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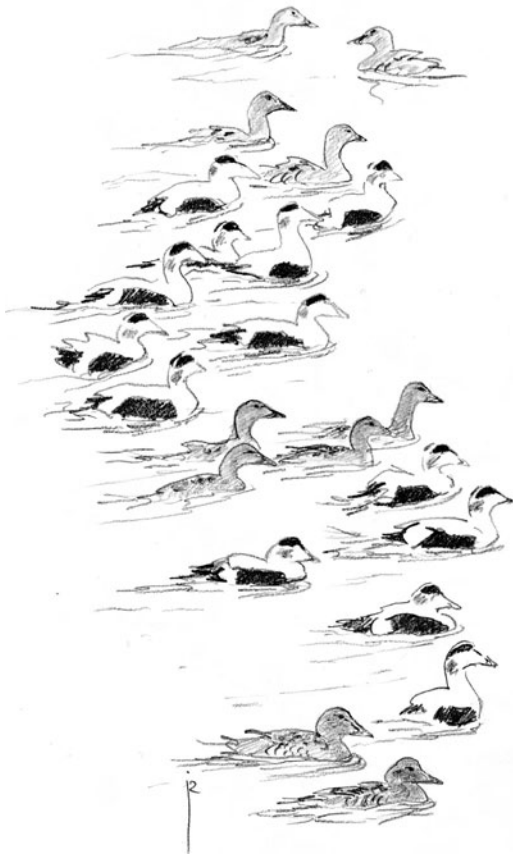
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Common Eider *Somateria mollissima* feeding activity and the influence of human disturbances

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We studied the impact of human disturbances on the feeding activities of Common Eiders *Somateria mollissima* wintering in Southwest Greenland. Eider activity and human disturbances (fast moving, open boats) were recorded during 9 days of observations in mid and late winter 2002. When most heavily disturbed, the feeding activity in the study area was reduced up to 60% on a daily basis. At the same time locomotion activity tripled. Logistic regression analyses showed that eiders attempted to compensate for lost feeding opportunities by rescheduling more feeding to periods where feeding conditions were relatively less profitable with respect to other variables. When undisturbed, eiders avoided feeding during high tide and intensified feeding at the start and at the end of the day, but these tendencies were levelled out if eiders were disturbed. When disturbed, the time interval and the distance to the last disturbance were both significant explanatory variables for the feeding activity. There was a cumulative effect of repeated disturbances on the feeding activity if disturbances were close in time and space (<1 h, <1 km). The day with the highest number of disturbances coincided with observations of nocturnal feeding the following night and may indicate that a critical threshold of disturbances was reached where eiders could not rely on a diurnal feeding strategy.

Key words: Common Eider, *Somateria mollissima*, human disturbance, time allocation, feeding activity, Greenland

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INTRODUCTION

The non-breeding season is important for migratory Arctic birds for the simple reason that this period typically represents two thirds or more of their annual cycle. Consequently, the availability and suitability of non-breeding areas and their management strongly influence their population dynamics (Newton 1998, Scott 1998). During the non-breeding period, birds must restore body reserves lost during the breeding season and they must maintain sufficient reserves throughout the winter to buffer against energy shortfalls (King & Murphy 1985, Blem 1990). The risk of not meeting these energy requirements may be severe at high latitudes; periodically inflicted by extreme weather conditions (Harris & Wanless 1984, Lovvorn 1994, Robertson

& Gilchrist 1998) or generally challenged by low temperatures and reduced daylength (Jenssen *et al.* 1988, Systad *et al.* 2000, Systad & Bustnes 2001). In addition, mortality threats often include natural predation, bycatch and hunting by man (e.g. Quinlan & Lehnhausen 1982, Denlinger & Wohl 2001).

Just as hunting and natural predation cause direct mortality, both will entail disturbances that potentially may affect population dynamics indirectly by altering an individual's investment in risk avoidance (Aebischer 1997, Frid & Dill 2002). Whether the energetic costs of this investment affects the body condition and ultimately the survival or reproduction of the bird depends on the potential of the bird to compensate by intensifying feeding later on or elsewhere (Madsen 1994, Madsen & Fox 1995, Kokko 2001). Studying dynamic

behavioural responses, e.g. a diurnal shift in feeding time allocation, can be a useful tool in assessing the impact of disturbance. Previous studies of disturbance impacts mainly dealt with direct behavioural responses, such as escape distances (Madsen & Fox 1995, Gill 2007) and only few with dynamic behavioural responses (Béchet *et al.* 2004).

