..	0,9	1,9	4,7
6,1	1,5	3,0	1,5	4,6
..	..	4,2
3,7	..	0,9	11,1	2,8	0,9
11,5	11,5	1,8	2,7	6,2	4,4	1,8
5,0	5,0
6,7	3,3	20,0	23,3
..	10,3	47,9	25,3	7,5	8,9	..
..	..	13,9	..	72,0	..	7,5	2,2

he thus displays the upper side of the stretched-out wing. This is not, however, in agreement with my observations. In a total of 57 checked cases the stretching was only 23 times performed on the side turning away from the female, but 34 times on the other side, which turned towards her. As the foot at any rate in the great majority of cases is held above the wing,

it can in contrast to the upper side of the wing be seen whether the stretching takes place on one or the other side. Probably the stretching of wing-leg from being an unritualized comfort displacement has developed into a display just because the foot is displayed so distinctly. Secondly the wing may have obtained a releasing value as well.

It seems probable that the function of the Kick-throw, which is performed when the male swims away from the courtship flock, is that of increasing the sexual tendency in the female and directing it towards the male in question. In this way pair-formation might be brought about. Observations have only in part been able to corroborate this hypothesis (cf. p. 187). The function of the Wing-display will probably also consist in an increase of the sexual tendency in the female (to secure complete copulation).

The white spot on the cheek of the male is of course always prominent, but perhaps is especially displayed in the Oblique and the threatening Crouched Posture (p. 184).

The Snarl-throw and Oblique Posture I have a clearly stimulating effect on the males mutually, as they very often are infectious. It is not surprising that these very activities synchronize the behaviour of the males. Both of them are mainly aggressively motivated, and the aggressive tendency in the courtship is first of all due to the presence of other males. Furthermore, they may of course have a stimulating influence on the female as well.

At any rate two courtship activities are accompanied by a call, *viz.* the Snarl-throw and the Kick-throw. The former is always made in the flock and the sound is always soft, while the latter often is made at a considerable distance from other Goldeneyes and the sound correspondingly is loud.

During the pre-copulatory ceremony the male lies laterally to the female or turned a little towards her. Perhaps the bill-dippings during which the bird moves backwards in the water, is of importance by carrying the male somewhat away from the female, without the escape tendency or decreasing intensity necessarily coming into play. After the Mock-preening the male rushes towards the female and the display posture can the better assert itself the longer it is maintained, *i. e.* the longer

TABLE II.

Origin and motivation of the early reproductive behaviour patterns of the Goldeneye (see text p.209).

De tidligt forekomm. yngledriftshandlingers oprindelse og motivation hos hvinanden.

		Origin oprindelse					Motivation		
		Displacement Oversprings- handling		Intention movement of Intentions- bevægelse til					
		Comfort act. Ryste- strækte- og pilnings- handling	Drinking movement Drikkebev.	Attack Angreb	Escape Flugt	Copulation Parring	Attack Angreb	Escape Flugt	Sexual Parrings-
I	Crouched Pos. <i>Dukket-pos.</i>	×	×	..	5	5	0
	Chasing <i>Jagning</i>	×	10	0	0
	Fleeing <i>Flugt</i>	×	..	0	10	0
	Head-bobbing <i>Lodret-hovedryk</i>	×	..	?	6	?
	Head-shaking <i>Hovedryst</i>	×	0	0	0
	Body-shaking <i>Kroppryst</i>	×	?	?	?
II	Snarl-throw I <i>Snerrekast-I</i>	×	7	2	1
	Snarl-throw II <i>Snerrekast-II</i>	×	×	..	6	3	1
	Oblique Pos. I <i>Skrå-pos.-I</i>	×	5	4	1
	Oblique Pos. II <i>Skrå-pos.-II</i>	..	×	×	4	3	3
	Crouched-up-down <i>Dukket-op-ned-pos.</i>	..	×	×	4	3	3
	Kick-throw II <i>Spjætkast-II</i>	..	×	..	×	..	2	4	4
	Kick-throw I <i>Spjætkast-I</i>	..	×	..	×	..	1	4	5
III	Vertical Drinking <i>Lodret-drik</i>	..	×	2	2	6
	Wing-display <i>Vinge-pos.</i>	×	2	2	6
	Mock-preening C. <i>Falsk-pilnings-k.</i>	×	×	×	1	1	8
	Copulation <i>Parring</i>	?	..	×	?	0	?10
	Post-copulatory Pos. <i>Efter-parrings-pos.</i>	?	×	?	?	8	?2
IV	Courtship Pos. ♀-pos.	×	..	1	8	1
	Inciting <i>Ophidsehandling</i>	×	×	..	4	4	2
	Copulation Pos. <i>Parringsstilling</i>	?	?	×	?	?	?10

