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BEHAVIORAL RESPONSES TO DECREASING DAY LENGTH IN WINTERING SEA DUCKS

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ABSTRACT.—Sea ducks generally are diurnal feeders, but large numbers winter above the Arctic Circle where day lengths decrease dramatically in winter. To determine how sea ducks cope with short day lengths, we studied different aspects of the behavior of three sympatric wintering species (Common Eider [*Somateria mollissima*], King Eider [*S. spectabilis*], and Oldsquaw [*Clangula hyemalis*]) at 70°N where day length is reduced to less than 4.5 h of twilight in midwinter. Numbers of both eider species remained fairly constant throughout winter, whereas Oldsquaws moved out of the area in midwinter. As day length decreased, eiders extended their feeding period into lower light intensities. Common Eiders and Oldsquaws spent a higher proportion of the day diving (underwater) when days were short, whereas King Eiders did not. As the days lengthened, King Eiders and Oldsquaws increased their total time diving at similar rates, which were faster than those of Common Eiders. Feeding at lower light intensities and increased proportions of time spent diving did not offset reduced feeding time in midwinter, and estimated time spent underwater during daylight on the shortest days was only 35% of that on the longest days in King Eiders, 51% in Common Eiders, and 39% in Oldsquaws. The ability to survive when days are short might be explained by use of stored nutrient reserves, night feeding, or high prey availability. *Received 23 July 1998, accepted 27 April 1999.*

ON NORTHERN SEAS during winter, air and water temperatures decrease and wind and waves increase, resulting in increased energy costs for wintering waterfowl (Nichols and Haramis 1980, Jenssen et al. 1989, Lovvorn 1994). In addition, day length decreases dramatically in winter, e.g. at 70°N the sun is below the horizon for two months, and day length is reduced to less than 5 h of twilight in late December. Sea ducks (tribe Mergini) mainly are diurnal feeders that depend on animal foods that include mollusks, echinoderms, crustaceans, and other invertebrates. In general, these prey species have low energy density, so large amounts of food are needed to maintain a positive energy balance (Goudie and Ankney 1986, Bustnes and Erikstad 1990, Guillemette et al. 1992, Guillemette 1998). This combination of short days and high food requirements is expected to adversely influence the energy budgets of wintering sea ducks.

To determine how sea ducks cope with decreasing day length during the arctic winter, we studied the behavior of three sympatric species that differ in body size, migration, and food habits. Common Eiders (*Somateria mollissima*; 1.8 to 2.5 kg) are year-round residents that feed mainly on mussels and echinoderms. King Eiders (*S. spectabilis*; 1.4 to 2 kg) have a similar diet but are long-distant migrants present only during winter (Bustnes and Erikstad 1988, Bustnes and Lønne 1995). Finally, Oldsquaws (*Clangula hyemalis*), are considerably smaller (0.5 to 1 kg), migrate short and long distances, and feed on much smaller prey, including snails, mussels, and epibenthic crustaceans (Johnson 1984, Sanger and Jones 1984, Goudie and Ankney 1986). We studied three nonexclusive mechanisms to compensate for reduced feeding time: (1) leaving in search of better feeding areas, (2) extending feeding periods into periods of lower light intensities, and (3) increasing the proportion of time spent feeding during daylight. We also estimated total diving times of the different species at varying day lengths.

STUDY AREA AND METHODS

Study area and general methods.—Our study was carried out in Kvalsundet (69°49′N, 19°02′E) about 15

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km northwest of Tromsø, Troms County, northern Norway, between November 1991 and April 1992. Kvalsundet is a sound 7 km long and 600 to 2,000 m wide that separates the islands of Kvaløy and Ringvassøy. Water depth reaches about 60 m, and the bottom substrate is diverse, consisting of several benthic community types described in Bustnes and Lønne (1995, 1997). Because of the warm North Atlantic Current, northern Norway is mostly ice free and mild compared with other areas at the same latitude. At this latitude, day length increases from less than 5 h (280 min) in midwinter to more than 20 h in April, including the two twilight periods. The sun is below the horizon from 20 November to 20 January.

