Some behaviour patterns of the Black Guillemot *Cepphus grylle*

STEN ASBIRK

(Med et dansk resumé: Tejstens adfærd)

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INTRODUCTION

The behaviour patterns of the Black Guillemot *Cepphus grylle* have until recently only been fragmentarily documented in a few rough descriptions by Darling (1938), Armstrong (1940), Winn (1950), and Williamson (1951). However, Preston has given a much more detailed description in his unpublished thesis from 1968, and the behaviour of the Pigeon Guillemot *Cepphus columba* has also been studied in detail by Storer (1952) and especially by Drent (1965).

The scope of the present paper is to describe some behaviour patterns of the Black Guillemot during the breeding season and to attempt an interpretation on the significance of the different postures.

I would like to acknowledge Dr. phil. Jon Fjeldså for advice during the study and for drawing the figures, as well as my family which patiently has helped me with much of the practical work in connection with the study. The Nature Conservancy Council has allowed me to work on the islands of Nordre Rønner and to use the buildings of the light-house. I would also like to express my gratitude to Mr. Per Bertelsen for much practical help and obligingness during the three years of study. Jan Dyck, Inge Hoffmeyer, Jon Fjeldså, Kent Forsgren and Sverre Sjölander critically read the manuscript.

MATERIAL AND METHODS

The investigation was made at the islands of Nordre Rønner in northern Kattegat (57°22'N, 10°56'E). A description of the study area is given elsewhere (Asbirk 1976 and 1979). Observations were made during the three summers of 1975 (25. April — 11. August), 1976 (29. April — 3. August) and 1977 (6. May — 1. August). The birds were watched from hides or from the light-house with a telescope (40 × 60). The observation hours totalled about 216 in the three years put together.

By individual colour-ringing I was able to sex many birds when they copulated. Later observations of these colour-ringed birds made it possible to identify if certain behaviour patterns were sex-related. Only by this method it is possible to tell, whether certain behaviour patterns exclusively took place between the mates of a pair or in other connections as well.

DESCRIPTIONS OF CERTAIN BEHAVIOUR PATTERNS

Escape behaviour

Direct flight

On extreme disturbance Black Guillemots may escape by flying, diving or both. Escape by diving is often seen during the chick-rearing period, when parent birds approach the colony with food in the bill. Herring Gulls *Larus argentatus* often spend much time in Black Guillemot colonies, trying to steal the food which the parents bring for their chicks. The fish-carrying birds often hesitate on the water near the colony before flying to the nest, and if they are attacked by a Herring Gull they often have to dive because it takes too much time to get on the wings.

The scream

When a human approaches a colony of Black Guillemots, the birds leave their nests and sit down on stones nearby or swim around on the water near the colony. A high-pitched and prolonged piping is heard from their widely

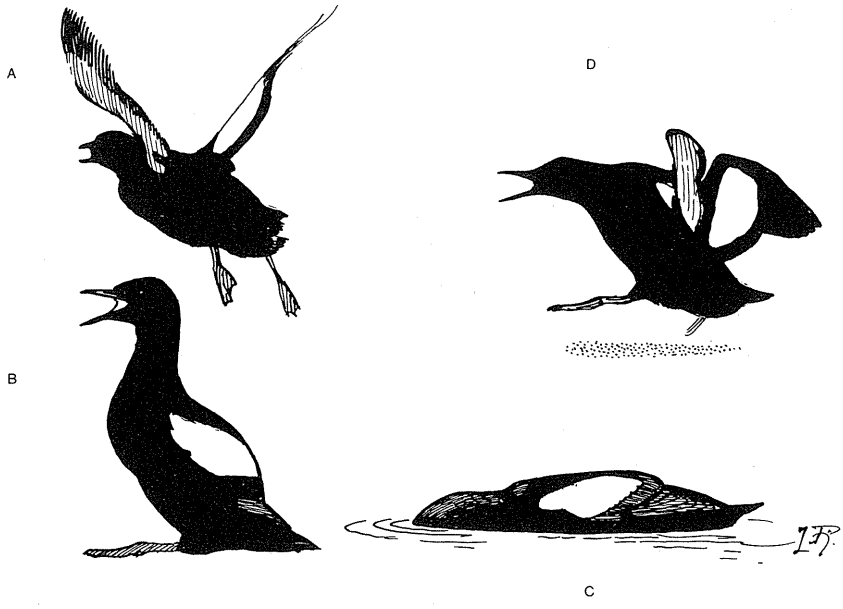

Fig. 1. Alarm postures. A Black Guillemot fleeing from attacking bird D. — B The scream. — C Bill-dipping.
Flugtbetonet adfærd. A Tejst flygter fra angribende fugl D. — B Alarmskriget. — C Næbdyppen.

