Comparative behaviour of sympatric moulting populations of Common Eider Somateria mollissima and King Eider S. spectabilis in central West Greenland



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Activity budgets and distribution patterns of Common Eider moulting at Disko Island, West Greenland, were studied and compared to the behaviour of King Eider moulting in the same general area (Frimer 1994b). Both species are diurnal feeders who spend most of the night resting. The daily foraging pattern was essentially similar in the two species, with peak intensity early and late in the day, and there was no significant difference in the amount of time spent foraging. However, while Common Eiders foraged near the rocky shoreline at depths of less than 15 m, King Eiders foraged mainly on silt bottom at depths of 15-25 m. Dabbling comprised between 10.7% and 45.6% of the foraging time in Common Eiders, and less than 1% in King Eiders. The total food niche overlap between the two eider species is estimated to be less than 16%. A low interspecific food competition may be crucial to the survival of the species in the late autumn and winter, when days are short and the birds spend most of the day foraging. Some adaptations of the species to their feeding habitats are discussed.

Keywords: Common Eider, King Eider, Feeding, Competition, Moult, Greenland

Central West Greenland, particularly the Disko Bay region, supports large numbers of moulting Common Eiders Somateria mollissima and King Eiders S. spectabilis in the autumn, with the latter being by far the more numerous (Frimer 1993). The Common Eiders (subspecies borealis) are West Greenland birds (Salomonsen 1950, 1968), possibly mixed with birds from northeast Canada (Abraham & Finney 1986). The King Eiders belong to the populations breeding in the eastern Canadian Arctic, who perform a moult migration to the area during July and August (Salomonsen 1968, Frimer 1994a). At Disko Island, the eiders undergo moult mainly in sheltered fjords and bays, where they often mix.

In 1991 and 1992, the moulting behaviour of King Eider was studied at western Disko Island (Frimer 1994b). The present paper examines the activity budgets of Common Eider moulting in the same general area and describes the distribution patterns of Common and King Eider in the investigation area. The behaviour of Common Eider is related to time of day and stage of tide, and compared with the behaviour of moulting King Eider. The study pays special attention to behavioural indications of niche segregation in these closely related and sympatric moulting species.

Study area

Observations were carried out during 11-20 August 1992 in the bay Ivisaarqut, near the mouth of the fjord Akulliit (Mellemfjord), western Disko Island (69° 45'N, 54° 50'W) (Figure 1). The coast of lvisaarout consists of basaltic cliffs and small reefs to the east and west, and a stony beach to the south. Preliminary vessel-based Van Veen grab sampling within the bay revealed that the bottom, at depths of up to about 15 m, is rocky and stony, but replaced by silt at greater depth. The hard bottom is partly covered with seaweed, and apparently has areas with Mytilus edulis (numerous dead shells on the beach).

The weather conditions in August were rather unstable, with periods of 129



Figure 1. The study area, Ivisaarqut, showing the 15 m depth-line and positions of buoys (•) and ranging poles (o). -----= border of bay.

strong winds, precipitation or fog, and heavy dew often occurred at night. During the study period the daily ambient temperatures ranged between -1 and 8°C. Local fjord winds from the west and northwest occurred almost daily from late morning to late afternoon. The tidal amplitudes are up to 2.2 m.

Apart from a few Red-breasted Mergansers *Mergus serrator*, Common and King Eider were the only duck species occurring in the area during the study period.

Materials and Methods

In order to help determine distribution patterns and foraging depths, the bottom profile of Ivisaarqut was mapped from a research vessel using combined echo sounder (Skipper 802)

and radar (Furuno). The depth of 15 m was marked with three buoys; two at the outer border of the bay and one at the southernmost point for this depth. In addition, two pairs of ranging poles were placed near the coast, each pair some distance apart, and aligned with the outermost buoys and parallel with the coast. A line drawn between the three buoys, according to the pointing directions of the ranging poles and the approximate curvature of the southernmost shoreline, roughly corresponds to the topographical 15 m line, and is here referred to as the 15 m depth-line (Figure 1).