the distance covered. The bill-dipping thus indirectly gives prominence to the posture shown later.

It is a well-known fact that the courtship as a whole must have some function in the pair-formation and that the pre-copulatory behaviour serves the performance of the copulation. The function of the post-copulatory behaviour, on the other hand, is unknown. The exaggerated performance of this behaviour in the Goldeneye suggests that it includes optical releasers, which must be directed towards the female. As the post-copulatory behaviour forms a transition between a period with intense activation of the sexual, aggressive, and escape tendencies and a period of "peaceful coexistence" of the mates, there is a possibility that it functions as a re-pairing display. This is corroborated by the fact that the post-copulatory behaviour in some other ducks (LORENZ 1952, LIND 1958) includes courtship activities.

Postscript.

In March-April 1959 some notes were made on the calls of the Goldeneye (2 ♂♂ and 6 ♀♀) in "Tierpark Hellabrunn", München.

Being together the males repeatedly utter an apparently hostile call reminiscent of the Snarl-call, but fainter and shorter. The same call may be uttered in Oblique I and II and a stronger variant may replace the Snarl-call, being repeated 2-3 times during the head-throw.

A call of a somewhat different timbre and similar to the last part of the Kick-throw call, but fainter, always accompany the stretching of the neck in the Crouched-up-down and now and then the Oblique II. The same call is uttered during the final stretching of the neck in the Mock-preening Complex (only one record). It seems that the probably strongly ritualized drinking movements are all accompanied by the same type of call. Vertical Drinking, which is only a little changed at the ritualization, is silent.

The inciting female may utter a faint *eeuu* during the upward bending of the head.

DANSK RESUMÉ

Hvinandens (*Bucephala clangula* (L.)) pardannelses- og parringsadfærd.

Fra slutningen af marts til midten af april 1958 iagttoges dagligt de hvinænder, der holdt til på vandet umiddelbart nordvest for Tipperne. I denne periode forekom meget hyppigt kurtiserings- og parringsspil. Nogle observationer kunne udføres på nært hold i Zoologisk have i København i vinteren 1956-57 og 1957-58.

Kurtiseringsspillet, der formodentlig leder til pardannelse, foregår typisk i flokke bestående af 1–2 hunner og flere hanner, men desuden også i andre situationer, således når en han kommer til et par (begge hanner udfører kurtiseringshandlinger), når en han nærmer sig til eller fjerner sig fra en flok eller et par, når en han kommer til en fremmed hun, og endelig nu og da hos enlige hanner tilsyneladende uden ydre foranledning. Hunnerne udfører også karakteristiske handlinger og bevægelser, men kun få i sammenligning med hannerne. Oftest svømmer eller dykker hunnerne bort, fulgt af hannerne. Til tider svømmer en han foran hunnen og dermed i spidsen for hele kurtiseringsflokken.

I parringsspillet, der foregår i direkte forbindelse med parringen og betinger dennes gennemførelse, udfører hannen ligeledes karakteristiske handlinger forskellige fra kurtiseringshandlingerne, medens hunnen ligger stille i parringsstillingen. Efter parringen svømmer hannen bort i en særlig positur.

Alle disse ritualiserede handlinger og positurer beskrives, og der foretages såvidt gørligt en bestemmelse af deres oprindelse, deres motivation (d. v. s. de tendenser eller drifter, der fremkalder dem) og i nogle tilfælde deres funktion i de ritualiserede handlingsforløb.