opened bills, and the coral red linings of the gape is clearly seen. Usually one bird starts the alarm-calling, but it quickly spreads to the nearby birds, and the result is a veritable piping concert. At low intensity the birds lie down in the resting position when uttering the scream, but typically the neck is stretched vertically in the air. When the motivation for flight is higher, the birds raise onto their tarsus, and just before flying they may stand on their feet, in wholly upright position. The body-feathers and the wings are kept tight to the body in this position.

The scream may also be heard after the birds have taken to flight, especially when they are scared very suddenly, e.g., when a Herring Gull or a Greater Black-backed Gull *Larus marinus* flies low over the colony, or when a loud, strange sound is heard from, e.g., an aeroplane.

The scream may also be heard, when Hooded Crows *Corvus corone cornix* approach the colony, and when a Black Guillemot is attacked by another Black Guillemot.

Bill-dipping

During this behaviour the birds swim around and dip their bills in the water for a moment. Part of the head up to above the eyes are dipped below the surface of the water. Bill-dipping is seen, when the birds are clearly nervous, e.g. at the appearance of a human in the colony. However, birds showing this behaviour show a weaker tendency to flee than those screaming. Between each bill-dip the birds swim around with erect necks, keeping an eye on the person or the event, which has made them nervous. This bill-dipping corresponds to the same behaviour in foraging birds, which look for fish under the water before diving. Bill-dipping clearly occurs in conflict situations, when the bird is inclined both to stay and to flee, and it may be considered a displacement behaviour.

Aggressive behaviour

The lunge

In a direct lunge the Black Guillemot runs towards the antagonist with its neck stretched

forward, the head held low, the bill half or wide open, so that the red gape is seen, and uttering a shrieking sound. The wings are lifted out from the body and eventually stretched up into the air, and the situation may lead to a flying attack against the intruder.

If the attacking bird is very aggressive, it may pursue its victim over long distances through the air, duplicating every evasive twist and turn and dropping to the water or landing which the intruder makes.

If the attacked bird does not leave out escape the lunge, it is bitten and grasped, while the attacker beats its wings and tries to scratch with its claws. The victim does the same in defence. If it gets free, it is nearly always pursued in the air in the »duet-flight«, as this behaviour was called by Drent (1965). The somewhat romantic expression may lead to the impression, that this is a courtship behaviour. However, this is not the case. Among the colour-ringed birds observed I have never seen this performed between members of the same pair. If the lunge is made on the water, the antagonist often dives and may be pursued under water.

Threatening

At a lower intensity aggression the Black Guillemots threaten in a hunched posture either standing or walking slowly towards an intruder. The neck is drawn in, and the bill points towards the antagonist, but is held a little downward (30-45°). The bill is typically held open, but no sounds accompany the act. The carpal joints are lifted out from the body, the secondaries are fanned, and the tip of the wings may be dragging along the ground.

On the water this posture is not so conspicuous, because the body is horizontal. However, the raised carpal joints and the fanned secondaries are distinctly seen, giving the threatening bird a hunched appearance.

Twitter-waggle

At a lower intensity aggression than in threatening the Black Guillemot performs a peculiar behaviour, which leaves no doubt that the bird is in a strong conflict. It stands in an oblique position, the neck is stretched forward, and the bill points downward. The bill is open, and a twittering sound is heard. The head is waggling from side to side, the wings are raised from the body and may be held stiffly over the back, so the white under-sides are exposed. Feathers on the back are raised. The bird typically rests on its tarsi, while performing this display, and the tail is often cocked up. The latter feature was termed aggressive by Drent (1965). However, the tail is not cocked up in the typical aggressive behaviour patterns of lunging and threatening, and this feature is rather a typical part of displays, which express strong conflicts in the birds between fleeing and attacking/staying, as in the twitter-waggle, hunch-whistle, and communal displays.

Twitter-waggling has been seen on the water on a few occasions, and then the body is held horizontally.