Behavioural observations were carried out from an elevated point near the shore, while counts were made from the ranging poles, using binoculars (10x) and telescopes (20-60x). Distance between the observer and the eiders ranged from 100 to 2,000 m, and did not appear to affect the behaviour of the birds.

The observational methods largely follow those in my previous studies on moult and behaviour of King Eiders (Frimer 1994a,b).

Sex and age ratios and state of moult

In flocks or subgroups selected at random over the widest range of flock size and observation distance as possible, the numbers of males and females were recorded. The plumage phase of all males was determined and divided into the following age and plumage categories: adult males (third calendar year or older) and immature males in full or partial alternate plumage, and males (adults as well as immatures) in basic plumage. It should be mentioned here that Common Eiders may not reach maturity until their fourth calendar year (Palmer 1976). Females occurred in very low numbers in the area and no attempt was made to determine their age and plumage. The proportion of males in wing moult was estimated by observing the remiges of birds flapping wings (Piersma 1987). Each male seen wing-flapping was recorded and the state of wing-moult expressed as being moulting or not moulting. For further details see Frimer (1994a).

Sex and age ratios and the proportions of males in each plumage phase and in wing moult were calculated from the sum of data collected over a 24-hour period.

Activity budgets and distribution patterns

Activities were recorded by instantaneous scan sampling (Altmann 1974) of individuals in randomly selected flocks, every 60 seconds for a minimum of 30 minutes or until the birds were out of sight. I attempted to obtain a minimum of 30 minutes of scans within each hour of the 24-hour cycle. Prior to scans, the number of birds in the sample flock was counted carefully to allow later estimates of how many birds were underwater. The proportion of individuals engaged in each activity was recorded according to the following categories: diving, interdive loaf (pausing between consecutive dives), dabbling (head-dip and up-end), comfort movements (preening, bathing, wing-flapping, stretching), swimming, resting (head on back, standing or sitting on shore) and other activities (flying, aggression). The number of birds submerged at any one time was calculated by subtracting the number of birds on the surface from the flock total. Pausing between dives at intervals of less than two minutes was defined as inter-dive loaf (this time interval was the maximum pause time, timed to the nearest minute, recorded between consecutive dives). Foraging was the time devoted to diving, inter-dive loaf and dabbling. Temperatures, level of tide, precipitation, wind and sea surface conditions were recorded at the beginning of each scan.

The total numbers of Common and King Eiders present within the bay were counted, usually every hour of the diurnal cycle, and the position of each individual was recorded and expressed as being within or on and outside the 15 m depth-line.

Data on sex and age ratios, state of moult, activities and distribution patterns were collected during four days, regularly distributed over the tidal cycle: 11, 14, 17 and 20 August.

Data analysis

statistical package The computer Execustat (Loll 1993) was used for the statistical analysis. The effect of the tide on the foraging behaviour was analysed using one-way ANOVA and following the procedure given in Fry (1993); the estimated proportion of time devoted to foraging within one hour of a sampling period constituted a unit of observation. Differences between Common and King Eider in the amount of time spent foraging was analysed using t-test. The patterns of presence of the two species were compared using Wilcoxon's Test on hourly proportions occurring within the 15 m depth-line. The level of significance accepted is P < 0.05. Before the parametric tests were performed, the data were arcsine transformed to obtain normally distributed samples (Sokal & Rohlf 1981).

Overlap in habitat use was calculated

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as the proportion of time spent by the Common Eider on and outside the 15 m depth-line plus the proportion of time spent by the King Eider within this line.

Results

Common Eider

Sex and age ratios

Of 360 birds sexed during the study period, 99% were males. On 11 August, when 89% of the recorded males were in full or partial alternate plumage (**Table** 1) and thus were aged, 75% were adults.

State of moult

The proportion of males in body moult peaked in the second week of August, and around this time the birds initiated wing moult (**Table 1**). The proportions of birds in wing moult given in **Table 1** should be taken with some caution, because the wing-flapping frequencies, and thus the recording likelihoods, of moulting and non-moulting birds may differ (see Frimer 1994a). However, this was not investigated.