We observed birds with a telescope on a car window mount and a Noctron night-vision scope with a 300-mm lens. All observations were made from roads running along the sound. Sea ducks were counted in the sound every second week.

Daily arrival and departure relative to light intensity.—Eiders arrived at and left the study area synchronously in monospecific flocks. We recorded the timing of 18 arrivals and 17 departures for King Eiders and 21 arrivals and 17 departures for Common Eiders at varying day lengths. We calculated the deviation in time of arrival ($Dev_{arrival}$) by subtracting time of arrival from time at start of morning twilight, and deviation in time of departure ($Dev_{departure}$) by subtracting time at end of twilight in evening from time of departure, using the standard definition of twilight (time when the sun is between 0 and 6° below the horizon). For eiders, $Dev_{departure}$ and $Dev_{arrival}$ yielded the birds' total active period in the feeding area at any given day length. Oldsquaw numbers were too few and the birds were too scattered to enable us to record their exact arrival and departure times. However, very few Oldsquaws were seen earlier or later than eiders, so we used the pooled data from eiders to estimate the total active period of Oldsquaws (see below).

Diurnal activity budgets.—The species we studied were very social and usually fed in flocks. Because it was difficult to follow individuals, we used scan sampling to determine activity budgets of entire flocks (Altmann 1974). We used a random numbers table to select available flocks independently of site, flock size, and activity. Total flock size was determined when all individuals were believed to be on the water surface. We conducted scans every 60 s for 10 to 30 min ($\bar{x}$ = 21.83 ± SE of 0.43) and counted the number of birds that were engaged in resting (resting, pausing between dive), comfort (preening, comfort movements), social (alert, aggressive, display), and locomotion (swimming, flying) behaviors. We estimated diving behavior by subtracting the previous four categories from total flock size. In this paper, we use diving as a measure of feeding behavior, but we note that other studies that used focal-sampling methods have included pauses between dives as part of feeding behavior (Campbell 1978, Paulus 1988).

For each sampling sequence, counts were converted to proportions, and successive scans from the same flock were combined to yield a single observation for statistical analysis. Size of recorded flocks varied from 1 to 180 individuals ($\bar{x}$ = 17.7 ± 1.88, n = 219) for Common Eiders, 1 to 540 ($\bar{x}$ = 60.7 ± 8.54, n = 164) for King Eiders, and 1 to 12 ($\bar{x}$ = 2.0 ± 0.21, n = 95) for Oldsquaws. King Eider flocks, especially those feeding on deep water, dived synchronously, enabling us to record time budgets of very large flocks. To ensure that sampling periods were evenly distributed, we divided the day into 3-h intervals (0600 to 0900, 0900 to 1200, 1200 to 1500, 1500 to 1800) and recorded time budgets for at least 2.5 h for each period, month, and species. Data were collected during daylight only; hence, activity data were obtained between 0900 and 1500 in midwinter and between 0600 and 1800 in late winter. The average (±SE) length per month of observation periods was 13.9 ± 1.9 h for Common Eiders, 13.7 ± 1.5 h for King Eiders, and 7.2 ± 0.9 h for Oldsquaws. Because Oldsquaws left the area in late December, no data on this species were obtained in January.

Statistics.—All statistical tests were performed with SAS (1990). Values are expressed as $\bar{x}$ ± SE, and P-values < 0.05 are considered significant. The Wilk-Shapiro test (PROC Univariate) was used to test for normality. When data were normally distributed, general linear models (PROC GLM) were applied; otherwise, we used nonparametric statistics.

RESULTS

Bird numbers.—Numbers of Common Eiders and King Eiders were relatively stable between mid-November and February (ca. 900 birds), although short-term decreases occurred in January (Fig. 1). From early March, the numbers of both eider species gradually declined to fewer than 200 birds by early April (Fig. 1). Oldsquaw numbers decreased from 110 birds in November to a minimum of 4 birds in late December and then increased slowly to more than 100 individuals by early February, after which numbers remained relatively stable until late April (Fig. 1).