Attacking birds may from a threatening posture change to twitter-waggling, if it has come too far away from its perch-site, or if it has attacked a territory-owner which is not disposed to leave its perch-site. Birds attacked may also twitter-waggle in response to the threatening posture of another bird instead of making a counterattack. If the lunge comes from behind, twitter-waggling is performed with the back towards the attacking bird, but regardless of the angle from which this behaviour is observed, it leaves no doubt that it is twitter-waggling. This behaviour pattern is also commonly seen during the communal displays on land.

In most situations with twitter-waggling the birds calm down, and this peculiarly looking behaviour probably has an appeasing effect. The exposed white under-sides of the wings are presumably an important stimulus in the appeasement.

Hunch-whistle

Pairs or single birds on their established perch-sites may use hunch-whistling as appeasement to approaching conspecifics. Sometimes only one of the mates does the hunch-whistling, but often both of them. The birds lie in a hunched posture with the tail cocked up, the wings tight to the body, and often with the head directed towards the intruder. The neck is drawn in, and the head is tossed upwards and backwards many times. The bill is closed in the lower position, but opened in the upper position, so that the red gape is blinking towards the intruder. The action is accompanied by a rising and falling piping. The orientation may change during the performance, as the birds turn their heads from side to side.

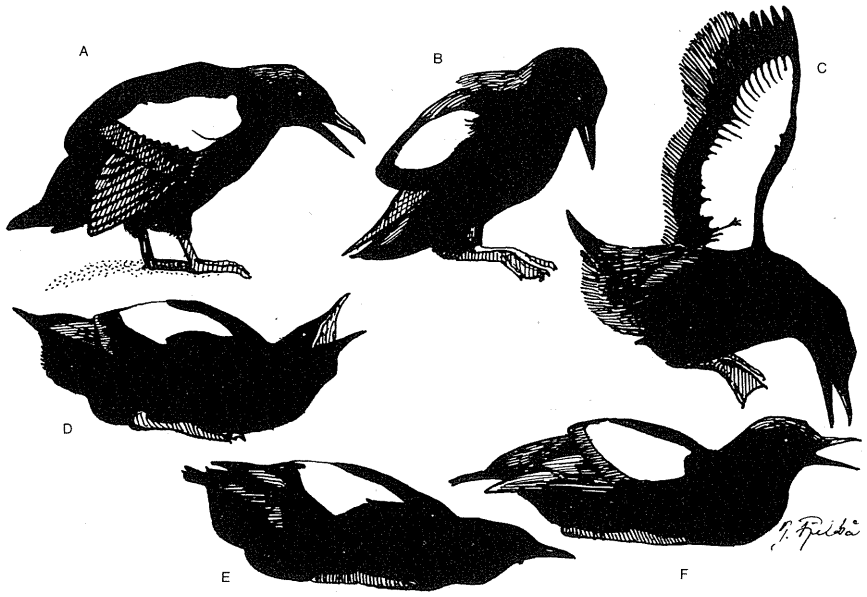

Fig. 2. Aggressive postures. A Threatening. — B-C The twitter-waggle. — D-E The hunch-whistle. — F The nest-song.
Aggressive positurer. A Truepositur. — B-C Hovedrysten. — D-E Hovedvippen. — F Territorie-sang.

Hunch-whistling is also seen between the mates in a pair, and it probably has an appeasing function. Thus, the hunch-whistle serves to keep intruders at a distance by lowering their aggressiveness. In addition, it serves to lower the flight tendency and/or the aggressiveness of the mate, so that they can keep together.

Nest-song

Black Guillemots sitting on top of their nests may utter a quick staccato piping at the approach of other Black Guillemots. The song is usually performed in the posture, in which the bird lies at the moment, most often the resting position. The neck is withdrawn, and the head directed slightly upward. The bill is half open, and the intruder is followed intensely with the eye. The wings may be lowered towards the ground as an intention movement to threatening.

The head-turning described by Preston (1968) as a special display, is probably a variation of the nest-song. The head is turned backwards, the bill touching the scapulars, but it alternates with the song, and the different orientation of the head is probably a mean of focusing the intruder.

Leap-frogging

This type of behaviour looks like a short flying attack, but the direction of movement is typically ahead of or parallel to the apparent object of the display. It often occurs during chasing on the water.

