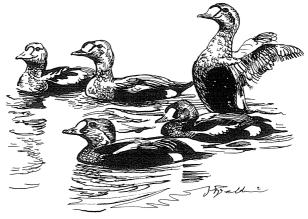
Adaptations by the King Eider *Somateria spectabilis* to its moulting habitat: review of a study at Disko, West Greenland

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(Med et dansk resumé: Kongeederfuglens Somateria spectabilis fældningsøkologi: sammenfatning af en undersøgelse ved Disko, Vestgrønland)

Introduction

Marine birds which live the whole year in the Arctic require special adaptations to survive. Their most conspicuous challenges are the long periods of short daylight and extensive ice cover over large parts of their distribution ranges. The marked seasonal limitations of food availability caused by these environmental factors, and the consequent high risk of starvation, exerts a strong selection force on the timing of migration, breeding and moult.

The King Eider *Somateria spectabilis* has a circumpolar breeding distribution in the high-arctic regions (Cramp & Simmons 1977). After breeding, the adult males and some of the females migrate to traditional areas where they undergo prebasic moult in the autumn along with a number of immatures and non-breeding adults who may have spent the summer south of their potential breeding range (Salomonsen 1968, Barry 1986, Alerstam 1990, Frimer 1994a). After completed moult, the eiders move to areas which remain icefree and spend the winter there, often close to the edge of the pack ice (Abraham & Finney 1986, Alerstam 1990).

One of the most important moult centres for King Eiders in the Arctic is West Greenland between c. 68-73°N, where more than 200000 King Eiders may be present in the autumn (Salomonsen 1967, 1968).

Schiøler (1926) examined a large number of King Eiders collected in several regions, including West Greenland, and his detailed descriptions and illustrations of King Eiders in various plumages have largely contributed to our knowledge of the timing and progress of their moult (Bauer & Glutz von Blotzheim 1969, Palmer 1976, Cramp & Simmons 1977). The significance of West Greenland for King Eiders was, however, first demonstrated by Salomonsen (1950, 1967, 1968). Under his authority more than 6000 King Eiders were ringed here between 1946 and 1974 (Salomonsen 1979). Ring recoveries have shown that the birds come mainly from breeding areas in the eastern and central Canadian Arctic (Fig. 1); those who have travelled farthest have come from Victoria Island (110°W) about 2500 km to the west (Salomonsen 1968, 1979). However, no detailed field studies of moulting King Eiders have previously been carried out in any of their moulting areas.

During 1990-1993 I stayed on Disko Island (Fig. 1), studying King Eiders. Various aspects of their moult ecology have been treated in Frimer (1993, 1994a, 1994b, 1995). The present paper reviews new and previously published information on the moult migration, timing of moult and feeding ecology during the moulting period of King Eiders, and discusses behavioural and physiological adaptations to the environmental features of the moulting sites at Disko Island.

The moulting habitat

The main part of Disko Island (8575 km²) is composed of Tertiary basaltic plateau mountains (up to 1904 m a.s.l.) with numerous U-shaped valleys. The easternmost part of the island has sandstone mountains with adjacent sandy beaches and a large shallow bay (Aqajarua/Mudderbugten). The western part has three rather narrow fjords and several smaller bays. The littoral zone varies from steep rocks, over boulder and clay to silt at river mouths.

The mean monthly temperatures are above zero in June through September, with July being the warmest month (c. 7°C), and below zero for the rest of the year, with March being the coolest month (c. -15° C) (Humlum 1987, Stonehouse 1989). The period of continuous daylight lasts from the second half of May to late July, and continuous darkness from late November to mid-January.

The highest concentrations of King Eiders are found in the narrow fjords of western Disko Island and in the eastern Disko Bay (Frimer 1993). The fjords may be ice-covered from November to mid-June, the Disko Bay from January to April (Frimer 1993). The fjords are up to about 200 m deep (Schmid & Piepenburg 1993). In Kangerluk/ Diskofjord, the density and biomass of the benthic fauna are greatest in the upper 60 m of depth, with about 3000-7000 individuals (>1 mm in size) and 31-35 g ash-free dry weight per m2 (Schmid & Piepenburg 1.c.). Curtis (1977) and Petersen (1978) give further information on the benthos communities and microhabitats of Disko Island.