Daily arrival and departure from the study area.—Common Eiders and King Eiders generally arrived at and departed from the area near the start and end of twilight, respectively (Fig. 2). The two species did not differ in their response to day length ($Dev_{arrival}$, $F = 0.003$, df = 1 and 36, $P = 0.95$; $Dev_{departure}$, $F = 0.70$, df = 1 and 31, $P = 0.41$), so data for the two species

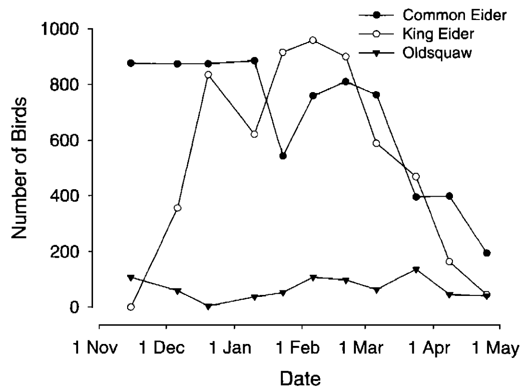

FIG. 1. Numbers of sea ducks wintering in Kvalsundet, northern Norway, between 18 November 1991 and 26 April 1992.

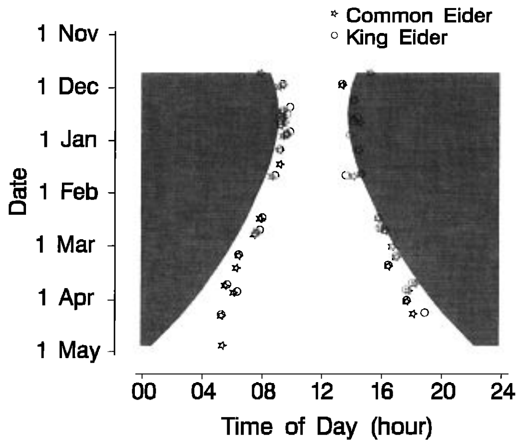

FIG. 2. Time of arrival to and departure from the Kvalsundet in relation to daylight for wintering Common Eider (stars) and King Eider (circles). Shaded areas = darkness, and white area = daylight (defined as the period when the sun is less than 6° below the horizon, including twilight periods). Data are from 1991–1992.

were pooled. As day length decreased, eiders arrived at and departed from the study area at lower light intensities ($Dev_{arrival} = 21.84 - 0.1 \times$ day length, $n = 39$, $r^2 = 0.80$, $P < 0.0001$; $Dev_{departure} = 57.83 - 0.14 \times$ day length, $n = 34$, $r^2 = 0.65$, $P < 0.0001$). As a result, the birds spent more time in the study area before and after the start of twilight when days were short than when days were long (Fig. 2).

Diurnal activity budgets.—Based on 219 sampling sequences for Common Eiders, the proportion of time spent in diving and locomotion decreased as day length increased (Table 1, Fig. 3). Monthly means of the proportion of daylight spent diving decreased from 0.257 ± 0.014 in December to 0.169 ± 0.026 in April. The proportions of time spent in comfort and social activities were positively correlated with day length (Table 1, Fig. 3).

As days lengthened, King Eiders ($n = 164$) increased the proportion of daylight hours spent in comfort activities, whereas locomotion activities decreased. The proportion of time spent diving did not change significantly (Table 1, Fig. 3), increasing slightly from 0.203 ± 0.020 in December to 0.263 ± 0.022 in March (Fig. 3).

In 95 sequences for Oldsquaws, the mean monthly proportion of time spent diving decreased from a peak of 0.546 ± 0.035 in November to 0.334 ± 0.043 in April (Fig. 3). As for Common Eiders, the proportion of time spent diving was negatively correlated with day length, whereas comfort activities were positively correlated with day length (Table 1). Social and locomotion activities did not show any trend, and the proportion of time spent engaged in these activities was very low (Table 1, Fig. 3).

