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Does heavy investment in foraging implicate low food acquisition for female Common Eiders *Somateria mollissima*?

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In the northern Baltic Sea, Common Eiders *Somateria mollissima* feed mainly on mussels, taken exclusively by diving. By comparing the rate at which food is ingested (prey mass taken per time unit) with the rate of digestion (gut contents divided by known transit time), we found that the digestion rate was the major constraint on energy assimilation of female Common Eiders in the western Gulf of Finland (Tvärminne), whereas in the central Gulf of Finland (Söderskär), the limiting factor was the ingestion rate. This indicates that females at Söderskär had to work harder to secure one meal. The density of Blue Mussels *Mytilus edulis* of suitable size for Common Eiders was significantly lower at Söderskär compared to Tvärminne and likely the main cause for the difference. We conclude that hyperphagia at the breeding grounds was possible among females at Tvärminne, but not among females at Söderskär. Nevertheless, these differences in feeding behaviour did not translate into differences in body weights at incubation onset or clutch size. This may be due to the insensitiveness of these parameters to the ambient conditions measured, or to the fact that 1997 was in fact a benign feeding year at Söderskär. Our results suggest that females of a migratory Common Eider population to a great extent rely on reserves accumulated on the wintering grounds, but that nutrients derived from the breeding grounds may be important for maintenance of body condition and for the overall health status of a laying female.

1. Introduction

The extra energy needed for egg formation and incubation in birds is mainly derived from an increase in feeding rate (King 1972, Murton & Westwood 1977, Jönsson 1997). The high rate of food intake, termed *hyperphagia*, appears to be the main means of pre-breeding fattening of typical capital breeders (*sensu* Drent & Daan 1980). Arctic-nesting geese and eiders that invest much in building vast endogenous nutrient reserves prior to migration are well known examples of species exhibiting such behaviour (reviewed in Rohwer 1992, but see Bromley & Jarvis 1993, Choinière & Gauthier 1995). For female Common Eiders *Somateria mollissima*, building nutrient reserves facilitates the continuous incubation, this ultimately bearing an anti-predator function as the nest-attending female is constantly covering her eggs (Korschgen 1977, Hario 1983). Because females do not eat during their 24–26-day-long incubation, they may lose up to 30% of their post-laying body weight (Hario 1983). To compensate for this weight loss, females build up substantial reserves of subcutaneous fat during winter, up to the start of the laying period (Gorman & Milne 1971, Korschgen 1977, Nehls 1995, Guillemette 2001).

Common Eiders feed on molluscs, crustaceans, urchins, and other sublittoral invertebrates, of which molluscs are by far the most favoured prey (notably mussels and cockles; Bagge *et al.* 1973, Nehls 1989, 1995, Guillemette *et al.* 1992, Hilgerloh 2000, Thingstad *et al.* 2000). All prey are swallowed whole and crushed in the muscular gizzard, and the shell fragments are passed through the intestine. Due to the comparatively low energy content and high inorganic content of their food, eiders must eat large quantities of food to meet the daily energy requirement, including the extra needs during hyperphagia (Bustnes & Erikstad 1990, Guillemette *et al.* 1992, Nehls 1995, Öst & Kilpi 1998). Less than 15% of the total dry weight of molluscs is comprised of organic "flesh" (the soft, unsegmented body), the rest being calcareous shell, carapace, plate, spines, or other nondigestible material. While feeding on molluscs, eiders ingest daily 0.5–2.5 kg of this inorganic matter (Swennen 1976, Thompson 1985, Bustnes & Erikstad 1990, Guillemette 1998, Öst & Kilpi 1998). Cracking the food's defences in the digestive tract and getting rid of them in the faeces makes up the most time-consuming component of eiders' feeding, at least when food is not in short supply. Eiders store food in their distensible esophagus, and supply their gizzard on demand (Guillemette 1994). The crushing activity of the gizzard probably reaches its maximum when the bird is in resting phase (Guillemette *et al.* 1992, Nehls 1995). Thus, by observing the bird's behaviour it is possible to infer the ingestion rate vs. digestion rate based on a few parameters in a simple model.