Activity budgets

Common Eiders were generally active in the daylight hours, with peak intensity early and late in the day, and spent most of the night and a period around midday resting (**Figure 2**). However, the diurnal foraging pattern was modified to some degree by the tide (**Figure 3**). Test of the effect of the tide (divided into four approximately three hour stages of the tidal cycle; high, falling, low and rising tide) on the foraging intensity: $F_{3.69}=3.34$, P<0.05; the Common Eiders foraged less

Table 1. Estimated proportions of maleCommon Eiders in basic plumage and in wingmoult during 11-20 August.

n = number of birds whose plumage and state of wing moult, respectively, were recorded.

Date in August	Basic Plumage (%)	п	Wing moult (%)	n	
11	11	254	7	31	
14	31	305	32	151	
17	64	146	25	83	
20	64	22	29	21	

frequently at falling tide than at low and rising (Tukey-Kramer tide HSD procedure; see Sokal & Rohlf 1981). At Disko. the Common Eiders fed exclusively by dabbling and diving. In 47 recorded dives, the dive time varied from 16 to 50 seconds (mean 30.1) at intervals of four to 99 seconds (mean 29.0) between consecutive dives. Dabbling was most intense in the early morning







Figure 3. The proportion (%) of time devoted to foraging in relation to stage of tide by moulting Common Eiders. Data are means of four observation periods (sunrise to sunset) during 11-20 August. Hatched part of bars = diving; open = inter-dive; shaded = dabbling.

(**Figure 2**), particularly around low tide (**Figure 3**), but this was not statistically significant ($F_{3,69}$ =2.02, P>0.1).

The proportion of time devoted to diving and inter-dive loaf was almost the same in all sampling periods (mean 15.2% of the 24-hour cycle) (**Table 2**), while the amount of time spent dabbling varied between 1.9% and 13.1%, corresponding to 10.7-45.6% of the foraging time. On average, the Common Eiders devoted 20.9% of the 24-hour cycle to foraging.

The intensity of comfort movements decreased during the study period (**Table 2**), in coincidence with an increasing proportion of birds having attained basic plumage (**Table 1**).

Resting was the most frequently observed behaviour during all sampling periods, except on 11 August, when the birds spent much time swimming and dabbling (**Table 2**).

Other activities (flying, aggression) together accounted for less than 0.5% of all activities during all sampling periods.

Distribution patterns of Common and King Eiders

The number of Common Eiders present

within the bay varied greatly both within and between sampling periods, because Common Eiders also used alternative areas for foraging and resting. The daily maximum number varied from 33 to 120 individuals. The greatest variations within sampling periods occurred on days with calm sea (17 and 20 August), when the Common Eiders tended to spend the midday resting period outside the bay. These variations did not appear to affect the estimates of the amount of time spent foraging (Table 2), indicating that the birds generally use the same area for foraging within a day or that the use of alternative feeding areas does not influence the overall foraging intensity.

While present in the bay, the Common Eiders spent most of the time within the 15 m depth-line (**Figure 4**), particularly during the periods of peak foraging intensity (mean 86.8% of the combined periods 0300-1100 and 1500-2200 h). In three of the four sampling periods flocks of Common Eiders spent the night in the bay close to the shore.

Presence of King Eiders (Figure 4) reflects the daily foraging pattern (Frimer 1994b). The daily maximum number present varied from 108 to 216 individuals during the study period. Unlike the Common Eiders, King Eiders spent most of the time in the bay on waters deeper than 15 m, and rested outside the bay both during the night and midday, irrespective of the weather conditions. The difference is statistically significant (z=8.63, P<0.001). In the periods of peak foraging intensity, which were essentially the same as for Common Eiders (Frimer 1994b), King Eiders spent on average 77.8% of the time on and outside the 15 m depth-line, giving an overlap in habitat use between the species of (100-86.8)% + (100-77.8)% = 35.4% within these periods. Common

Table 2. Activity budgets (% of 24 hours) of moulting Common Eiders. n = total number of behavioural records.