Efficiency of compensation.—When combining data on the proportion of time spent diving at different day lengths (based on activity budgets) and data on the total active period (time

TABLE 1. Relationship between the proportion of time spent in various activities and day length for wintering Common Eiders, King Eiders, and Oldsquaws in northern Norway, 1991–1992.

	Common Eider		King Eider		Oldsquaw	
Activity	r_s	P	r_s	P	r_s	P
Diving	−0.282	0.0001	0.122	0.1208	−0.343	0.0007
Resting	−0.071	0.2900	0.029	0.7141	0.159	0.1241
Locomotion	−0.149	0.0275	−0.299	0.0001	0.032	0.7588
Comfort	0.517	0.0001	0.259	0.0008	0.404	0.0001
Social	0.295	0.0001	−0.062	0.4295	0.073	0.4797

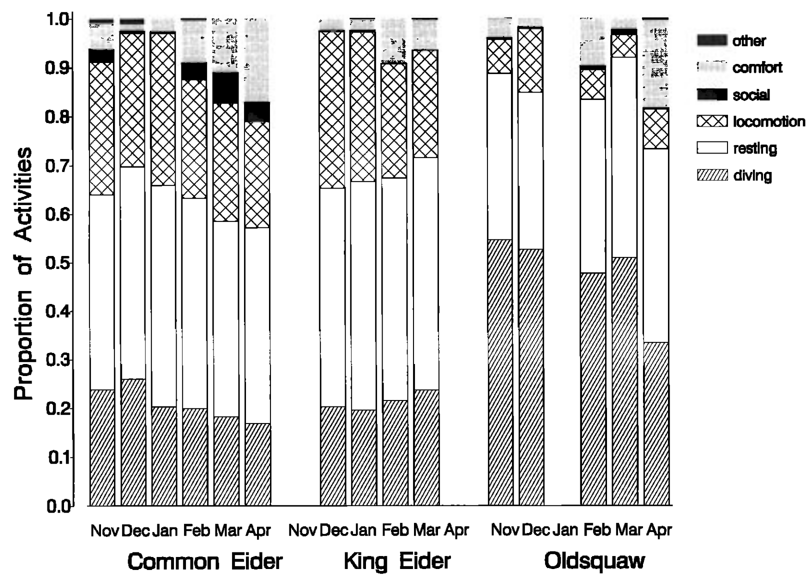

FIG. 3. Monthly means of activities (cumulative proportions) for three sea duck species wintering in Kvalsundet, northern Norway, 1991–1992. Resting includes loafing and pauses between dives.

between arrival and departure), Common Eiders were estimated to dive for a mean of 100 min/day, King Eiders for 102 min/day, and Oldsquaws for 232 min/day. Common Eiders increased the estimated diving time from a minimum of 73 min/day during the shortest days to a maximum of 144 min/day during the longest days (Fig. 4, Table 2). The corresponding values for King Eiders were 57 and 161 min/day, and for Oldsquaws 148 and 382 min/day (Fig. 4, Table 2). The full GLM model revealed a significant increase in time spent diving relative to day length for all three species (Table 2). However, significant differences existed among species in how much time they devoted to diving and/or how steeply the time spent diving increased as day length increased (Table 2). Oldsquaws spent significantly more time diving than did either species of eider (Fig. 4). Common Eiders and King Eiders spent similar amounts of time diving, but King Eiders increased their diving time at a faster rate as day length increased (Fig. 4, Table 2).

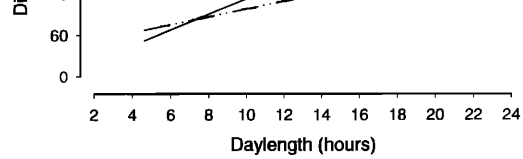

FIG. 4. Relationship between estimated diving time and day length in wintering sea ducks at Kvalsundet, northern Norway, 1991–1992. Regression lines are: Common Eider, diving = 43.156 + 0.092 × day length(min), $r^2 = 0.13$, $P = 0.0001$; King Eider, diving = 0.355 + 0.187 × day length(min), $r^2 = 0.34$, $P = 0.0001$; Oldsquaw, diving = 124.45 + 0.175 × day length(min), $r^2 = 0.22$, $P = 0.0001$. The slopes are not significantly different for King Eider and Oldsquaw (see Table 2).