A town (Qeqertarsuaq/Godhavn) with about 1100 inhabit ants is situated on southernmost Disko Island, and a settlement of about 70 inhabitants exists at the fjord Kangerluk. Human activity is mainly confined to the southern parts of Disko, from Eqaluit/Nordre Laksebugt to Aqajarua, where rather intensive hunting of eiders may take place from 15 August when the hunting season opens (Greenland Home Rule 1990). The hunting rate on King Eiders is generally low in the remote western parts of Disko Island (Frimer 1994b).

In recent years, trawlers from Ilulissat/Jacobshavn, eastern Disko Bay, have been dredging clams in Aqajarua in summer and autumn (Frimer 1993).

The moult migration Post-breeding males

In contrast to the colonial-breeding Common

Eider *Somateria mollissima*, King Eiders usually nest solitarily and dispersed over tundra areas, often close to freshwater ponds and streams (Abraham & Finney 1986, Barry 1986).

In King Eiders, as in many other waterfowl, the male deserts the female early in the incubation period and move to the nearby sea. In the eastern Canadian Arctic, it usually takes place between late June and mid-July, peaking in early July (Abraham & Finney 1986), which seems to be typical throughout the breeding range (Dement'ev & Gladkov 1967, Thing 1976, Meltofte 1977, Meltofte et al. 1981, Barry 1986, Elander & Blomqvist 1986). The post-breeding males gather in flocks with non-breeders and failed breeders, and during July the birds begin their south- and eastward migration, heading mainly for West Greenland (Abraham & Finney 1986). The major routes are through Lancaster Sound and over central Baffin Island (Fig. 1), where large numbers of migrating adult males have been recorded between mid-July and mid-August (Wynne-Edwards 1952, McLaren & McLaren 1982). Some may pass through Hudson Strait (Abraham & Finney 1986).

Post-breeding females

Compared to other ducks, eiders produce small clutches (Koskimies & Lahti 1964, Fjeldså 1977). The average clutch size of King Eiders is c. 4.5 eggs (Lamothe 1973). The young have a very high metabolic rate and become thermally independent of the adult shortly after hatching. This is probably the reason why very weak family-bonds have evolved (Koskimies & Lahti 1964, Fjeldså 1977; see below).

In King Eiders, hatching commonly takes place between mid-July and early August (Fraser 1957, Parmelee & MacDonald 1960, Lamothe 1973, Hussell & Holroyd 1974, Thing 1976, Montgomerie et al. 1983). The young are not fed by the adults (Cramp & Simmons 1977), but are conducted to the sea or larger lakes by the female shortly after hatching, usually via streams and ponds (Abraham & Finney 1986). King Eiders exhibit the same tendency to form crèches as do Common Eiders (Cramp & Simmons 1977, Abraham & Finney 1986), thus enabling post-incubating females to leave their still flightless young to join the moult migration (Palmer 1976, Barry 1986). Consequently, females depart from the breeding grounds over a wider time-scale than do males. Large numbers of females depart in the first half of August, while others stay until early September, and some may even moult near the breeding areas while acFig. 1. Map of Northeast Canada and Greenland (Disko Island inserted), showing location of places mentioned in the text.

Kort over Nordøstcanada og Grønland (Disko indsat) med lokaliteter nævnt i teksten.



companying young (Lamothe 1973, Palmer 1976, Abraham & Finney 1986, Barry 1986).