Here, we investigated the effect of human disturbances (fast moving open boats) on the time spent feeding by Common Eiders *Somateria mollissima* wintering in the Southwest Greenland open water area. This area is internationally important as a winter quarter for seabirds (Boertmann *et al.* 2004), and constitutes the major wintering area for breeding populations of Common Eider in Eastern Canadian Arctic and West Greenland (Lyngs 2003, Mosbech *et al.* 2006). Estimated, 460 000 Common Eiders winter here (Merkel *et al.* 2002). Based on official harvest records around 60 000 Common Eiders were bagged annually in West Greenland in the period 1993–2001 (The Greenland Home Rule Department of Hunting and Fishing) and nest surveys in western Greenland confirmed suspicions about a major decline in the breeding population prior to 2001 (Frich *et al.* 1998, Merkel 2004a).

Seabird hunting (including eider hunting) and coastal fishing activities are practiced from fast moving, open boats during wintertime in Southwest Greenland and can cause extensive levels of traffic in the coastal areas, especially near cities and settlements (Merkel 2004b). Disturbances induced by this boat traffic are the subject of this study. We aimed to assess the impact of human disturbances on the feeding activity of eiders relative to natural variables that may influence the feeding, such as flock size, tide level, and light conditions. These are variables that previously have been documented as important determinants of feeding activities in eider ducks (Minot 1980, Guillemette *et al.* 1993, Systad *et al.* 2000, Guillemette *et al.* 2004). As measured by the level of feeding activity in predefined study transects, we also wanted to investigate the relationship between feeding time allocation and the frequency of disturbance, and finally, we wanted to determine if eiders compensate for lost feeding opportunities by intensifying feeding later on.

METHODS

Study area

The study area includes a shallow water coastal area, Nepisat (64°10'N, 51°53'W), at the mouth of the Nuuk fjord system (Fig.1). Within the Greenland Open Water

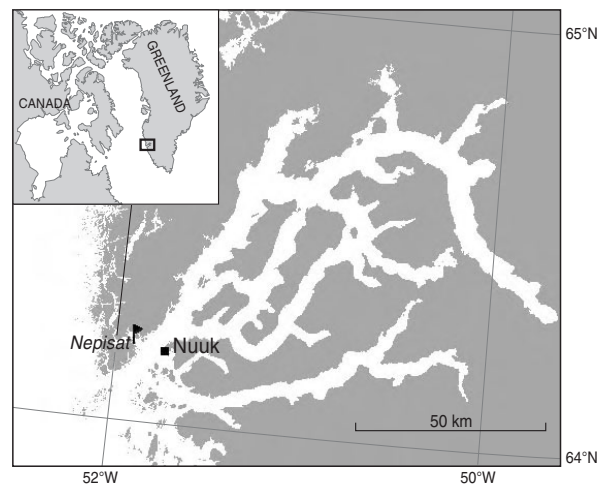


Figure 1. The capital Nuuk and the Nepisat study area, Southwest Greenland.

Area, the Nuuk fjord and coastal area constitutes key wintering areas for both King Eiders *S. spectabilis* and Common Eiders, with estimated numbers of c. 12 000 and 57 000 birds, respectively (Merkel *et al.* 2002). The municipality of Nuuk inhabits a human population around 14 000, of which 2486 persons were licensed as recreational hunters and 132 as commercial hunters in 2001. In the period 1993–2001 the hunters bagged on average $11\,579 \pm 1071$ eiders (both species) during fall, winter and spring, or approximately 15% of the total annual eider kill toll in Greenland (The Greenland Home Rule Department of Hunting and Fishing). The Nepisat study area is primarily occupied by Common Eiders, feeding on a mixture of soft-bottom and hard-bottom prey species, primarily bivalves and polychaetes (Merkel *et al.* 2007). The Common Eiders in the Nepisat area are primarily diurnal feeders (Merkel *et al.* 2008). According to systematic counts in the study area in 2002 (8 and 26 February, 30 March) 2.4% of the eiders in Nepisat were King Eiders, however, in the following observation protocol we did not distinguish between the two species. Up to c. 8000 eiders was observed during the study period. The Nepisat area is located only 6 km from Nuuk city and as a consequence it is often exposed to high levels of boating activity (Merkel 2004b, Merkel *et al.* 2008). Tide levels change approximately 4.5 m from low tide to high tide.