Date in August 11	Diving	Inter- Dabbl dive 7.5 13.1	Dabbling	21.4 Comfort	Swimming Resting		Other	п
	8.1		13.1		25.2	24.6	0.0	5,433
14	7.0	6.4	3.1	17.7	16.0	49.4	0.4	16,692
17	8.6	7.2	1.9	16.6	19.7	45.8	0.3	9,928
20*	8.6	7.5	4.5	10.6	23.4	45.3	0.0	4,644

*Proportions were calculated assuming that the eiders were resting during three night hours (22.00-01.00 h) not sampled.



Figure 4. Patterns of Common Eider and King Eider presence (% of daily maximum numbers) within the bay Ivisaarqut. Data are means of four observation periods during 11-20 August. Solid part of bars = <15 m of depth (see text); open = \geq 15 m of depth. O = no records. ? = not sampled. Circles = sunrise (open) and sunset (closed).

Eiders were, however, not seen diving or dabbling at depths of 15 m or more. Hence, the overlap in use of foraging habitat was probably not greater than 22.2%.

Discussion

Common Eider

In mid-August, the Common Eiders occurring at Disko consist almost exclusively of males, with c. 75% being adults. A similar sex ratio has been recorded at Disko in mid-July, but with adult males making up 45-50% of the recorded birds (Frimer & Nielsen 1990). The Common Eider is a scarce breeder in the Disko Bay region, and a minor proportion of the birds recorded in August may have bred locally, while the majority probably have come from breeding grounds in west Greenland north of Disko (Salomonsen 1967) from and/or northeast Canada (Abraham & Finney 1986). Most postbreeding males move into the area during July and initiate body moult in the second half of the month (Salomonsen 1950). In mid-August the birds were in late body moult and beginning wing moult.

The foraging pattern largely agrees with other studies of Common Eider activities in areas with small tidal amplitudes, with peak intensity early and late in the day (Pethon 1967, Dunthorn 1971). Foraging took place at depths of less than 15 m, which is typical of Common Eider (Bergmann 1939. Pethon 1967, Ydenberg & Guillemette 1991). The amount of time devoted to diving and inter-dive loaf was almost the same in all sampling periods, whereas the proportion of time spent dabbling varied markedly. Most dabbling took place near shore in the early morning. The birds were most dabbling certainly mainly for amphipods Gammarus spp., who were observed swarming close to the shore morning low tide on several at occasions. This is further supported by the fact that the birds mostly were dabbling by head-dipping, rather than by up-ending.

It is unclear why the Common Eiders foraged less at falling tide than at low and rising tide. The proportion of time spent dabbling did differ not significantly between the four tidal stages, suggesting that the availability of amphipods did not vary markedly with the tide. Thus, other prey species may have been involved. Marked tidal influence on the daily foraging pattern of Common Eiders has been described from areas with large tidal amplitudes or where food items are more available at certain stages of tide (Player 1971, Cantin et al. 1974, Campbell 1978, Minot 1980). In the present area, with moderate tidal amplitudes, the foraging pattern of Common Eiders was probably mainly governed by the birds' internal need for food, and to a lesser degree by environmental (physical or biotic) factors, while the choice of foraging technique was influenced indirectly by the time of day.

The amount of time devoted to comfort movements decreased during the study period as the proportion of birds having attained basic plumage increased, suggesting that comfort movements, to some degree, are correlated with the state of body moult.

Swimming showed no trend in relation to any one other behaviour class.

The birds spent a period around midday and most of the night resting, resting being the most frequently observed behaviour during most sampling periods.

Other activities than those discussed were rarely observed, although time spent flying may be underestimated, because flying Common Eiders, except at take-off and landing, were not sampled. It is my impression, however, that moulting Common Eiders (including birds capable of flying) prefer to move by swimming rather than by flying.

Comparison of the behaviour of moulting Common and King Eider

In the following, all comparisons with King Eider refer to data in Frimer (1994a,b).

Post-breeding male King Eiders arrived at Disko mainly in early August; by mid-August 1992 males (including adults and immatures) made up about 75% of the King Eider population, the rest being immature and non-breeding adult females, which probably had spent the summer south of the potential breeding range. Post-breeding females arrived in the area during the second half of August, and by the end of the month the sex ratio was close to parity.