The moult migration of the females is poorly understood, and their major moulting areas unknown. Duvall & Handley (1946) and McLaren & McLaren (1982) observed about 10000 and 22000 females, respectively (assumed to include King as well as Common Eiders), passing east through Lancaster and Eclipse Sound in mid- to late August (Fig. 1). Dalgety (1936) reported thousands of female King Eiders at the Eglinton Fjord - Clyde Inlet area of eastern Baffin Island in mid-August 1934 (Fig. 1). Salomonsen (1968, 1979) assumed that the latter area is a major moulting site for female King Eiders of the eastern Canadian Arctic, and stated that adult females do not undergo wing moult in West Greenland. The age-determination of two females ringed here as "adults" were rejected by Salomonsen (1979) as being unreliable. However, recent investigations of the autumn arrival and moult of King Eiders at Disko have shown that adult females do moult here (Frimer 1994a). This discrepancy indicates that the adult females have previously been overlooked at Disko, perhaps due to their arrival in worn plumage with reduced age-class characteristics (Frimer 1994a), or that a recent change in the moult migration pattern of females has taken place. Their time of arrival at Disko (see below) falls perfectly into the pattern of moult migration of females observed in Lancaster Sound. They may thus follow the same routes as the adult males.

Females with young leave the breeding areas in early September (Salomonsen 1950, Fraser 1957, Parmelee & McDonald 1960). Little information is available on their timing and routes of migration, but there is some evidence that they migrate between mid-September and mid-October along the major routes used in spring (Abraham & Finney 1986). This is in good accordance with observations from Disko, where juveniles have been recorded from mid-September (Frimer 1994a).

In Lamothe's (1973) study area on Bathurst Island, in 1971 and 1972, failed breeders and nonbreeding females (presumed to include adults and immatures) left the breeding area during the second half of July.

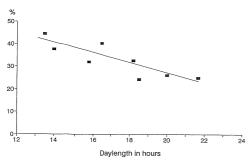


Fig. 2. Proportion (percent) of daylight hours that King Eiders devoted to foraging, in relation to daylength. Y = 71.5 - 2.2X (t = -3.98, df = 6, P < 0.01). Data from Frimer (1994b).

Andel (procent) af dagslystimerne som Kongeederfuglene anvendte til fouragering, sammenholdt med daglængden. Data fra Frimer (1994b).

Immatures

Immatures, particularly females, may follow the adults to the breeding grounds in spring, but most immatures apparently spend the summer south of the breeding areas (Palmer 1976, Salomonsen 1967). Fairly large numbers of immatures and non-breeding adult King Eiders occur along the coasts of Disko Island in the summer (Salomonsen 1950, Frimer & Nielsen 1989).

Time of arrival at Disko Island

The adult males arrive at Disko between mid-July and mid-August, peaking in early August (Salomonsen 1968, Frimer 1994a). The adult females arrive during the second half of August (Frimer 1994a). Judging from Lamothe's (1973) data on the time of departure of failed breeders and nonbreeders (see above), the females arriving at Disko in the second half of August may include these categories.

The autumn population size

The autumn (September) population of King Eiders at Disko Island has recently been estimated to comprise 15000-20000 individuals (Frimer 1993). The population may have declined markedly in recent years, or the autumn distribution has changed, because the former very important moulting area Aqajarua has now been almost abandoned. Boertmann (1979) counted about 2800 and 2500 King Eiders here in July 1975 and July 1976, respectively, and (Salomonsen (1950) reported about 30000 King Eiders in the area on a single day in August.

Time of moult

Adult males undergo body moult between early July and late August, peaking in early August (Frimer 1994a). Thus, the adult males may initiate body moult while still on the breeding grounds (e.g., Meltofte et al. 1976, Palmer 1976), and body moult is well in progress in most males when they arrive at Disko. Soon after arrival, between mid-August and late September, they undergo wing moult (Schiøler 1926, Frimer 1994a).

The adult females arrive in worn alternate plumage and undergo body and wing moult from late August and into October (Frimer 1994a).

At Disko, many immatures moult about two weeks earlier than the adult males, and flightless immatures of either sex is commonly seen here in the second half of July (Frimer 1994a). These birds have probably spent the summer in or near the moulting area. Immatures who have come from distant areas (see Lamothe 1973, Frimer 1994a) presumably moult shortly after arrival (see also Palmer 1976).