The trailing bird alights from the water with whirring wings, and with its wings held stiffly over the back, gliding forward, lands with a splash a few feet in front of the leading bird. After landing the wings typically remain raised for some seconds. During the short flight, the legs hang straight down, and the bill is open, but I have not been able to hear, if any call accompanies this display.

Leap-frogging is most often seen during the communal displays, but once I saw it in a presumably newly formed pair. One of the mates began billing (see later) but without mutual response from its mate, and it then performed a leap-frog flight ahead of the mate.

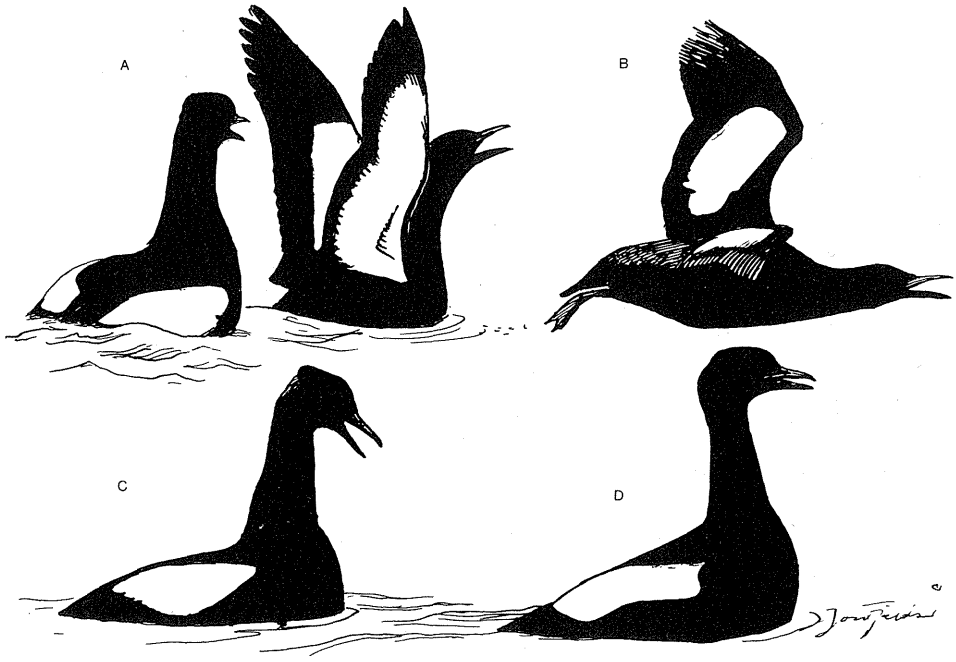

Fig. 3. Communal display postures on the water. A-B Leap-frogging. — C-D Two birds in line formation.
Fællesspil i vandet. A-B Springen buk adfærd. — C-D To fugle i linjeformation.

Leap-frogging is always performed very rigidly and stereotyped, and it looks like a highly ritualised behaviour pattern. It presumably originates from aggressive behaviour, where a redirecting or changed orientation of the attack has taken place. The behaviour may have an appeasing effect and/or be a part of the courtship.

Communal displays

During communal displays a mixture of postures is seen, which may express tendencies of escape, aggression and courtship.

It is uncertain what starts the communal displays. Suddenly one bird swims quickly towards a nearby individual. Its neck is erect, the bill wide open, and the breast pulsates deeply as a loud two-syllabled peeping call is given. The carpal joints may be held away from the body or the wings may be raised and held stiffly over the back. The tail is often cocked up. In the water the rear of the body may be lowered under the surface and the breast raised from the water. On land the displaying bird assumes a very upright posture and walks strutting around on its toes.

The individual at which the display is directed, immediately assumes a similar strutting posture and swims away ahead of the first bird. When several birds participate in the display a line formation may be formed in this way (Fig. 3 C-D). On other occasions, the individual at which the display is directed may swim towards the initiator of the display. When the two birds meet they turn and swim parallel with strutting necks, plowing through the water, or they may dive and chase one another under the water. More seldomly they directly attack one another with beating wings and scratching feet before diving. This may develop into an alteration of underwater chases, chases on the water surface using wings for propelling itself, and flight chases.

Bill-dipping, leap-frogging and twitter-waggling are frequently included in the communal displays.