By comparing the rate at which food is ingested (prey mass taken per time unit) with the speed of digestion (gut contents divided by known transit time), Guillemette (1994) showed that the low defecation (digestion) rate had a profound impact on the feeding efficiency of wintering Common Eiders in Canada. Being lower than the ingestion rate, the digestion rate was the major constraint on energy assimilation. This means that Common Eiders did not need to maximize their ingestion rate (feeding effort) to permit their digestive system to work at the maximum capacity. Theoretically, an efficient animal relying on food that is plentiful but of poor nutritional value, should replenish its storage before it empties completely so that the gut always operates at maximum capacity (Sibly 1981, Sibly & Calow 1986). Wintering eiders in Canada whose meal size and feeding bout duration were regulated by the gut capacity clearly fulfilled this requirement.

However, when ingestion rate falls below the digestion rate, digestion cannot reach its maximum capacity and, what is more, the bird is no longer in a positive energy balance during which body reserves accumulate (theoretical framework presented by King 1961). In Common Eider females, this may bear consequences on reproductive investment in the form of lowered clutch size or reduced ability to withstand physiological stress during incubation. In this paper, we compare the digestion rate and ingestion rate of pre-laying Common Eider females at two localities in the Gulf of Finland, in the northern Baltic Sea. We aim to determine whether possible differences in foraging investment reflect differences in food acquisition, and whether birds in either of the two populations are in a negative energy balance prior to breeding. As in many other circumpolar areas, Common Eiders in the Baltic are currently declining (CAFF Circumpolar Seabird Working Group 1997). Reasons are largely unknown, but food deficiency has been one of the most widely speculated issues lately (e.g. Pihl *et al.* 2001).

2. Material and methods

We compare the pre-laying feeding rates of Common Eider females at two localities in the Gulf of Finland, situated at opposite ends of a blue mussel gradient in the Gulf. At the western site, Tvärminne archipelago (59°50′N/23°15′E), the Eider population is stable and mussel stocks are larger than at Söderskär bird sanctuary, 130 km eastwards (60°15′N/25°25′E), where Eiders have been declining at 7% per year since 1986, and mussels are smaller in size (median shell length

3 mm against 5 mm at Tvärminne, maximum length ranging 10.8–13.9 mm in 1996–1998 at Söderskär and 24.7–30.6 mm at Tvärminne; Hario *et al.* 1999, Westerbom *et al.* 2002). The study was conducted in 1997 when there were about 1500 and 1078 breeding pairs of Eiders at Tvärminne and Söderskär, respectively. In both areas, most of the population breeds on rocky islets partly covered with low shrubby vegetation (mainly juniper bushes), and the rest breeds on partly wooded islands. More detailed descriptions of the nest-site selection of the populations are given by Hario and Selin (1988) (Söderskär) and Kilpi and Lindström (1997) (Tvärminne).

The Baltic Sea is a small marginal sea with low salinity and few benthic species. The available diet spectrum for eiders in the central Gulf of Finland seems comparatively narrow (there are no crabs or urchins in the Baltic), the main food items are small, and there is no tide and consequently no easy exposure of mussel beds for surface feeding and dabbling. Vertically, the greatest biomass of Blue Mussels *Mytilus edulis* lie at depths of 5–8 metres (Westerbom *et al.* 2002). Eiders in the Gulf of Finland need to secure mussels primarily by diving.

2.1. Pre-laying foraging behaviour

Feeding effort is measured as the duration of the feeding bout, based on the assumption that the mean feeding bout indicates the mean time that is required to fill up the esophagus with 80 g of mussels (Guillemette *et al.* 1992). Longer feeding bouts then translate into lower feeding efficiency and lower ingestion rate (meal size divided by the length of the feeding bout).

A foraging cycle is composed of a feeding bout and a subsequent resting bout. Feeding bouts are composed of successive dive-cycles, each of which consists of diving and pausing before the next dive (Ydenberg & Forbes 1988). The resting bout follows a completed feeding bout when the gut contents have been filled, and the end of the resting bout demarcates consecutive foraging cycles.