Feeding behaviour and diet of moulting King Eiders

King Eiders are primarily daytime feeders who spend most of the night resting (Frimer 1994b). Consequently, the daytime feeding intensity is negatively correlated with daylength (Fig. 2).

King Eiders are gregarious outside the breeding areas. At Disko, they usually feed in dense rafts of up to about 70 individuals with highly synchronized diving, but feeding by single birds or loose flocks with unsynchronized diving is not uncommon (Frimer 1994b). The maximum diving depth recorded at Disko is about 30 m (Frimer 1994b). In a study area in Akulliit/Mellemfjord, in the early moulting season (mid-August), most feeding took place at depths of 10-25 m (Frimer 1995).

The King Eider is an opportunistic feeder and may show great seasonal variation in diet (Cramp & Simmons 1977). At Disko, moulting King Eiders feed mainly on soft-bottom benthos but also explore hard-bottom habitats (Frimer in prep.).

The stomachs of 109 moulting King Eiders collected at Disko Island during 1990-1992 contained the remains of at least 41 prey species, including many 20-40 mm bivalves but few polychaetes (Frimer in prep.). The bivalves *Mya truncata, Serripes groenlandicus* and *Cardium ciliatum* together accounted for 83% of the diet by estimated wet weight (Fig. 3). All stomachs contained food (on average 11.1 items), and the species composition and number of items per stomach varied only slightly over the three study years, indicating that the benthic community at Disko Island was rather stable and sufficient to support the large number of King Eiders moulting in the area (Frimer in prep.). This was also reflected in the foraging behaviour of the moulting birds, displaying a similar foraging intensity to non-moulting birds and showing no signs of stress (Frimer 1994b). Thus, food is apparently not a limiting factor for King Eiders at Disko.

Interspecific food competition

The King Eider is the most numerous waterfowl at Disko in the autumn. The closely related Common Eider (subspecies *borealis*) moults in the same general area, but in much smaller numbers. Frimer (1993) estimated 3200-4800 Common Eiders at Disko Island in the autumns of 1990-1992.

The habitat exploitation of Common Eiders differs markedly from that of King Eiders. Common Eiders generally feed at lower depth and spend more time dabbling than do King Eiders. The food niche overlap between the two eider species has been estimated to be less than 16% in the moulting season (Frimer 1995).

The other common marine duck occurring in the area, the Long-tailed Duck *Clangula hyemalis*, moults in a few restricted sites at Disko of which at least one is totally outside the main moulting areas of King Eiders.

The autumn migration

In November, when the fjords and bays of western Disko Island become ice-covered, the post-moulting King Eiders congregate at the mouth of the fjords and, particularly, in the eastern Disko Bay (Frimer 1993). During November and December, the great majority of the eiders leave the Disko Bay region and migrate to Southwest Greenland where they spend the winter (Salomonsen 1967, Frimer 1993).

Conclusions

Environmental factors affecting the timing of migration and moult

Availability of open water is undoubtedly the principal factor influencing the timing of autumn (and spring) migration of King Eiders (Salomonsen 1967, Abraham & Finney 1986, Frimer 1993). The moult migration, however, takes place long before new ice begins to form in the breeding areas. As stated by Salomonsen (1968), this timing of migration is linked to the coming prebasic moult: because of the short ice-free period in the high Arctic, King Eiders leave the breeding grounds as soon as possible and move to low-arctic areas where the risk of being caught by new ice in the flightless state is low, and where autumn days are longer. West Greenland is one of the nearest lowarctic areas with suitable moulting habitats for King Eiders breeding in the central and eastern Canadian Arctic (Salomonsen 1968, 1979).

The timing of moult in King Eiders appears to be adapted to the constraints imposed by the moulting

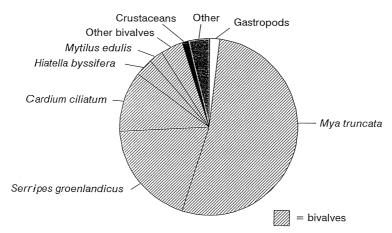


Fig. 3. Distribution on prey species (wet weight) of the autumn food of King Eiders at Disko Island, 1990-1992. Data from Frimer (in prep.).