Behavioural observations

In the winter of 2002 we made behavioural observations from dawn to dusk (i.e. including the twilight periods before sunrise and after sunset) from a small island (camp island) in the Nepisat area at nine dates:

26–27 January, 2–6 February, 31 March, and 1 April. Observations were made from a hide at an elevated point (~10 m) using a Leica Televid 77 telescope (32x). We recorded eider activity in 12 predefined transects, which were laid out in 10° intervals, starting at 0° (North). Transect widths were fixed according to the field of vision of the telescope when pointing at a given angle (0°, 10°, 20°... 110°). Transects had a mean length of 2249 m (range 1510–2500 m) and covered an area of 3.9 km². The size of the total area that could be observed from the observation point was c. 12 km². Eiders were primarily at the inner 1300–1500 m of the transects, at which we measured water depths (close to high tide) between one and 40 m (mean 19 m). Beyond 1500 m depths gradually increased and averaged 48 m (range 14–181 m). For each transect we counted the total number of birds and subsequently observed randomly selected groups of birds (usually 1–3 groups of 5–30 individuals/transect) continuously for 75 s to classify their behaviour into three categories: feeding (diving and inter-dive pauses), locomotion (swimming or flying), and other activity (resting, comfort and social behaviour). The number of birds engaged in feeding (including inter-dive surface time) was estimated by counting the number of birds disappearing from the surface during the scan period. The duration of the scan period (75 s) was based on sequences of focal-animal sampling (Altmann 1974), which showed that inter-dive pauses rarely (5%) exceeded 75 s (mean 48.4 ± 1.3, range 22–114 s). Feeding did not include the longer resting and diet processing phase (8–17 min, Guillemette *et al.* 1992) which complete a feeding bout. We surveyed all transects in sequence each hour throughout each day. Eider activity was observed at night or in twilight periods using a Swarovski NC2 night vision scope (3x). We walked the coastline of the camp island, on average three times per night, and included observations of a roosting area located just behind the camp island. The results of the night observations are reported elsewhere and only referred to in the discussion (Merkel *et al.* 2008). Between dawn and dusk the study area was kept under observation for disturbances, i.e. boats. We determined the track of each boat as it passed through the study area by measuring its angle and distance from the hide at regular intervals. Similarly, locations of flocks were determined from angle and distance measurements, using laser binoculars (Zeiss Harlem II 8x56 and Leica Geovid 7x42 BDA). Eider flocks and boat routes were subsequently mapped in GIS, allowing us to calculate the distance between boats and eiders. Time is referred to as local time (UCT–3 h). Infor-

mation gathered after 30 March is corrected (minus one hour) for daylight saving time (summertime) to make comparison possible throughout the observation period.

Data analysis

To analyze the influence of different variables on the feeding activity of Common Eiders we used the PROC GENMOD procedure in SAS, applied the logit transformation and assumed a binomial error structure (SAS 2001). The genmod package allows groups of e.g. birds to be the observation unit and not the individuals, in contrast to traditional logistic regression. Our response variable for feeding was the number of birds engaged in feeding relative to the total number of birds observed in the flock. We corrected for overdispersion by scaling the error variance (quasibinomial error structure) and by applying the *F*-test of deviance when comparing different logistic regression models. Overdispersion occurs when the residual deviance is substantially larger than degrees of freedom, and was in our case maybe caused by social interactions among birds, i.e. the behaviour of one bird may be influenced by others. Prior to logistic regression analyses we explored the independence of observations using an autocorrelation procedure in the statistical package R. For each day, correlation coefficients *r* were calculated between consecutive observations and between observations with time lags up to c. 20 observations. For consecutive observations correlation coefficients varied between –0.24 and 0.35 and were significant in four of nine dates. In one of these four days the autocorrelation continued to be significant for observations with time lags of two and three observations (*r* = 0.31 and 0.19). Apart from this there was no meaningful detection of autocorrelation in the data, and we therefore chose not to model autocorrelation in the logistic regression analyses.

Initially, we considered 7 independent factors as explanatory variables for feeding activity. These were: the *tide* level (calculated in meters on an hourly basis); the nearest twilight period (time in min to the nearest *twilight* period, either dusk or dawn); the *chill factor* (from observations of temperature and wind speed); *abundance* (the number of birds present in a given transect); the passed *undisturbed time* since the last disturbance (in min); the *disturbance distance* to the last disturbance (to the nearest 10 m); and the number of *repeated disturbances* (number of boats within a given distance and time period). Continuous variables were organized into discrete variables to reflect expectations that changes in e.g. *abundance*, *disturbance distance* or *repeated disturbances* had larger impact on feeding ac-

tivity at the low end of the sampling scale compared to the high end. The intervals used for discrete variables (see Table 2) were based on visual inspections of data and general considerations not to generate badly skewed datasets.