DISCUSSION

The three species of sea ducks that we studied behaved differently when days were short than when days were long. However, in no case did the altered behavior result in a constant daily feeding time.

Movements.—All of the Oldsquaws left the area during the darkest period, whereas Common Eiders and King Eiders showed small temporary declines in numbers. Although Oldsquaws commonly winter in northern Norway,

TABLE 2. Analysis of covariance (type 1, mean sum of squares) comparing estimated total time of diving in relation to daylight for Common Eiders, King Eiders, and Oldsquaws (see Fig. 4) in northern Norway, 1991–1992.

Effect	df	MS	*F*	*P*
		All species		
Day length	1	725,058	124.04	0.0001
Species	2	628,873	107.59	0.0001
Day length × species	2	37,847	6.48	0.0017
Error	472	2,758,921		
		Common Eider vs. King Eider		
Day length	1	394,063	87.18	0.0001
Species	1	11,747	2.59	0.1078
Day length × species	1	53,107	11.74	0.0007
Error	379	1,713,041		
		Common Eider vs. Oldsquaw		
Day length	1	394,041	55.58	0.0001
Species	1	1,171,305	165.21	0.0001
Day length × species	1	45,323	6.39	0.0120
Error	310	2,197,751		
		King Eider vs. Oldsquaw		
Day length	1	790,855	91.94	0.0001
Species	1	811,248	26.49	0.0001
Day length × species	1	636	0.10	0.7508
Error	255	1,607,049		

conditions in the study area may have been too harsh when days were shortest, forcing the birds to leave in pursuit of better feeding areas. Alternatively, the Oldsquaws may have died (we have no evidence for this). Long movements during winter are common among waterfowl in response to food shortages or other adverse conditions (Nilsson 1970, Lovvorn 1989, Suter and van Erden 1992). The difference among species may be caused by different tolerances for harsh conditions. Smaller species usually have higher mass-specific metabolic rates than larger species and are prone to higher heat loss (Calder 1974). Although Oldsquaw prey have a higher energy density than prey of eiders (Johnson 1984, Sanger and Jones 1984, Goudie and Ankney 1986), their prey may be more mobile (e.g. crustaceans and fish) and thus probably are more energy-consuming to catch. In addition, stored nutrient reserves are important for wintering ducks (Paulus 1988), and larger species have better possibilities to store energy reserves and can withstand adverse periods better than small species (Calder 1974).

The body condition of individuals also may affect their ability to remain within a certain area. Guillemette et al. (1992) showed that Common Eiders in poor condition employed a risk-prone feeding strategy in which they used a habitat where food was less predictable but had a higher energy content (crabs). Movements to such habitats may explain the temporary reductions in numbers of all three species when days were short.

Daily arrival and departure from feeding areas.—Both eider species generally arrived in the study area at first light until mid-March. After that, they arrived no earlier than 0530 h, even if twilight started earlier. They departed close to the end of twilight in the afternoon. Day length thus explained much of the arrival and departure patterns of the birds. However, the birds fed at lower light intensities when days were short, especially in December and January when feeding was extended into the afternoon darkness. Eiders started feeding 123 min earlier and stopped 108 min later relative to the start and end of twilight, respectively, on the shortest days compared with the longest days. Thus, being able to feed under conditions of low light seems to be a mechanism by which sea ducks compensate for short days. Few studies of waterfowl have investigated factors influencing the start and termination of activity periods, but light conditions have been considered important (Paulus 1988). Raveling et al. (1972) suggested that a certain level of light was needed to trigger morning flights in Canada Geese (*Branta canadensis*), and Hein and Haugen (1966) reached the same conclusion for Wood Ducks (*Aix sponsa*). Hein and Haugen (1966) also found that Wood Ducks reduced the duration (the time between the first and last birds leaving the roost) of morning and evening flights, and that the flights started at lower light intensity as day length decreased.