Efterårsføden ford elt efter vådvægt for Kongeederfugle ved Disko, 1990-1992. Hvidt: snegle; stribet: muslinger; sort: krebsdyr; gråt: andre bytteemner. Data fra Frimer (in prep.).

habitat. The preferred moulting sites, the sheltered fjords and bays, may become ice-covered in November. Moreover, the daylight period shortens rapidly during the autumn, from continuous daylight in late July to continuous darkness in late November. Considering that moulting King Eiders daily spend 6 hours foraging (Frimer 1994b), and that they (if possible) restrict foraging to the daylight hours, they should complete flight-feather growth before the end of October; otherwise, they would have to cover part of their need for food at night, and also risk to get caught in new ice (Frimer 1994b). It should be mentioned, however, that even though the timing and progress of moult in King Eiders would appear to be adapted to specific environmental constraints, it resembles that of several other seaducks (e.g., Joensen 1973).

Like several other seaducks, male King Eiders usually undergo body moult before wing moult from the brightly coloured alternate plumage into the less conspicuous basic (eclipse) plumage which may be an adaptation to the increased risk of predation in the flightless state. The prebasic moult schedule of many species is somewhat plastic, however. If, for example, breeding is delayed, the onset of moult may be postponed until breeding is nearly complete, but the progress of moult is then accelerated so that the bird completes its moult almost on schedule (Hahn et al. 1992). This appears to be the case even in King Eiders, as shown by an adult male in alternate plumage who arrived in Akulliit in early September 1992, at a time when all other males in the area had attained basic body plumage. Shortly after arrival this male initiated body moult and shed the flightfeathers while still mainly in alternate plumage, so his moult schedule resembled that of females arriving at Disko in the second half of August.

Why do King Eiders moult in restricted areas?

Flightless King Eiders are vulnerable to predation and extremely shy (Frimer 1994b), and need extra energy for feather growth. Hence, the birds require sheltered areas (fjords and bays) where they are protected from predators and disturbance, and where rich food supplies are available within their usual diving depth range (c. 0-30 m). The need for open water and daylight restricts the moulting habitat mainly to the low-arctic region.

As already mentioned, there are good indications that food is not a limiting factor for King Eiders at Disko. It is therefore advantageous for King Eiders to utilize this food-rich habitat while it is ice-free, before moving on to the winter quarters.

The quality of Disko Island as a moulting habitat for King Eiders

The habitat requirements of moulting King Eiders appear to be fulfilled in the remote (undisturbed) western and northern parts of Disko Island (Frimer 1994b, in prep.). Human activity, such as hunting and dredging for clams, has apparently made the southern parts less suitable for King Eiders, and the former important moulting area Aqajarua has now been almost abandoned (Frimer 1993).

Ground and aerial surveys of the moulting areas north and south of Disko Island (see Salomonsen 1967) should be conducted, to obtain more precise information on the distribution and numbers of moulting King Eiders in West Greenland. Future studies should also focus on females at Disko. Due to their late arrival in the area, females are particularly vulnerable to disturbance (Frimer in prep.), and may thus be good indicators of environmental change.

Acknowledgments

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Resumé

Kongeederfuglens Somateria spectabilis fældningsøkologi: sammenfatning af en undersøgelse ved Disko, Vestgrønland

Vestgrønland mellem ca 68° og 73°N, og især Disko Bugt regionen, har længe været kendt som et vigtigt fældningsområde for Kongeederfugle (Salomonsen 1968). I sensommeren og tidligt på efteråret samles adskillige tusinde fugle her, især voksne hanner og ungfugle, for at fælde svingfjerene. De fleste kommer fra ynglepladser i højarktisk Canada, medens en mindre del (ikke-ynglende fugle) har tilbragt sommeren i eller nær fældningspladsen.