Once started, this type of behaviour is very infectious, and frequently up to 15-20 birds were seen strutting together. Bouts of communal displays may last for a few minutes till about a quarter of an hour.

The communal displays most often have

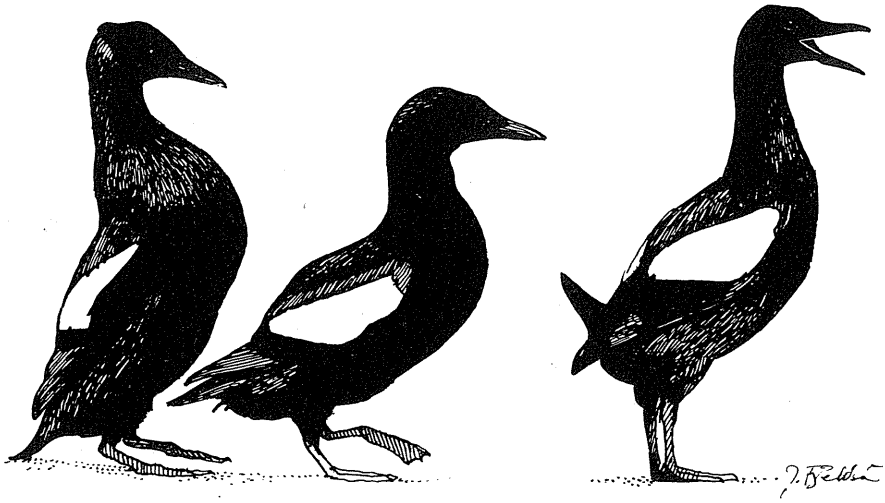

Fig. 4. Communal display postures on land.
Fællesspil på land.

been described as occuring on the water, but I have just as often seen it on land. In my study area, communal displays on land were most common on the harbour pier. When approaching the colony of 25-30 pairs in the harbour pier, one may be able to start a communal display by forcing the birds close together. Typically two birds from adjacent nest territories initiate the display, but it may also be started by a non-breeding individual. Within short time other individuals gather in the vicinity of the initial two birds, and some birds even travel long distances (up to about 75 m) to join the displaying groups. On a few occasions incubating birds were seen to leave their nest and participate in the displays.

Compared with other non-mate interactions it was characteristic for the strutting displays that they typically evoked an identical behaviour in the display partner.

Courtship behaviour

Circling

Prior to copulation the male assumes an upright posture with its neck erect and the bill pointing downwards. A series of quick staccato sounds is heard. He begins to strut around the female lifting his feet high as he walks. If she is ready for copulation, she raises and walks around in a circle in a hunched posture. If she has moved only in order to avoid the advances of the male, she soon lies down again with upright neck and her bill towards the male.

Invitation

If the female is ready for copulation, she lies down after some time of circling with the male. She lies flat with her neck stretched out along the ground, the bill pointing straight out, and her tail cocked up. During copulation she normally stays in this position, but may raise her head to the normal resting position or direct her bill upward towards the male. This is often seen, if the male hesitates in copulating and stands for long time trampling on the back of the female.

Copulation

A short moment after the inviting of the female the male mounts with trampling feet, keeps his upright posture and presses down his tail to make cloacal contact.