When constructing the logistic regression models we followed the procedure described in Hosmer and Lemeshow (1989). First, we analyzed each explanatory variable separately to identify candidates qualified for multiple logistic regressions ($P < 0.2$, F -test). Subsequently, multiple logistic regressions were applied to all qualified main effects plus all first order interactions. Second order interactions (or higher) were not considered, except in one case, where two first order interactions included the same variable. The model was subsequently reduced by removing non-significant factors one by one according to the Type 3 F -test of deviance. A significance level of 10% was applied in the model reduction procedure (Hosmer & Lemeshow 1989).

To make the maximum use of data, we constructed two logistic regression models (Table 2). Model 1 is based only on days that included human disturbances and included the variables *undisturbed time*, *disturbance distance* and *repeated disturbances*, whereas Model 2 also includes days with no human disturbances and treats *disturbance* as presence or absence. The level of feeding activity is presented as the observed proportion of individuals actively feeding or as the change in feeding odds (odds ratio) when one variable changes (e.g. from low tide to high tide) while the others are fixed.

The testing of differences between two proportions, representing the means of two sets of proportions, was compared by a two-sample t -test after arcsine transformation (Zar 1999). For correlation analyses we used the Pearson product moment correlation coefficient r . To test for differences in mean number of birds over time we used one-way ANOVAs. Assumptions of normality and homogeneity of variances were tested using the Andersen-Darling test and Bartlett's test, respectively. For tests other than logistic regression analyses, we used a significance level of 0.05. Average numbers are reported as means \pm SE.

RESULTS

Overall activity

As counted by the hour the study transects had a mean sum of 844 ± 93 birds present between dawn and dusk ($n = 82$ counts, range 69–1696). There was a steady increase in the number of eiders around dawn and the

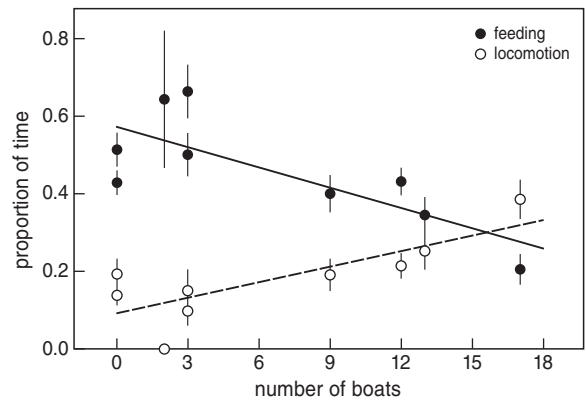


Figure 2. The daily number of disturbances (boats) in the Nepisat study area and the daily mean (\pm SE) proportion of birds engaged in feeding or locomotion among Common Eiders wintering in Nuuk, Southwest Greenland.

birds gradually moved out of the area again around dusk. Despite fluctuations within days, the mean number of birds did not change significantly between 9:00 and 16:00 when averaged for all days (814 ± 46 ; ANOVA, $F_{7,62} = 0.87$, $P = 0.53$). The only detected change was a seasonal change: significantly fewer eiders occupied the study area in late March/early April compared to January/February (386 ± 27 vs. 956 ± 42 ; $n = 28$ vs. 54 ; ANOVA, $F_{1,80} = 84.7$, $P < 0.001$).

As calculated on a daily basis there was a decrease in the feeding activity as the number of human distur-

Table 1. Logistic regression statistics based on test of deviance on Common Eider feeding activity on days with human disturbances (Model 1) and on days with and without disturbances (Model 2). See Table 2 for details on parameters.

| Parameter | df | F-value | P |
|-------------------------------|-------|---------|--------|
| Model 1 | | | |
| Tide | 1,257 | 7.13 | 0.008 |
| Abundance | 1,257 | 9.34 | 0.003 |
| Undisturbed time | 1,257 | 11.16 | 0.001 |
| Disturbance distance | 2,257 | 8.61 | 0.0002 |
| Repeated disturbances | 1,257 | 3.66 | 0.057 |
| Undisturbed time x Abundance | 1,257 | 6.86 | 0.009 |
| Model 2 | | | |
| Disturbances | 1,689 | 2.9 | 0.088 |
| Tide | 1,689 | 6 | 0.014 |
| Abundance | 1,689 | 13.07 | 0.0003 |
| Twilight | 1,689 | 6.51 | 0.011 |
| Disturbance x Tide x Twilight | 4,689 | 2.25 | 0.063 |

bances (number of boats) increased ($r = -0.77$, $P = 0.015$). More and more time was instead allocated to locomotion activity as the number of disturbances increased ($r = 0.79$, $P = 0.012$). Approximately, the observed locomotion activity tripled when comparing days with few or no disturbances with days having the highest number of disturbances (Fig. 2).