Oprindelsen undersøges ved en analyse og i nogle tilfælde ved en sammenligning med andre ænder.

Motivationsbestemmelsen er vanskeligere. Der fremføres argumenter for den antagelse, at såvel kurtiserings- som parringsspillet fremkaldes af samtidigt tilstedeværende angrebs-, flugt- og parringsdrift (ved parring forstås kopulation og ikke pardannelse). Den årsagsforskelle, der nødvendigvis må være, er af kvantitativ og ikke kvalitativ art, d. v. s. den beror på væsentlige forskelle i disse drifters indbyrdes styrkeforhold såvel som i deres absolutte styrke.

Oplysninger om de enkelte handlingers motivation fås først og fremmest fra deres oprindelse, deres orientering og deres relative hyppighed i de forskellige kurtiseringssituationer (tabel I). Forudsætningen for den sidstnævnte metode er antagelsen af, at styrken af de tre drifter i hver af disse situationer gennemgående står i et bestemt forhold til hinanden forskelligt fra de styrkeforhold, der forefindes i de andre situationer, og afhængigt af de situationsspecifikke stimuli.

Tabel II sammenfatter bestemmelserne af de behandlede handlingers oprindelse og motivation. Oversprings- og intentionsbevægelser, der indgår i handlingerne, er angivet ved kryds, og driftstyrken ved en grov talangivelse stigende fra 0 til 10. Der er kun taget hensyn til den relative driftstyrke.

Hannens kurtiseringshandlinger:

I Skrå-positur-I (fig. 2) holdes halsen skråt fremad-opad, eller rykkes gentagne gange frem til denne stilling og tilbage (fig. 3). Positionen udgøres af en sandsynligvis aggressiv intentionsbevægelse. I Skrå-positur-II indgår desuden en drikkebevægelse, idet næbbet føres frem lavt over vandet og til tider berører dette, inden det løftes til

skråstillingen. I begge positurer er angrebsdriften stærkest; parringsdriften spiller en relativt større rolle i positur II end i I.

I Snerrekast-I (fig. 4) kastes hovedet langt tilbage over ryggen, og der udstødes i denne stilling en svag, snerrende lyd, hvorefter hovedet atter slynges frem. Dette hovedkast er sandsynligvis opstået af bl. a. en aggressiv dykkeintention. En noget lignende bevægelse forekommer som ritualiseret dykkeintention uden for kurtiseringsspillet (fig. 15). Angrebsdriften er stærk i Snerrekast-I. I Snerrekast-II er samme bevægelse koblet til Skrå-positur-I, og flugtdriften spiller en lidt større rolle end i Snerrekast-I.

Spjætkast-I udføres i tre faser som vist i fig. 5. I anden fase sprøjtes vandet bagud, idet fødderne slynges op over vandet. Sandsynligvis virker såvel føddernes farve som vandsprøjtet som udløser, der kan være særligt virksomme ved pardannelsen ved at øge hunnens parringsdrift. I tredje fase udstødes en kraftig todelte lyd. Parringsdriften spiller en relativt stor rolle i Spjætkast-I, omend den absolutte styrke formodentlig er ret lille; flugtdriften er større end angrebsdriften. Spjætkast-II (fig. 6) indledes med halsstrækning, og halsen lægges længere tilbage over ryggen, men er ellers som foregående. Muligvis spiller angrebs- og flugtdriften her en lidt større rolle. Begge Spjætkast er afledt af en flugtpræget dykkeintention koblet til en drikkebevægelse.

Dukket-positur (fig. 7) har truefunktion og indtages af både han og hun og også uden for kurtiseringsspillet. Den er altså kun bestemt af angrebs- og flugtdrift. I posituren indgår en aggressiv dykkeintention. De hvide kindpletter er muligvis udløser, og samme funktion har de sikkert i Skrå-positurerne.