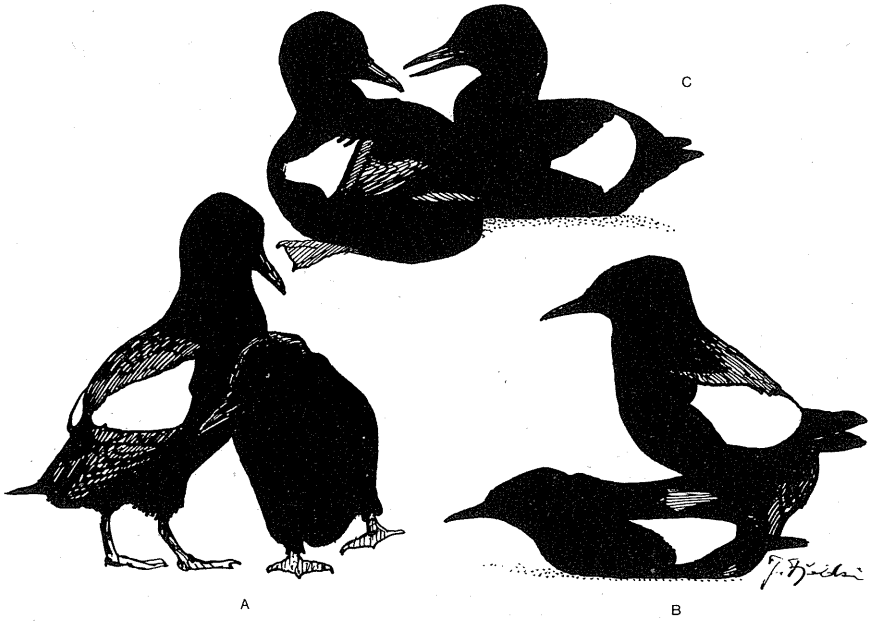

Fig. 5. Pair behaviour. A Precopulatory circling, male to the left, female to the right. — B Copulation. — C Billing on land.
Par-adfærd. A Cirklen, han til venstre, hun til højre. — B Parring. — C Næbben på land.

Often the copulatory act is finished by the female in the way, that she raises and throws the male off. He may however also finish the copulation by pecking the back of the female's head, after which she raises and throws the male off.

After copulation the mates lie down preening. This behaviour does not seem to me to be ritualised, as the male always preens his belly feathers and the female her back feathers and the feathers around her cloaca. It merely seems to be an action of getting the plumage in order.

Billing

This behaviour pattern is only seen between the mates in a pair. Two birds lying or standing near one another face each other and bob their bills alternately from side to side. Their bills normally point a little downwards (30-45°), and the action is accompanied by a rapid staccato sound from both birds. The call is similar to that heard during circling. At high intensity the bill is opened while piping. The opened bill is otherwise characteristic of the aggressive behaviour of the species. When it is seen by the mates of a pair, it is in situations when they have been seperated for a long time, or when one bird does not response to the billing of its mate.

When the birds meet after a time of separation, a greeting ceremony is often seen, beginning with hunch-whistling in one or both birds followed by mutual billing with open bills and ending in typical billing with closed bills. The aggressive tendencies are clearly diminishing in the course of the greeting ceremony, corresponding to conditions in the gulls (Tinbergen 1959). Thus billing apparently strengthens the pairbond, and Drent (1965) has suggested that invitation to billing presumably plays a role in pair formation.

When billing is performed standing the tail may be cocked up. On the water the mates also bill, while circling around themselves and around one another. This circling should not be confused with the precopulatory circling, which always takes place on land. The Puffin *Fratercula arctica* is the only species known to copulate on the water (Lockley 1955, Myrberget 1962).

Interference between neighbour pairs

Evidence that a social hierarchy may exist among pairs of Black Guillemots is given by the following example. Three nests situated linearly 1 m apart in the harbour pier were closely studied from a hide. The male at the middle nest (nest 1) was clearly very aggressive, and spent most of its time attacking the pair to the right (nest 90), which always withdrew when attacked and was clearly subordinate. Despite the fact that pairs normally sit above their nests when ashore, this pair was prevented from doing so, and established a perch-site about 4 m away in a neutral area of the harbour pier, where no other nests were found. On the other hand, the pair to the left (nest 137) of the aggressive male was clearly dominant. That pair always laid quietly on top of the nest, completely ignoring the presence of other individuals. The aggressive male of the middle pair never tried to attack or threaten this pair. In fact the subordinate pair was excluded from breeding, although the female was at least 6 years old. Their nest was taken over by another pair, which was also subordinate, but apparently had a higher social position than the excluded pair. They were able to slip into their nest, although frequently attacked by the male of nest 1.

The reproductive success of the mentioned pairs was highly different: the dominant pair laid their two eggs first, followed by the pair in the middle (also two eggs); one subordinate pair was totally excluded from breeding and the other one laid only one egg and very late in the season. That year (1976) however, none of the pairs hatched eggs. The dominant pair in nest 137 because their nest had been partly filled with sand and sea-weed, so that the eggs lay rather exposed and rolled out of the nest. The pair in nest 1 experienced the same partly filling out of their nest, and in addition their nest was parasitized by a strange pair, which placed their two eggs in it. The subordinate pair laying one egg in nest 90 was disturbed so much, that they were not able to incubate the egg to hatching.