Birds exposed to human disturbances (Model 1)

The initial simple logistic regression step showed that there was a tendency for higher feeding activity at the low end of the *chill factor* scale ($P = 0.02$). However, this result was caused by observations on a single very

cold day, and the number of observations were too few ($n = 25$) to adequately represent the other variables in the proceeding analyses. All other explanatory variables qualified for multiple logistic regression ($P < 0.2$). A stepwise reduction of model 1 ($P > 0.1$) resulted in the removal of the *twilight* factor and all first order interactions except for one, the *undisturbed time x abundance* interaction term (Table 1). Based on the *F*-test of deviance, the *undisturbed time* factor was the single most important factor in explaining the variation in the estimated feeding probability of the eiders, partly as a main effect partly through the interaction with *abundance*. Birds that were recently disturbed (<1 h vs.

Table 2. Parameter estimates for logistic regression models on Common Eider feeding time allocation on days with human disturbances (Model 1) and on days with and without disturbances (Model 2). Variables that are part of an interaction term are not listed as main effects. The three columns to the right show the observed proportions of individuals feeding (mean \pm SE) corresponding to the variables included in the logistic regression models.

| Parameter | Logistic regression | | | | | Observed feeding proportion | | |
|-------------------------------|---------------------|-------|------------|----------|----------|-----------------------------|------|----------|
| | Estimate | SE | Odds ratio | χ^2 | <i>P</i> | Mean | SE | <i>n</i> |
| Model 1 | | | | | | | | |
| Intercept | -3.743 | 0.584 | | | | | | |
| Tide | | | | | | | | |
| High (above average) | 0 | 0 | 1.00 | | | 0.37 | 0.03 | 146 |
| Low (below average) | 0.747 | 0.283 | 2.11 | 6.98 | 0.008 | 0.57 | 0.05 | 119 |
| Disturbance distance | | | | | | | | |
| <0.5 km | 0 | 0 | 1.00 | | | 0.32 | 0.05 | 48 |
| 0.5–1.0 km | 0.982 | 0.413 | 2.67 | 5.66 | 0.02 | 0.43 | 0.05 | 64 |
| 1.0–2.0 km | 1.387 | 0.352 | 4.00 | 15.52 | 0.0001 | 0.52 | 0.04 | 153 |
| Repeated disturbances | | | | | | | | |
| No, 0–1 | 0.780 | 0.419 | 2.20 | 3.54 | 0.06 | 0.52 | 0.03 | 213 |
| Yes, 2–5 | 0 | 0 | 1.00 | | | 0.23 | 0.05 | 52 |
| Undisturbed time x Abundance | | | | | | | | |
| <1 h >100 | 0 | 0 | 1.00 | | | 0.21 | 0.03 | 41 |
| <1 h <100 | 1.510 | 0.401 | 4.52 | 14.19 | 0.0002 | 0.45 | 0.05 | 97 |
| 1–5 h >100 | 1.691 | 0.482 | 5.42 | 12.3 | 0.0005 | 0.55 | 0.09 | 34 |
| 1–5 h <100 | 1.814 | 0.427 | 6.13 | 18.07 | 0.0001 | 0.56 | 0.06 | 93 |
| Model 2 | | | | | | | | |
| Intercept | -1.166 | 0.201 | | | | | | |
| Abundance | | | | | | | | |
| <100/transect | 0.625 | 0.175 | 1.87 | 12.83 | 0.0003 | 0.44 | 0.02 | 531 |
| >100/transect | 0 | 0 | 1.00 | | | 0.33 | 0.03 | 167 |
| Disturbance x Tide x Twilight | | | | | | | | |
| Yes High 2–6 h | 0.503 | 0.304 | 1.65 | 2.74 | 0.098 | 0.34 | 0.04 | 118 |
| Yes High <2 h | 0.485 | 0.324 | 1.62 | 2.24 | 0.135 | 0.35 | 0.04 | 90 |
| Yes Low 2–6 h | 0.462 | 0.317 | 1.59 | 2.13 | 0.145 | 0.41 | 0.04 | 110 |
| Yes Low <2 h | 0.832 | 0.300 | 2.30 | 7.67 | 0.006 | 0.45 | 0.04 | 138 |
| No High 2–6 h | 0 | 0 | 1.00 | | | 0.32 | 0.04 | 82 |
| No High <2 h | 1.055 | 0.352 | 2.87 | 8.99 | 0.003 | 0.53 | 0.05 | 64 |
| No Low 2–6 h | 1.045 | 0.35 | 2.84 | 9.01 | 0.003 | 0.53 | 0.05 | 70 |
| No Low <2 h | 1.325 | 0.418 | 3.76 | 10.07 | 0.002 | 0.52 | 0.08 | 31 |