Diurnal activity budgets.—Compared with most other waterfowl, sea ducks spend substantial amounts of time feeding, probably as a result of their low-quality diets (Paulus 1988). Thus, if sea ducks feed little in darkness, they would be expected to spend a larger proportion of the day feeding during short days than during long days. Common Eiders and Oldsquaws met this expectation, reducing the proportion of the day spent diving from 26% to 13% and from 53% to 20%, respectively, from midwinter to spring. A similar pattern was found for Common Eiders wintering in the Gulf of St. Lawrence, Canada, where birds fed for 56% of the daylight hours in midwinter and for 33% in spring, including pauses between dives (Guillemette 1998). In our study, Common Eiders and Oldsquaws reduced the time used for loafing, comfort, and social activities on short days. Common Eiders often display and form pairs in fall (Spurr and Milne 1976), and in our study males stopped displaying in midwinter but resumed again as the days lengthened (G. H. Systad unpubl. data). In nocturnally feeding waterfowl, increased feeding rates were found during daytime in seasons when nights were short, indicating that birds were compensating for restricted feeding periods (Nilsson 1970, Tamisier 1972, Paulus 1988). Goudie and Ankney (1986) proposed that because the smallest species had to feed for most of the day, they were less able to adjust their feeding behavior relative to environmental factors. The high diving rate of Oldsquaws (53% of the time underwater) in midwinter in our study may be close to the maximum possible rate for the species.

Contrary to the other two species, King Eiders did not decrease the proportion of the day spent feeding as day length increased. Indeed, they dived for 20% of the daylight hours in December and 24% in March. Many waterfowl species commonly exhibit high feeding rates in autumn to build up nutrient reserves, reduce their feeding rates in winter, and then resume high feeding rates in spring before migration and breeding (Tamisier 1972, Miller 1985, Paulus 1988). The increased proportion of time that King Eiders spent diving late in the season may have resulted from their preparing for migration out of the area in late March.

Compensation for lost feeding time.—For all three species, active periods in midwinter were several hours shorter than in early spring. Guillemette (1998) found that Common Eiders in the Gulf of St. Lawrence (50°N) compensated for reduced day length by feeding more intensively so that the absolute time spent feeding and diving was similar throughout the season. In our study, the estimated times spent diving on the shortest days were only 35%, 51%, and 39% of those on the longest days for King Eiders, Common Eiders, and Oldsquaws, respectively. Thus, the compensation mechanisms employed did not result in equal feeding times. The difference in day length between the Gulf of St. Lawrence and northern Norway is large. During the shortest days in our area, day length (twilight) is only half of that in the Gulf of St. Lawrence (280 vs. 557 min).

How, then, do sea ducks survive the winter at 70°N? Several possible explanations exist. First, increasing body reserves in fall may enable sea ducks to survive on stored reserves (Paulus 1988). Second, feeding at night may have occurred even though we did not observe it at the roosting sites for Common Eiders. Sea ducks generally are considered to be diurnal feeders (Player 1971, Campbell 1978, Goudie and Ankney 1986, Guillemette et al. 1992), but captive Common Eiders have been observed feeding at night (Swennen 1976). Extended feeding after dark by Common Eiders also has been observed at blue mussel (*Mytilus edulis*) beds that were exposed at low tide (Nehls 1995). Third, the low absolute time spent diving in midwinter versus early spring could be explained by prey depletion and/or reduced prey quality; e.g. urchins are an important food for both eider species in the area (Bustnes and Erikstad 1988), and Bustnes and Lønne (1995) found that the density of green urchins (*Strongylocentrotus droebachiensis*) decreased in kelp forests during winter. Moreover, green urchins start spawning in late February (N. Hagen pers. comm.), which reduces their energy content. Finally, changes in foraging profitability might have compensated for short days. In a recent study of Common Eiders, ingestion of food per unit time was higher in midwinter than in spring, and gizzard size increased to cope with the higher processing rates during the coldest period (Guillemette 1998).

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