Taking all three years together the dominant pair laid 3 × 2 eggs, hatched 2 × 2 eggs, and fledged 2 × 2 young. The pair in the middle laid 3 × 2 eggs, hatched 1 × 1 and 1 × 2 eggs, and fledged 2 × 1 young. The subordinate pair being excluded from breeding in 1976 laid two eggs in 1975, hatched one or two eggs, but fledged no young. In 1977 they changed to another nest, laid two eggs, hatched two eggs, and fledged one young. The second subordinate pair bred at another nest site in 1975, laid 2 eggs, but no one hatched. In 1977 they laid 2 eggs, hatched both of them, but fledged only one young.

DISCUSSION

The behaviour patterns of the Black Guillemot very closely resemble those described for the Pigeon Guillemot by Drent (1965). Drent (1965) tried to compare some behaviour patterns of Pigeon Guillemot, Razorbill *Alca torda*, and Common Guillemot *Uria aalge*. He points out, that billing runs like a red thread through auk behaviour, and this is also the case in Cassin's Auklet *Ptychoramphus aleutica* (Thoresen 1964), and Little Auk *Alle alle* (Ferdinand 1969). Much more analyses should be made on auk behaviour, before rigorous tracing of homologies may be performed.

At present it is only indicated, that communal displays are widespread among the auks (Conder 1950), that the twitter-waggle of the Black Guillemot corresponds to appeasement gesture no. three in the Common Guillemot (Nørrevang 1958), and that the hunch-whistle of the Black Guillemot corresponds to head-bobbing in Cassin's Auklet (Thoresen 1964), to head-flicking in the Puffin (Lockley 1955, Myrberget 1962), and to »le rejet de la tête« in the Razorbill (Bédard 1969).

The performance and function of the different displays in the Black Guillemot corresponds to a high degree to the postures in gulls described by Tinbergen (1959). The threatening posture of the Black Guillemot may thus correspond to the »aggressive upright« in the gulls, twitter-waggling corresponds well to the »choking« of the gulls (especially for the Black-headed Gull *Larus ridibundus*), and the hunch-whistle resembles the »head-tossing« of the gulls.

The communal display and the aggressive behaviour patterns have striking similarities to the corresponding behaviour patterns of the divers *Gaviidae* (see Dunker 1975, Sjölander 1968, Sjölander & Ågren 1972). These similarities to other groups of birds may indicate taxonomic relationships, although parallel trends also play a role e.g. in the bill-dipping behaviour of the divers and the alcids.

Ecological aspects of the communal displays

Communal displays are well-known in many colonial birds and in some territorial birds (Bastock 1967), but their significance has been much disputed.

Past describers of communal Black Guillemot displays have classified it as the courtship behaviour. Establishment of pair-bonds presumably takes place at the breeding locality in the early spring, but it is characteristic, that the communal displays are performed throughout the entire breeding season, and a courtship function is not immediately convincing.

Observations on colour-ringed individuals have shown that normally only one of the mates in a pair takes part in the communal displays, while the other may be incubating the eggs or doing something else. If both mates take part in the display, they do not act as a pair but as individuals. Preston (1968) found the same to be true in his study, and Drent (1965) stated the same fact in the Pigeon Guillemot.

Preston (1968) has suggested that, since first-year birds do not participate in the communal displays, the aggregations of birds may represent a pool of potential breeders, from which a mate could be selected. This hypothesis is at least not quite correct, as I several times have seen two-years-old individuals retiring from strutting communal displaying adults in the same way as first-year specimens as described by Preston (1968:92). These two-years-old birds are sexually mature birds capable of breeding (Asbirk 1979) and thus constitute part of the potential breeders.

It has also been suggested, that such communal displays serve to facilitate breeding synchrony through mutual stimulation of a breeding population (Darling 1938). However, there is little evidence of breeding synchrony in the Black Guillemot (Preston 1968, Asbirk 1979). For instance the period of egg-laying nearly covers a period of two months in my study area, and in the subcolonies there is even as little synchrony. Further the communal displays are performed throughout the whole breeding season, which would not be expected, if they served merely to synchronize breeding.

I suggest another function of the communal displays, namely population regulation through establishing a peck order or certain dominance relationships between the birds (see also Wynne-Edwards 1962). The existence of a social hierarchy has been presented by the above mentioned example of behaviour between neighbour pairs, and the combination of aggressive and evasive elements together with appeasing postures in the communal displays gives good possibilities of establishing dominance relationships between birds. However, it still remains to be documented whether certain individuals always retire or show appeasement postures to certain other and more dominant individuals in these displays. Once such dominance relationships have been established, the reproductive success of subordinate individuals may be reduced at high population densities by suppressing the full reproductive development for the season in question or by frequent disturbances, and they may even be totally excluded from breeding.