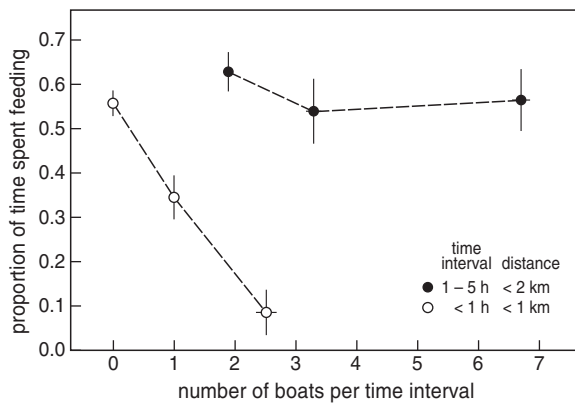


Figure 3. The observed feeding activity (mean proportion of individuals \pm SE) for Common Eiders in the Nepisat study area in relation to the number of disturbances (boats; \pm SE), within the specified distance and time interval since the last disturbance.

1–5 h) were less likely to feed (Table 1), and this tendency was stronger at high abundances (<100 vs. >100 birds per transect). Thus, birds gathered in large flocks after a recent disturbance had very low feeding odds, while birds in smaller groups approached normal feeding activity much faster. The variables *disturbance distance* and *tide* both came out as significant main effects. The odds for feeding at low tide was a factor 2.1 times higher than at high tide and there was a gradual increase in feeding odds as the distance between the observed eiders and the boats increased (Table 2). In addition, there was an effect of *repeated disturbances*, with feeding odds being a factor 2.2 lower than for birds not disturbed or disturbed only a single time (Table 2). When repeated disturbances occurred within a relatively short period of time and distance (<1 h, <1 km) there seems to be a cumulative effect on the feeding activity, approaching zero when disturbed three times within one hour (Fig. 3, lower curve). In contrast to this, the feeding activity observed 1–5 hours after one or several disturbances appeared to be rather constant and independent of the number of boats (Fig. 3, upper curve). At disturbance levels of 1–3 boats/h significantly more time was allocated to locomotion activity (0.20 ± 0.04) compared to periods 1–5 h after the last disturbance (0.07 ± 0.02 ; $t_{132} = 2.72$, $P = 0.007$).

Disturbance vs. no disturbance (Model 2)

The mean feeding activity observed on days with no human disturbances was 0.46 ± 0.03 , and this value was significantly smaller than the feeding activity observed in undisturbed periods on disturbed days (0.59 ± 0.03 , $t_{258} = 2.39$, $P = 0.017$). The mean proportion

of eiders engaged in locomotion was 0.16 ± 0.02 on days with no disturbances.

Logistic regression on the full dataset, including days with no human disturbances, differed from Model 1 in several ways. The variable *twilight* remained significant throughout the analysis and a dichotomous variable for *disturbance* (Yes/No) interacted with both *twilight* and *tide* (Table 1). The impact of *tide* was highly significant during midday (twilight 2–6 h) when birds were undisturbed, whereas this tendency was levelled out when exposed to disturbances (Table 2). The odds for feeding were lowest when high tide occurred around midday on days with no human disturbances. At all other periods feeding odds were higher in the absence of human disturbances (Table 2).