I Dukket-op-ned-posituren (fig. 8) er en sikkert stærk aggressiv variant af trueposituren koblet til en overdrevet drikkebevægelse: Først indtages en vandret truepositur, så strækkes hals-hoved til lodret og smækkes atter lynhurtigt ned i truestillingen. Handlingen bestemmes af tilsyneladende samme motivation som Skrå-positur-II, men i denne indgår der en intention til aggressiv fremadsvømning, i Dukket-op-ned derimod en intention til aggressiv dykning. Afstanden til andre hvinænder bestemmer, hvilken af de to handlinger der udføres.

I kurtiseringsspillet kan hannen rykke hovedet hurtigt op og ned i sandsynligvis en intentionsbevægelse til opflyvning, men der er sikkert ikke tale om nogen speciel kurtiseringshandling. De ret hyppige hovedryst er sikkert uritualiserede overspringsbevægelser, som dog kan optræde som et ritualiseret opflyvningssignal (tabel I). Kropryst er muligvis svagt ritualiseret.

Hunnens reaktion på hannernes kurtisering:

Den kan nu og da angribe hannerne (det omvendte sker ikke), men indtager oftest en stærk flugtpræget positur (fig. 9). Desuden kan den lave en »Ophidseshandling«, der består i en truepositur rettet mod

een han, efterfulgt af en anden positur rettet mod en anden han (oftest magen); hovedet løftes i denne positur til lodret, idet halsen stadig holdes lavt (fig. 10). Ophidsehandlingen er først overvejende aggressivt præget, derefter overvejende bestemt af flugt- og parringsdrift.

Hunnens parringsstilling viser muligvis en vis ambivalens med Dukket-positur.

Hannens parringsspil:

Lodret Drikke-positur (fig. 11) og Vinge-positur er begge oprindeligt overspringsbevægelser, førstnævnte en drikkebevægelse og sidstnævnte en strækkebevægelse. De er begge tydeligt ritualiseret og nu overvejende bestemt af parringsdriften, men sandsynligvis også af nogen angrebs- og flugtdrift p. gr. a. hunnens tilstedeværelse. I Vinge-posituren er foden sikkert særlig virksom som udløser (seksuelt stimulerende).

Disse to positurer udføres gentagne gange og alternerer med sandsynligvis uritualiserede overspringsbevægelser som hovedryst og gnidning af brystfjerene med næbbet.

Til sidst udføres Falsk-pilnings-komplekset (fig. 12): Først laves flere næbdyp og -ryst, hvorved fuglen rykker baglæns i vandet, derefter stikkes næbbet i rygffjerene, og idet det føres frem igen, løftes nogle vinge- eller skulderfjer. Den hurtige fremadbevægelse slutter i en strakt stilling, samtidig med at fuglen farer hurtigt frem mod hunnen. De første dele af komplekset er afledt af pilningsbevægelser i overspring, sidste del muligvis af en drikkebevægelse. Parringsdriften når i denne parringsspilhandling, der altid efterfølges af parring eller forsøg herpå, maximal indflydelse. De indledende næbdyp og -ryst har tilsyneladende betydning ved at bringe fuglen lidt bort fra hunnen, så den afsluttende positur kan fastholdes længere tid.

Under parringen bider hannen sig fast i hunnens nakke, hvilket er nødvendigt for parringens gennemførelse; det har muligvis en aggressiv oprindelse. Desuden udfører hannen serier af svirrende vingslag, oprindeligt sikkert af balancehensyn, nu uden tvivl med stimulerende betydning.

Efter-parringsposituren (fig. 13) er stærkt flugtpræget og har muligvis funktion som et genpardannelsesspil. Hos nogle andre ænder forekommer der kurtiseringshandlinger i den tilsvarende situation, men hos hvinanden forefindes ingen næsten eensidigt flugtpræget kurtiseringshandling svarende til den stærke flugttendens hos hannen efter parringen.