The ultimate significance of the evolution of such behaviour patterns may be dispersion of the breeding pairs in relation to the food resources. Preston (1968) has shown, that there were behavioural differences between normal density groups and high density groups of Black Guillemots. The communal displays were seen much more frequently in the high density groups and Preston (1968) presumes that behavioural differences were responsible for the reduced laying in these groups. Elsewhere (Asbirk 1979) I have presented evidence that reduced reproduction leads to more frequent changes of nests in the Black Guillemot, which normally retains its nest from year to year, and the result will be dispersion of the nests and most possibly some birds might move elsewhere, which will lead to the most efficient utilization of the inshore food resources.

DANSK RESUMÉ

Tejstens adfærd

Nogle af Tejstens adfærdsmønstre beskrives ud fra studier på Nordre Rønner i årene 1975-77. Beskrivelserne omfatter flugtadfærd (Fig. 1), aggressiv adfærd (Fig. 2), fællesspil (Fig. 3 og 4), parringsadfærd (Fig. 5) og adfærd mellem nabopar (rangorden). Funktionen af de forskellige adfærdsformer søges belyst, og specielt betydningen af fællesspillene diskuteres. Tidligere mente man, at fællesspillene var en del af pardannelsesadfærden, men da spillene finder sted igennem hele ynglesæsonen, lyder

denne forklaring ikke umiddelbart overbevisende. Desuden viser observationer af farveringmærkede individer, at det normalt kun er den ene af magerne i et par, som deltager i et bestemt fællesspil.

Det er også blevet foreslået, at deltagerne i fællesspillene kunne repræsentere en pulje af yngledygtige fugle, fra hvilken en mage kunne udvælges. Denne teori støttes af, at et-årige ikke-yngledygtige individer aldrig deltager i fællesspillene. På den anden side har jeg ofte set to-årige individer undgå fællesspillene, til trods for at Tejsten kan yngle i en alder af to år.

Synkronisering af yngleforløbet er en af de ældste forklaringer på fællesspil hos fugle. Imidlertid er Tejsternes ynglen meget lidt synkroniseret, f.eks. strækker æglægningsperioden sig over to måneder på Nordre Rønner. Hvis spillene udelukkende tjente synkroniseringsformål, skulle man heller ikke forvente at se dem udført igennem hele ynglesæsonen.

Jeg vil i stedet foreslå en anden funktion af fællesspillene, nemlig bestandsregulering. I afsnittet »interference between neighbour pairs« er givet et eksempel på, at der synes at være en rangorden imellem Tejste-parrene. I fællesspillene giver kombinationen af angrebs- og undvigemanøvrer sammen med pacificerende positurer gode muligheder for at etablere bestemte dominansforhold imellem fuglene. Der mangler imidlertid stadig dokumentation for, at underlegne fugle viser pacificerende adfærd overfor dominerende fugle i fællesspillene.

Er rangordensforhold én gang etableret, kan underlegne individers ynglesucces reduceres ved at undertrykke deres fulde reproduktive udvikling for den indeværende sæson, og ved stor bestandstæthed kan underlegne individer blive helt afskåret fra at yngle.

Den biologiske betydning af sådanne adfærdsmønstre kan være spredning af yngleparrene i forhold til føderessourcerne. Fællesspillene forekommer meget hyppigere i tætte grupper af ynglende Tejster end blandt spredte par. Preston (1968) formoder, at denne adfærdsmæssige forskel er årsagen til en mindre kuldstørrelse i de tætte kolonier. Fører fællesspillene til en reduktion af ynglesuccessen blandt de implicerede underlegne fugle, vil de være tilbøjelige til at skifte redested (Asbirk 1979). Den tætte koloni vil således spredes langs kysten, hvilket er fordelagtigt for arten, idet en sådan spredning giver den mest effektive udnyttelse af de kystnære fødeemner, som Tejsten lever af.

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Authors address: Zoological Museum, Universitetsparken 15, 2100 København Ø.
Present address: Helgesvej 1, 4000 Roskilde.