For sampling foraging cycles, we used focal animal sampling (Altmann 1974). However, we did not cut the focal sampling time at 30 min as did Guillemette *et al.* (1992), but continued the observation for as long as the bird was engaged in active feeding. This was because the duration of feeding behaviour was of primary interest, and therefore, the sessions should be long enough to obtain an adequate estimate of the distribution of durations (Altmann 1974). Focal pairs were chosen randomly by scanning the surrounding shorelines for resting pairs. In order to ensure that the esophagus contents had been digested, only pairs that had been resting for at least 30 min were chosen. Thus, the first pair in view entering the water after resting for at least 30 min was selected. The birds were then followed using binoculars (10×) or telescopes (20–40×) for their entire series of foraging cycles, and their behaviours were categorised as: (1) diving, (2) resting, and (3) other activities, separately for the female and the male. Observation was stopped when the focal birds remained inactive for at least 20 min, indicating that the pair had entered a longer roosting period.

Only the first two behavioural categories are treated here. Of the various behaviours of the third category, one needs to be mentioned. The most typical threat display given by the female, "chin-lifting", was very common, readily interrupting her foraging behaviour on many occasions, but was mostly of short duration, and, when not exceeding her normal recovery time following a dive (termed "pause", roughly half a minute long), was omitted (i.e., merged into pause).

As a sampling unit we use the mean duration of an activity of an individual female. At Söderskär, all nesting females have been colour-ringed since 1992, and thus, the measured variables could be related to the proximity of the female's laying start, known from direct observation at her nest. At Tvärminne, females were not individually marked and thus their laying date was not known. At Söderskär, however, proximity to laying was not correlated with female feeding intensity during the 19 days spanning the start of laying (16 days before laying + 3 consequtive laying days; Fig. 1a; Spearman rank correlation between number of days and the percentage of feeding bouts of total observation time, $r_s = -0.12$, $n = 58$, $P > 0.3$), whereas in males there was a highly significant negative correlation between laying proximity and feeding intensity (Fig. 1b; $r_s = -0.58$, $n = 58$, $P < 0.001$). Therefore, the com-

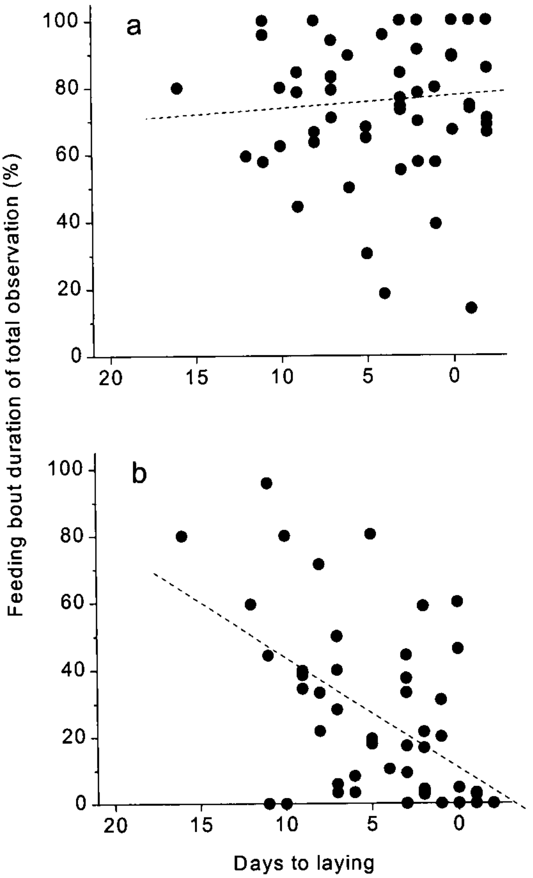

Fig. 1. The relationship between the days to laying start (day 0) and the proportion of active feeding of total observation time for individually known females (a) and their mates (b) at Söderskär, based on 58 completed foraging cycles of 21 different pairs in 1996–98 (Hario in prep.). Data extend to laying of the 3rd egg (on day 2; day 0 marks the laying of the 1st egg) after which most females gradually commenced incubation, being out of sight by daytime. Broken lines show linear regression equations fitted to the data for illustrative purposes only (see text).

parison between the data from Tvärminne and Söderskär is made on females only. The calendar timing of the observation periods at both sites roughly match, making comparisons feasible, and median laying dates were only 5 days apart in 1997 (24 April at Tvärminne, 29 April at Söderskär; Hario *et al.* 1999).