DISCUSSION

This study shows that human disturbances in the form of boating seriously affected eider feeding activity in the Nepisat area (Fig. 2), and it shows that eiders attempted to compensate for disturbances by rescheduling some feeding to periods that were relatively less profitable with respect to other variables. Bearing in mind that we made behavioural observations within fixed transects in the study area, the second conclusion is made under the assumption that the observed eiders constitute a fixed local population, with no substantial daily immigration and no use of alternative habitats on the same day. We believe that these assumptions were not seriously violated. (1) We began observation in mid-winter when there was no longer influx due to autumn- or moult migration (Lyngs 2003, Mosbech *et al.* 2006). (2) The number of birds in the study area remained constant until the end of the observation period (early April). (3) When disturbed the eiders fled to nearby sites and gradually reoccupied the Nepisat area. (4) Highly regular movements were observed on a daily basis between our study area and a roosting site that was located next to our observation point (Merkel *et al.* 2008). (5) The day with the highest number of disturbances coincided with nocturnal feeding the following night, indicating a direct response of daytime events (Merkel *et al.* 2008). (6) Satellite telemetry indicated high site fidelity among Common Eiders marked in the Nuuk coastal area (including Nepisat) with a mean core area (50%) of 8.1 km², and a mean distance between roosting sites and daytime activity centres of only 1.7 km (Merkel *et al.* 2006). (7) Among 32 Common Eiders marked with satellite transmitters, 72% used only one wintering area. The remaining 28% used on average

2.1 sites. For most of these birds, the shift was permanent (within the same season). No birds were tracked forth and back between two sites on the same day (Merkel *et al.* 2006). It remains unknown whether the decline in the number of eiders in early April was related to human disturbances, food depletion (Merkel *et al.* 2007), or pre-migratory movements (Mosbech *et al.* 2006). According to Mosbech *et al.* (2006) spring migration in the Nuuk area started in mid-April in 2000 and 2001.

This study does not distinguish between hunting and fishing activities since both use fast moving, open boats as operating platforms during wintertime in Southwest Greenland, and often the activities are combined. However, shots were released within or close to the study area in only a few cases and appeared to arise from rare hunting opportunities en route to fishing destinations. The disturbance response may also depend of the speed by which the boat approaches (Dill 1974), but in this study it proved difficult to record the speed of boats accurately. However, the vast majority of the boats observed travelled at 15–25 knots most of the time.

Evidence of disturbance impacts

We observed a decrease in feeding activity in the study area when the daily number of boats in the study area increased (Fig. 2). This indicates that boating generated disturbances that induced direct costs to the eiders in the form of lost feeding opportunities, including the time needed to relocate the same or a similar ideal feeding spot. In addition, as feeding activity went down locomotion activity went up and induced increased energy expenditure due to additional movements. This was even more evident on a short temporal scale (Fig. 3). As the number of boats approached three per hour the feeding activity was close to zero and locomotion activity nearly tripled compared to undisturbed periods. Increased energetic cost due to risk avoidance is the most common consequence reported for waterbirds in studies of human disturbances (see review by Madsen & Fox 1995). A factor less commonly considered, and indeed quantified, is the extra cost of feeding when conditions are less favourable (but see Béchet *et al.* 2004). Our results indicate that eiders avoided feeding during high tide if undisturbed, and when undisturbed they intensified feeding in the morning and again prior to the dusk twilight period (Table 2). In contrast, it appears that when disturbed, the eiders attempted to compensate for lost feeding opportunities by feeding more at high tide and during midday. On days with human disturbances the feeding activity was significantly higher in undisturbed periods compared

with days that had no human disturbances at all. The preference to feed more at the start and at the end of the day is probably related to the fact that eiders in the Nepisat area normally do not feed at night (Merkel *et al.* 2008). The cost for not doing so is not straightforward, since it will depend on feeding conditions the remaining period of the day. However, the cost of feeding more at high tide levels will clearly compromise the energy budget. Work against buoyancy and drag are the dominant components in the costs of feeding in diving birds (Stephenson *et al.* 1989, Lovvorn & Jones 1991). In our study area the tide level changed approximately 4.5 m from the low tide to high tide, corresponding to a mean water depth of c. 14.5 m at low tide and c. 19 m at high tide (the inner 1500 m of the transects).

Disturbance vulnerability

Bell & Owen (1990) referred to the Common Eider as particularly sensitive to hunting disturbance. The responses to human disturbances observed for the eiders in our study area may be used as an argument to support this. However, as argued by Gill *et al.* (2001) and Stillman *et al.* (2007), the response or the amplitude of the response to human disturbance may not be directly related to disturbance vulnerability. They argue that species showing a strong avoidance of human disturbances may not be those most seriously affected. Strong avoidance may be interpreted as having the capacity to respond, whereas no response may reflect that birds are already stressed and therefore need to accept the higher risk of ignoring the threat. In the same way Gill *et al.* (2001) argues that birds that do not leave a disturbed site may not do so simply because they have no alternative site to go to. They may therefore be more severely impacted than those leaving the disturbed area. The same argument can be used to explain the relationship between flock size (*abundance*) and the *undisturbed time* factor in our study (Table 2). We found that eiders in small flocks resumed feeding activity much faster than eiders in larger flocks. This does not necessarily mean that large eider flocks are more severely affected by disturbances than small flocks, rather that Common Eiders have a tendency to gather in large flocks when they are not feeding. The tendency for non-feeding birds to gather in large flocks is a well known behaviour for eider ducks in Greenland (Merkel *et al.* 2002) and elsewhere (Goudie *et al.* 2000).