Ritualiseringsprocesserne har sandsynligvis medført følgende: Nårsomhelst angrebs-, flugt- og parringsdrift er tilstede samtidigt hos en hvinand, kan fremkaldes kurtiserings- eller parringsspilhandlinger. Er parringsdriften stærk og stærkere end de andre to drifter, udføres parringsspil, er parringsdriften svag, udføres kurtiseringspil. Enhver af disse handlinger svarer til et bestemt motivationsforhold,

der dog kan variere inden for snævre grænser. Atypiske handlinger eller blandingsformer vil muligvis kunne fremkomme, når motivationsforholdet ændres fra det, der bestemmer een handling, til det, der bestemmer en anden. Bortfalder parringsdriften, udføres kampadfærd, bortfalder angrebs- og flugtdriften udføres parring.

Literature.

- BAGGERMAN, B., BAERENDS, G. P., HEIKENS, H. S. and MOOK, J. H. 1956: Observations on the behaviour of the Black Tern (*Chlidonias niger*) in the breeding area. – *Ardea* **44**, p. 1–71.
- BERNHARDT, P. 1940: Beitrag zur Biologie der Schellente (*Bucephala clangula*). – *Journal f. Ornith.* **88**, p. 488–497.
- BOASE, H. 1924: Courting display of the Goldeneye on salt water. – *Brit. Birds* **18**, p. 69–71.
- BREWSTER, W. 1911: Courtship of the American Goldeneye or Whistler (*Clangula clangula americana*). – *Condor* **13**, p. 22–30.
- GUNN, D. 1939: On the courtship-display of the Goldeneye. – *Brit. Birds* **33**, p. 48–50.
- HAARTMAN, L. VON 1945: Zur Biologie der Wasser- und Ufervogel im Schärenmeer Südwest-Finnlands. – *Acta Zool. Fenn.* **44**, p. 1–128.
- HEINROTH, O. 1910: Beobachtungen bei einem Einbürgerungsversuch mit der Brautente (*Lampronessa sponsa*). – *Journal f. Ornith.* **58**, p. 101–156.
- 1911: Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. – *Verh. d. V. intern. Ornith.-Kongr. Berlin*, p. 589–702.
- HINDE, R. A. 1953: The conflict between drives in the courtship and copulation of the Chaffinch. – *Behaviour* **5**, p. 1–31.
- 1955–56: A comparative study of the courtship of certain Finches (*Fringillidae*). – *Ibis* **97**, p. 706–745; *ibid.* **98**, p. 1–23.
- JOHNSGARD, P. A. 1955: Courtship activities of the Anatidae in Eastern Washington. – *Condor* **57**, p. 19–27.
- LIND, H. 1958: Eine Untersuchung über das Balzverhalten der Kolbenente (*Netta rufina*). – *Zs. Tierpsychol.* **15**, p. 99–111.
- (in press): The activation of an instinct caused by a “transitional” action. – *Behaviour*.
- LORENZ, K. 1941: Vergleichende Bewegungsstudien an Anatinen. – *Journal f. Ornith.* **89** (Festschrift), p. 194–293.
- 1951: Ueber die Entstehung auslösender “Zeremonien”. – *Vogelwarte* **16**, p. 9–13.
- 1952: Comparative studies on the behaviour of the Anatinae. – *Avicultural Magazine*.
- MILLAIS, J. G. 1913: British diving ducks I. – London.
- MORRIS, D. 1957: “Typical intensity” and its relation to the problem of ritualisation. – *Behaviour* **11**, p. 1–12.

- MOYNIHAN, M. 1955: Some aspects of reproductive behaviour in the Black-headed Gull (*Larus ridibundus*) and related species. – Behaviour suppl. IV, p. 1–201.
- 1958: Notes on the behaviour of some North American gulls. II: Non-aerial hostile behaviour of adults. – Behaviour **12**, p. 95–182.
- TINBERGEN, N. 1952: “Derived” activities; their causation, biological significance, origin, and emancipation during evolution. – Quart. Rev. Biol. **27**, p. 1–32.
- TOWNSEND, C. W. 1910: The courtship of the Goldeneye and Eider Duck. – Auk **27**, p. 177–181.
- WEIDMANN, U. 1956: Verhaltensstudien an der Stockente (*Anas platyrhynchos*). 1. Das Aktionssystem. – Zs. Tierpsychol. **13**, p. 208–271.