At Söderskär, observations were made in April–May from a lighthouse tower overlooking the entire study area (a 2.5 ha island). Due to the elevated lighthouse position in close proximity to the eiders, the colour ring combinations of females were readily identifiable. A total of 23 completed series of foraging cycles of 11 different females were recorded (ranging 1–5 per female, mean 2.1). For females sampled more than once, mean values for all focal periods were used as independent data points in statistical analysis.

At Tvärminne, we used high vantage points on rocky islets in sampling a total of 25 females. In two cases, the bird was lost from sight before any foraging cycle was completed; for these two females, only data on dive duration were included in the analyses. Despite the fact that birds from Tvärminne were not individually known, we believe that the probability of repeated observations of the same birds was small because of the large number of pairs present and our constantly changing observation sites (only one focal pair selected at each vantage point). Pre-nesting eiders show high fidelity to their feeding sites in close proximity to the shoreline of their nesting island (pers. obs.). MH collected the data at Söderskär and MÖ at Tvärminne.

2.2. Blue Mussel sampling

The occurrence of Blue Mussels was surveyed in 1997 by SCUBA diving in May–July (O. Mustonen & J. T. Lehtonen, unpubl.). All sampling sites were represented by hard bottom mussel beds frequented by foraging eiders. The salinity ranges from approximately 5.5‰ at Söderskär to 6–7‰ at Tvärminne (Perttilä *et al.* 1995). Benthic sampling was done by placing a 21 × 21 cm metal frame on the bottom and removing all material from within the frame into a bag. Samples were taken at a depth of 8 m, representing an optimal depth for mussels in the areas (O. Mustonen & M. Westerbom, pers. comm.). Three parallel samples (each sample 21 × 21 cm) were taken from each sampling site at both localities during the same calendar week (4 sampling sites from Söderskär i.e. a total of 12 samples, and 5 from Tvärminne i.e. a total of 15 samples).

The samples were first sieved through a 0.1-mm mesh screen and then frozen. The sampled mussels were later subdivided into 4 size classes (I: 1.8–3.5, II: 3.6–6.5, III: 6.6–19, and IV: > 19 mm long), by sieving them through 4 different mesh screens. The mean length of mussels in each size class was separately approximated for Söderskär and Tvärminne, by measuring the length of mussels in subsamples with a vernier calliper (100 mussels/size class/study area). The biomass of mussels, defined as the dry flesh weight of mussels/m^2, was calculated by substituting the estimated mean length of mussels of a certain size class into the biomass equation of Öst and Kilpi (1998), and multiplying this value by the number of mussels in that size class. The total biomass of mussels of preferable size for eiders (Öst & Kilpi 1998) was defined as the pooled dry flesh weight of mussels/m^2 excluding the smallest size class; this also excluding the varying effect of yearling mussels in samples (the annual growth rate of Blue Mussels in central Gulf of Finland averages only 2.3 mm/year; Westerbom *et al.* 2002).

2.3. Data on breeding performance

Measurements of reproductive performance (laying date and/or hatching date, clutch size) were obtained by direct observation at Söderskär. At Tvärminne, laying was timed by the egg floatation test (Kilpi & Lindström 1997). At both sites, females were captured on average on day 20 of incubation and weighed (to the nearest 10 g with a Pesola spring balance). Using regression equations for weight against incubation time (see Laurila & Hario 1988, Kilpi & Lindström 1997) we back-calculated the weight at incubation onset (i.e. the post-laying weight) separately for Söderskär and Tvärminne, and separately for open habitats and wooded islands at Tvärminne (only open habitat found at Söderskär). This was done because weight loss during incubation was found to depend on the type of breeding habitat (open/wooded) (Kilpi & Lindström 1997).