In mid-August the prebasic moult was well in progress in most Common and King Eiders occurring in the area. The two species resemble each other in being daytime feeders, who spend most of the night resting. The daily foraging pattern of both species was essentially diurnal, with peak intensity early and late in the day. The mean foraging time (% of 24 hours) for Common Eiders was 20.9% (SD=5.49, n=4), compared to an estimated 24.0% (SD=2.36, n=8) for King Eiders: the difference is not statistically t=1.42*P*>0.1). significant (df = 10,However, the species differed markedly in the following points:

(1) Common Eiders foraged mainly on the hard bottom fauna at depths of less than 15 m (**Figure 4**), and on amphipods swarming near shore, while King Eiders foraged mostly on the silt bottom fauna at depths of 15-25 m, although diving was observed at any depth down to about 30 m.

(2) Common Eiders spent between 10.7 and 45.6% (mean 27.0%) of the foraging time dabbling near the shore, while King Eiders dabbled less than 1% of the foraging time, and mainly offshore.

(3) Common Eiders spent the night resting near shore, while King Eiders rested far offshore.

The difference in diving depth corroborates earlier assumptions that Common Eiders, to a large extent, feed at lower depth than King Eiders (Brun 1971, Gjøsæter & Sætre 1974, Bustnes & Erikstad 1988) and, consequently, differ from King Eiders in the diversity and/or proportions of prey species in their diet (Cramp & Simmons 1977, Bustnes & Erikstad 1988).

Resting close to the shore provides shelter from winds and waves, but also makes flightless birds more vulnerable to predation by humans and Arctic Foxes Alopex lagopus. The following factors may account for the different resting strategies performed by the two eider species. Since dabbling requires less energy than diving it should be the preferred method of feeding, other factors being equal. It may thus be advantageous for Common Eiders to be present near the shore around dawn when amphipods are available and, in the costs for reduce addition. movements between feeding and resting sites. Considering that King Eiders feed at greater depth, and consequently at greater distance from shore, these factors are of less importance to King Eiders.

Interspecific food niche overlap

The present data give no basis for measuring to what extent the two eider species compete, but a maximum index of the food niche overlap can be assessed. The total food niche overlap can be calculated as the product of overlap indices for different independent food niche dimensions, in this case foraging habitat and foraging technique. The overlap in use of foraging habitat was 22%. Assuming that food items caught by diving differ from those caught by dabbling, the foraging technique can be considered an independent niche dimension. The amount of time spent dabbling by King Eiders within the 15 m depth-line was close to nil. Thus, the mean overlap in foraging technique was (100-27)% = 73%. A maximum index of the food niche overlap is estimated to $0.22 \times 0.73 = 0.16$ or 16%.

An essential food niche dimension, not investigated during this study, is diet. In a study of sympatric wintering King and Common Eiders in northern Norway, Bustnes & Erikstad (1988) found a food overlap of 0.15 (Morisita's index). The food overlap varies. however. greatly between areas. indicating that diet and habitat are closely coupled (see Bustnes & Erikstad 1988). Therefore, the habitat and food overlap indices cannot be multiplied directly in a calculation of the overall food niche overlap, and other formulas must be used (e.g. Morisita 1959, MacArthur 1968, 1970, Cody 1974, Fjeldså 1981). Taking other dimensions into account, e.g. food selection by bottom foraging, foraging efficiency and, in this case, diving depth within the 15 m depth-line, the total food niche overlap in the present study area would be expected to be considerably less than 16%. In other words, it is far below the limiting exploitation of c. 50%suggested by Cody (1974). It can be concluded that Common and King Eiders, in the present area, occupy well segregated food niches, and that this segregation appears to rest upon all marked behavioural differences observed.

Although there were no indications in this and my previous study of King Eider behaviour that the species had difficulties in obtaining sufficient food, food availability may become critical later in the moulting season, because of the rapidly decreasing daylength of the arctic autumn and the species' diurnal feeding behaviour (Frimer 1994b); a low interspecific food competition could therefore very well be crucial to the survival of the species. A similar and perhaps even more pronounced

situation may be expected in areas where the species' wintering ranges overlap (Lack 1968), such as southwest Greenland for the populations in question (Salomonsen 1967).