An alternative indicator for disturbance impacts is the dynamic behavioural response, which in contrast to the direct response (e.g. avoidance distance) considers the response on a longer time scale (e.g. feeding time allocation on a daily basis). This tool has not been

widely used in impact studies of human-induced disturbances (but see Béchet *et al.* 2004). In our case the analyses of feeding activity clearly show that eiders in the Nepisat area have the capacity to adapt to human disturbances, as indicated by the change in feeding time allocation when disturbed. What remains unanswered is whether the observed change in behaviour fully compensates for the unbalanced energy budget imposed by the lost feeding opportunities and the additional work effort. If nocturnal feeding is a durable strategy to balance the energy budget, then it would appear that they possess a large potential for compensating even more if needed. Among days where we know the history about daytime events, the eiders only had to rely on nocturnal feeding a single time (Merkel *et al.* 2008). If, on the other hand, nocturnal feeding as a supplement to diurnal feeding is durable only as a short-term solution, then the incidence of nocturnal feeding could indicate that the number of disturbances on this particular day were close to the limit of what they were capable of compensating for. We tend to believe that the last suggestion is the more likely one. If supplemental feeding at night was a competitive strategy we would expect this to occur more often. Although we realize that we have studied the eiders for only a limited period of time, we know from observations in remote fjord habitats east of Nuuk that Common Eiders are capable of practicing nocturnal feeding as an exclusive foraging strategy (Merkel *et al.* 2008). However, feeding conditions are different in these areas, in such a way that visual cues are probably less important (Merkel *et al.* 2008). Eiders in our study area spent between 43% and 66% of daylight hours feeding if not frequently disturbed. This is at the very high end of that reported on Eider feeding time during winter (Goudie *et al.* 2000) and gives support to the interpretation that the eiders were at the threshold limit for maintaining energetic needs at the day with the highest disturbance level (after which nocturnal feeding was observed). Although the net-consequences of the disturbances were not quantified in this study, the factors identified as important for eider feeding activity should be considered when dealing with eider management in Southwest Greenland or similar wintering areas highly exposed to human disturbances.

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SAMENVATTING

Voor vogels die in arctische gebieden broeden is de winter een periode die van grote invloed is op de overlevingskansen. Met dit idee in het achterhoofd werd onderzocht wat het effect van menselijke verstoring is op de tijdsbesteding van overwinterende Eiders *Somateria mollissima* in het zuidwesten van Groenland. De activiteiten van de Eiders werden gedurende negen volledige dagen in de winter van 2002 geregistreerd. Tegelijkertijd werden alle menselijke verstoringen (in de vorm van langsvarende motorjachtjes van lokale vissers of jagers) in kaart gebracht. Op dagen met veel verstoringen besteedden de Eiders 40% minder tijd aan voedsel zoeken dan op dagen zonder verstoring, terwijl aan vliegen driemaal zoveel tijd werd besteed. De Eiders compenseerden de verloren eettijd door meer tijd aan eten te besteden op minder geschikte tijdstippen. Zo gingen ze ook voedsel zoeken tijdens hoogwater, waardoor ze bijna 5 m dieper moesten duiken om hun voedsel te bereiken. Bovendien vervaagden de normale foerageerpieken aan het begin en eind van de dag doordat de vogels de hele dag actief bleven voedsel zoeken. Het effect van verstoring was het sterkst wanneer bootjes op korte afstand passeerden (<1 km) en wanneer verstoringen elkaar snel opvolgden (binnen een uur). In de nacht volgend op de dag met de meeste verstoring gingen de Eiders ook 's nachts voedsel zoeken, wat er op wijst dat compensatie tijdens daglicht niet meer voldoende was. Regulering van het bootverkeer (bijvoorbeeld door varen tijdens laagwater te verbieden) wordt als maatregel geopperd om mogelijk nadelige effecten op de overwinterende Eiders te voorkomen. (JP)

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