2.4. Statistical analyses

Mean values are given with standard errors, tests are two-tailed, and the significance level is set at 0.05. The similarity of variances was tested with Bartlett's test. When data were normally distributed and did not show heteroscedasticity, a parametric test was applied; otherwise differences were tested with non-parametric tests or a transformation was applied.

3. Results

3.1. Feeding vs. resting bout duration

Feeding bouts were on average three times longer at Söderskär (45.0 ± 6.6 min, Fig. 2a) than at Tvärminne (15.2 ± 1.7 min; Mann-Whitney $U = 12.00$, $n_1 = 11$, $n_2 = 23$, $P < 0.001$), whereas resting bouts were of similar average duration (7.9 ± 1.5 min vs. 10.9 ± 1.3 min; one-way ANOVA, $F_{1,30} = 1.129$, $P = 0.592$, Fig. 2b). Dive durations did not differ among sites (Söderskär 34.9 ± 3.8 sec, Tvärminne 36.0 ± 1.9 sec; ANOVA $F_{1,31} = 0.075$, $P > 0.1$, Fig. 2c), indicating that there were no differences in dive depth. This means that the longer feeding bouts at Söderskär were an outcome of more dives, not of longer surface pauses between dives as the surface pauses on average increase with dive length (due to increasing physiological stress). The total time of being submerged during a feeding bout was 24.7 ± 6.4 min at Söderskär compared to 7.2 ± 1.0 min at Tvärminne, a highly significant difference (Mann-Whitney $U = 29.00$, $n_1 = 11$, $n_2 = 23$, $P = 0.004$).

3.2. Blue Mussel populations

The mussel population structure at Söderskär differed significantly from Tvärminne, the density of larger mussels being significantly lower at Söderskär (Kolmogorov Smirnov test, $D = 0.36$, $n_1 = 3374$, $n_2 = 3051$, $P < 0.001$, Fig. 3a). The estimated mean size of mussels was 3.4 mm at Söderskär and 5.6 mm at Tvärminne. Consequently, the total biomass of mussels of suitable size for Common Eiders, i.e. the pooled dry flesh weight of mussels/m^2 excluding the smallest size class, was fivefold greater at Tvärminne ($\bar{x} = 10.8 \pm 4.9$ g/m^2) compared to Söderskär (1.9 ± 0.4 g/m^2) (Mann-Whitney U-test, $U = 131$, $n = 27$, $P < 0.05$, Fig. 3b).

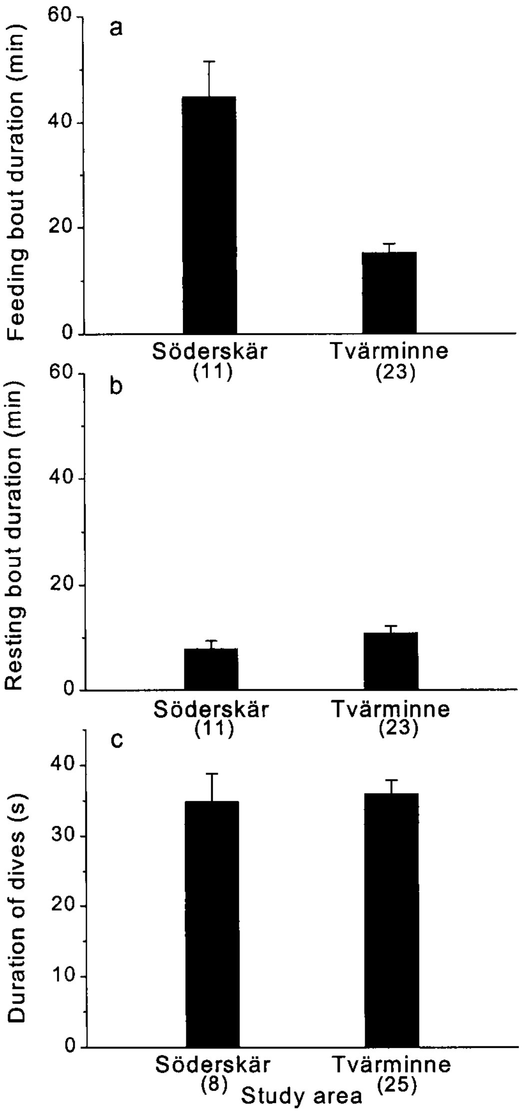

Figure 2. The mean (+ SE) length of the feeding bout (a), resting bout (b), and duration of dives (c) for females at Söderskär and Tvärminne in 1997. Number of observed females in parenthesis.