Denne artikel sammenfatter resultaterne af en undersøgelse foretaget i 1990-1993 under mit ophold på Disko, tillige med tidligere publiceret materiale vedrørende Kongeederfuglens fældningstræk, fældning, adfærd og føde i fældningstiden. Dette resumé begrænser sig dog til resultaterne af undersøgelsen ved Disko.

De voksne hanner ankommer til Disko omkring den første uge af august. Ved ankomsten er kropsfældningen af yngledragten tydeligt fremskreden, og det varer således ikke mange dage efter ankomsten før hannerne har



King Eiders at Disko in July. Photo: Ole Frimer. Kongeederfugle ved Disko i juli.

antaget den uanselige *eclipse* dragt. Fra midten af august til sidst i september skifter de voksne hanner svingfjerene (Frimer 1994a). Svingfjerene fældes samtidig og fuglene er ude af stand til at flyve i godt tre uger.

De voksne hunner ankommer i sidste halvdel af august. I modsætning til hannerne er hunnerne ved ankomsten stadig i fuld, men meget slidt yngledragt. De skifter krops- og svingfjerene næsten samtidig fra sidst i august til et stykke ind i oktober (Frimer 1994a).

Efterårsbestanden ved Diskos kyster blev anslået til 15 000-20 000 individer, hvilket inkluderer et ukendt antal voksne hunner (Frimer 1993, 1994a). Kongeederfuglens foretrukne fældningshabitat er uforstyrrede fjorde og bugter (Frimer 1993).

Kongeederfuglen søger næsten udelukkende føde om dagen og hviler det meste af natten (Frimer 1994b). Derfor ses fuglene om efteråret bruge en stadigt stigende andel af dagtimerne til fouragering efterhånden som dagen bliver kortere (Fig. 2). Ved Disko fouragerer fuglene hovedsageligt på dybder op til omkring 30 m (Frimer 1994b). De synes at foretrække muslinger på 20-40 mm's længde og at undgå de fleste havbørsteorme. Hos 109 Kongeederfugle indsamlet ved Disko i 1990-1992 (Frimer in prep.) udgjorde muslingerne Mya truncata, Serripes groenlandicus og Cardium ciliatum vægtmæssigt tilsammen 83% af efterårsføden (Fig. 3). Byttedyrsammensætningen og det gennemsnitlige antal byttedyr i maverne varierede ubetydeligt gennem de tre undersøgelsesår, hvilket tyder på stabile fødeforekomster for Kongeederfugle ved Disko. Fældende Kongeederfugle viste ingen adfærdsmæssige tegn på stress, og synes ikke at bruge mere tid på fouragering end ikke-fældende Kongeederfugle (Frimer 1994b). Føden synes således ikke at være en begrænsende faktor for Kongeederfuglene ved Disko.

Kongeederfuglen er den talrigeste havand ved Disko om efteråret. Alm. Ederfugl *Somateria mollissima* fælder også i området, med en efterårspopulation på 3200-4800 individer (næsten udelukkende hanner) langs Diskos kyster (Frimer 1993). Frimer (1995) beregnede føde-nicheoverlappet mellem de to ederfuglearter til at være mindre end 16% i fældningstiden. Også Havlitten *Clangula hyemalis* fælder i området, men det drejer sig om højst et par tusinde fugle fordelt på nogle få afgrænsede fældningspladser.

I november fryser Diskos fjorde og bugter til, så fuglene tvinges ud til fjordmundingerne og ind i den endnu isfri østlige Disko Bugt (Frimer 1993). I løbet af november og december forlader Kongeederfuglene regionen og trækker til åbentvandsområdet i Sydvestgrønland, hvor de tilbringer vinteren.

Undersøgelsen konkluderer bl.a., at den korte isfri periode på de højarktiske ynglepladser og de føderige habitater i Vestgrønland har været afgørende for udviklingen af Kongeederfuglens fældningstræk, samt at tidspunktet for fældningstrækket og fældningen synes at være styret af isforholdene og daglængden i fældningsområdet.

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