Adaptations that support the ecological differences between Common and King Eider

The two eider species are morphologically closely related. Both species show sexual dimorphism of body size, with the females being somewhat smaller than the males (see Cramp & Simmons 1977, Ericson 1987).

The Common Eider is a large (male borealis c. 2000 g) and heavily-built duck with a comparatively long bill, well adapted for tearing anchored mussels off a rocky substrate. It is known to specialise on Mytilus edulis for much of the year, with ability to show opportunistic and seasonal shifts to other immobile or slow moving prev types and to use various foraging techniques (see Cramp & Simmons 1977 for a review). Generally, it prefers to feed in the sublittoral zone. The Common Eider is subdivided into several subspecies, which vary in a number of aspects, including size of body and bill (Palmer 1976, Cramp & Simmons 1977, Mendall 1986, Ericson 1987).

The King Eider is monotypic. It is smaller (male c. 1700 g) than the Common Eider and has a shorter bill (Cramp & Simmons 1977). Food analyses of King Eiders suggest that the species has a varied diet, with molluscs, crustaceans and echinoderms comprising important parts of the food (Cramp & Simmons 1977, Bustnes & Erikstad 1988). The King Eider uses a wide range of foraging techniques (Lamothe 1973, Frimer 1994b), but it is specialised in so far as it prefers to forage by diving to comparatively great depth.

Goudie & Ankney (1986) argued, as a corollary to Bergman's (1847) rule, that for syntopic and closely related species that differ primarily in body size, the smaller species should have diets with higher energy density and/or should spend more time foraging to compensate for their relatively higher metabolic demands per unit of body mass. For diving ducks, this relation would be expected to be even more pronounced in cases where the smaller species forages at greater depth than the larger species, because diving time and the energetic costs for diving increase with depth (Houston & McNamara 1985, Nilsson 1972, Draulans 1982, Ydenberg 1988, Ydenberg & Guillemette 1991). In the present study, the estimated proportion of time spent foraging did not differ markedly between King and Common Eiders. At Disko, moulting King Eiders feed primarily on Mya truncata and Serripes groenlandicus (about 70% of the diet by wet weight) (Frimer, in prep.), which have a larger flesh:shell ratio than Mytilus edulis (Petersen 1978). presumed to be important food of Common Eiders at Disko. It therefore seems likely that King Eiders, to some extent, balance their higher metabolic demands per unit body mass and greater costs for diving by having diets with a higher energy yield per unit body mass. than those of the Common Eider. This implies, however, a significant overlap in prey size selection between the eider species, because the flesh:shell ratio varies with size in bivalves (Petersen 1978). At Disko, about 90% (by estimated wet weight) of the diet of moulting King Eiders consist of bivalves, mainly of 10 to 40 mm length (Frimer, in prep.). No data on prey size selection of Common

Eiders exist from Greenland. In a study of the diet of Common Eiders in Denmark (nominate mollissima), they primarily preyed on Mytilus edulis (91% by number), which were on average smaller than the most numerous size class (30 mm) (Jensen & Petersen 1990). In the German Wadden Sea, Common Eiders tend to select mussels of 30 to 55 mm length (Nehls & Ruth 1994) and in the Gulf of St. Lawrence, Canada, Guillemette et al. (1992) found that wintering Common Eiders preyed mainly on Mytilus edulis of one to 25 mm length and green sea urchins Strongylocentrotus droebachiensis ranging from 10 to 46 mm in diameter.

Houston & McNamara's (1985) model for single-prey loaders showed that as dive time increases, a diving bird should become less selective to maximize the rate of energy gain, because rejection of prey becomes more costly. Goudie & Ankney (1986) suggest that smaller species may have to consume alternative items more frequently when foraging than larger species, because larger species with lower energy demands per unit body mass (and larger prey) can afford to ignore alternative items when desired items are not found. The fact that King Eiders generally have a more varied diet than Common Eiders supports these general theories.

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