3.3. Breeding data

Clutch size was similar at Söderskär (5.1 ± 0.1, n = 50) and Tvärminne (4.9 ± 0.1, n = 123) in 1997 (independent t-test, t_{171} = 1.13, P = 0.17). Also, the body weight of females at the start of incubation did not differ between the sites (2051 ± 21 g, n = 50 vs. 2089 ± 16 g, n = 127; independent t-test, t_{175} = 1.34, P = 0.18).

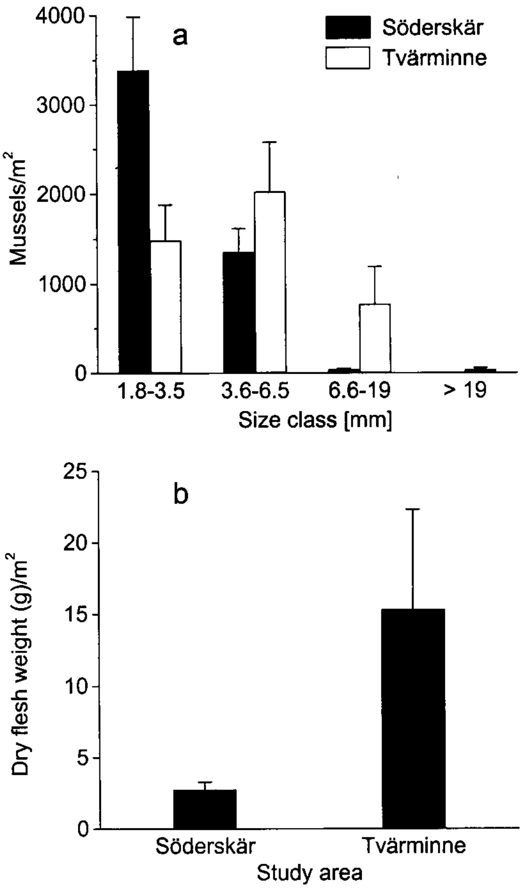

Fig. 3. The mean (+ SE) density of mussels belonging to different size classes (a), and biomass/m^2 of mussels larger than 3.5 mm (b) from Söderskär (n = 12 samples) and Tvärminne (n = 15).

4. Discussion

In birds, food is moistened and swallowed quickly (reviewed by, e.g., Campbell & Lack 1985). If food availability drops to a low enough level, however, this can result in a longer process of feeding than merely deduced from the elimination of the nondigestible exoskeletons of the prey. In eiders, hyperphagia prior to laying is common, whereas during egg laying females are believed not to eat (Korschgen 1977, Parker & Holm 1990, Christensen 2000). However, the need to secure extra body reserves for breeding may require feeding to continue throughout the laying period, at least if food acquisition is low. This was seen at Söderskär where females' feeding bout duration did not show a decreasing trend up to and including the laying of the third egg (in many cases the penultimate egg of the clutch, after which the incubation gradually starts and the female stays at the nest during the daytime; Fig. 1).

4.1. The ingestion–digestion dichotomy

We make the premise that feeding bout duration indicates ingestion effort in Common Eiders (Guillemette *et al.* 1992, Guillemette 1994, Nehls 1995). Ingestion rate is then a product of division of esophageal contents (mass of ingesta, in grams) by the duration of the feeding bout (in minutes). Digestion, on the other hand, involves the sequential mechanical and chemical breakdown of food components when making them suitable for absorption. Digestion rate is then a product of division of the total gut contents by the transit time. According to Guillemette (1994), the mean esophagus content is 80 g of mussels, the total gut contents averages 165 g of mussels, and average transit time through the alimentary tract is 63.5 min (Swennen 1976). Because the end result of digestion is the absorption of nutrients and water, only mussel shells are being used as a common denominator in our comparison of ingestion and defecation rate. Therefore, all our estimated rates are reported in terms of mussel shells ingested, processed, and defecated. The 80 g of mussels in the esophagus is equivalent to 68.3 g of shell material (mean dry shell weight of total mussel weight averaging 85.4% in Baltic Blue Mussels; Öst & Kilpi 1998), and the 165 g of gut content is equivalent to 140.9 g of shell material.

At Tvärminne, the ingestion rate 4.5 (68.3 / 15.2) clearly exceeds the defecation rate 2.2 (140.9 / 63.5), which is in line with the prediction of an efficient animal permitting its digestive system working at the maximum rate and storing food. In contrast, the ingestion rate of females at Söderskär, 1.5, (68.3 / 45.0) is far lower than the defecation rate (2.2, see above), indicating that food is not supplied into the gizzard fast enough to equal the gizzard's working capacity, and thus the rate of ingestion, and not of digestion, was the major constraint on energy assimilation.

However, one could argue that the transit time used here (63.5 min) is too long, exaggerating the difference between ingestion and defecation rates in favour of Tvärminne, i.e. reducing the defecation rate (gut contents divided by the transit time) sufficiently to become below the ingestion rate (esophagus content divided by the feeding bout) (for the problem, see Guillemette 1994). Yet, altering the transit time to equate the rate at which food was ingested results in a 93-min transit time at Söderskär [(2.2 / 1.5) × 63.5] and a 31-min transit time at Tvärminne [(2.2 / 4.5) × 63.5], which does not make sense. In contrast, the transit time given by Swennen (1976) was based on 13 trials in which colour differences of four different prey types were recorded and timed in faeces of two non-starved Common Eiders. These transit times ranged from 51 min to 75 min, averaging 63.5 min (Swennen 1976: Table 19). This seems a good parameter for constructing defecation rates in Common Eiders, and can be used with confidence.

Feeding bouts at Tvärminne were very similar in duration as compared to values reported from local populations in Canada (13.2 min, Guillemette *et al.* 1992; 10–20 min, Ydenberg & Guillemette 1991), or the German Wadden Sea (10–20 min, Nehls 1995). Resting bout durations, on the other hand, are roughly of the same magnitude across all studies (8–20 min). Thus, processing the meal seems to be an equally "easy" task across localities, whereas collecting the meal is far more laborious for females feeding in an area of low prey density including small prey size.

4.2. Does hyperphagia occur on the breeding grounds?

Blue Mussel densities at Tvärminne were manifold compared to those at Söderskär, and Söderskär females worked three times as long to complete one feeding bout. The low food availability had a profound effect on foraging by increasing the length of feeding bouts, so that energy assimilation in Söderskär females was constrained by the ingestion rate. This is in sharp contrast with the females at Tvärminne who were not food limited and apparently in a positive energy balance. At least in theory, hyperphagia on the breeding grounds was possible among females at Tvärminne, but not among females at Söderskär. It is noteworthy that these differences in feeding behaviour did not translate into differences in body weights at incubation onset or clutch size. Perhaps the food situation in 1997 at Söderskär was not bad enough to affect breeding parameters measured? Indeed, 1997 was a good year in terms of a higher-than-average body weight and a clutch size larger than ever since 1983 at Söderskär (Hario *et al.* 1999). Furthermore, the density and biomass of Blue Mussels were found to be recovering from the previous year low (Westerbom *et al.* 2002), and serum chemistry profiles of incubating Söderskär females indicated a better nutritional status in 1997 compared to 1998 and 1999 (Hollmén *et al.* 2001). It may also be that indicators such as body weight and clutch size simply are not particularly sensitive to variations in food acquisition on the breeding grounds.

It may be that food at the northern Baltic breeding sites, at the end point of a 1000 km long spring migration flight (Alerstam *et al.* 1974) is mainly for the maintenance, and food intake on the wintering grounds and/or stopover sites may have a larger impact on fecundity. Comparing our results with previous studies on eiders reveals that large differences in the reliance on local vs. imported food resources seem to exist even among different populations of the same species (Korschgen 1977, Parker & Holm 1990, Christensen 2000, Guillemette 2001).

What are the ecological consequences of females working harder for their livelihood at Söderskär? Comparing the two areas, the population trend is the only difference detected so far (Hario *et al.* 1999). Yet, population trends show closer response to changes in recruitment rate than to clutch size or female body weight (Hario & Selin 1988). Perhaps females at Söderskär were still not yet working at the uppermost limit of their capabilities when looking for suitable-sized mussels, or they made use of various alternative prey species, notably of Baltic Tellins (*Macoma balthica*). At Tvärminne, tellins have not been observed in the faeces of Common Eiders (Bagge *et al.* 1973, Hario *et al.* 1999, M. Westerbom, pers. comm.), whereas they were common at Söderskär in 1997. Tellins are burrowing clams and possibly more difficult to collect than clustering Blue Mussels. They also seem to be an energetically poor substitute for mussels and are directly avoided by Eiders in areas with access to mussel beds (Hilgerloh 2000). However, this reasoning does not change the main result of this study: heavier investment in foraging does implicate lower acquisition of preferred-sized food, notwithstanding the possible enlargement of diet spectrum into alternative prey.

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Selostus: **Ilmentääkö Suomenlahden haahkojen ahkera ravinnonotto ravintovarojen niukkuutta?**

Keväällä 1997 Söderskärin haahkanaaraat olivat ravinnonotossa (simpukkasukeltelussa) kolme kertaa pitempiä ajanjaksoja kuin Tvärminnen naaraat (kuva 2). Silti niiden ruokailun lepojaksot ja sukellusajat olivat yhtä pitkiä. Söderskärin naaraat jatkoivat ravinnonottoa munintakautenaan siihen asti kunnes aloittivat haudonnan; tuolloin koiraiden ravinnonotto oli jo kokonaan loppunut (kuva 1) ja ne pelkästään vartioivat puolisoaan. Yhden ruokailurupeaman kaikkien sukellusten yhteenlaskettu aika (pinnanalainen aika) oli Söderskärin naarailla keskimäärin 28 minuuttia ja Tvärminnen naarailla 7 minuuttia. Söderskärin naaraat tekivät siis huomattavasti enemmän töitä saadakseen kupunsa täyteen. Kupuun mahtuu kerralla 80 g sinisimpukkaa ja lihasmahaan 20 g. Koko ravintoannoksen läpimenoon ruuansulatuksessa kuluu aikaa runsas tunti. Suhteuttamalla tämä aika ravinnonottoon käytettyyn aikaan laskettiin naaraille tehokkuusindeksi. Se osoitti Söderskärin naaraiden joutuvan sukeltelemaan siinä määrin paljon ravintonsa eteen, etteivät ne enää kykene lisäämään varastorasvojensa määrää, toisin kuin Tvärminnen naaraat, jotka teoriassa olisivat kyenneet vielä lihottamaan itseään. Söderskärillä haahkalle sopivankokoista sinisimpukkaa oli merkitsevästi harvemmassa kuin Tvärminnessä (kuva 3), mikä saattaa olla syy havaittuun aikaeroon ravinnonotossa. Pesyekoossa ja naaraiden ruumiinpainossa ennen munintaa ei kuitenkaan ollut eroja alueiden kesken. Ilmeisesti naaraiden jatkuva ravinnonotto pesimävesillä ennen munintaa on lähinnä ehkäisemässä munapesyeeseen ja pitkään haudontaan talvialueilla kerättyjen energiavarantojen ennenaikaista ehdyttämistä. Siten pesyekoko ja naaraan kunto määräytyvät talvialueiden olosuhteista, eivätkä Suomenlahden ravintovarat ainakaan nykyisellään edellytä naaraiden tinkivän pesyekoosta ja kunnostaan.

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