DIGESTIVE-RATE CONSTRAINT IN WINTERING COMMON EIDERS (*SOMATERIA MOLLISSIMA*): IMPLICATIONS FOR FLYING CAPABILITIES

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ABSTRACT.—Rates of ingestion and digestion for wintering Common Eiders (*Somateria mollissima*) feeding on blue mussels (*Mytilus edulis*) were estimated using information on average meal size, feeding- and resting-bout durations, and transit time. Rate of ingestion of mussel shells is two times higher than defecation rate; as a consequence, shells accumulate in the gut as ingestion progresses. On average, eiders shot when flying ($n = 92$) had 1.1% of their body mass as prey compared with 3.7 and 6.4% for eiders foraging in small and large flocks ($n = 77$), respectively, suggesting that eiders tend to minimize the transportation of surplus mass when flying. Wing loading of the Common Eider averages $2.0 \text{ g} \cdot \text{cm}^{-2}$, which is among the highest values determined for a bird species capable of flight. Maximum gut contents were between 8 and 11% of body mass for eiders foraging in large rafts; such mass of food significantly increases wing loading and is associated with a reluctance or a possible inability to take flight. I hypothesize that meal size in Common Eiders is regulated in response to flight limitations that result from the added mass of a meal. *Received 11 June 1992, accepted 29 January 1994.*

INGESTION AND DIGESTION have been studied as two consecutive processes in few bird species (Kenward and Sibly 1977, Worthington 1989). Most studies dealing with the foraging ecology of an animal assume that the rate of ingestion of prey maximizes energy assimilation (Schoener 1987 and references therein). However, the rate at which food is assimilated or metabolized may be constrained by ingestion when food is scarce, and by digestion when food is abundant but of poor quality (Sibly 1981). Energy assimilation may be limited by the digestive process because food ingested must be broken mechanically and digested by gastric and intestinal agents before being absorbed and metabolized by the animal. In fact, if the digestion rate is lower than the ingestion rate, it is less likely that ingestion would be maximized (Verlinden and Wiley 1989). If so, an efficient animal should adopt a feeding strategy that would permit its digestive system to work at the maximum rate. One such strategy is to gather food in a storage organ so that the gizzard and the intestine can be supplied on demand. Although such a strategy in a bird species would maximize its digestive output and, thus, energy assimilation, it also increases the amount of food carried and could reduce the energetic efficiency of flight. In addition, an increase in the body mass of a bird resulting from stored food could decrease maneuverability during takeoff, thereby increasing the risk of predation.

Wintering Common Eiders (*Somateria mollissima*) regularly alternate ingestion bouts with resting bouts when foraging (Guillemette et al. 1992). Prey are captured in the subtidal zone by making dives in series and are stored in their distensible esophagus as ingestion progresses. The food is then processed in their powerful gizzard and in the intestine, where prey are crushed and digested. The diet of Common Eiders is characterized by a low energy density ($\text{kJ} \cdot \text{g}^{-1}$ wet mass) as they swallow molluscs, echinoderms, and crustaceans whole with their exoskeletons. This increases considerably the inorganic content of their food, and eiders must compensate by ingesting a large amount of material (ca. 2 kg) in order to meet their daily energy requirements (Guillemette et al. 1992).

In this paper I examine whether the rate of digestion limits the process of energy assimilation in wintering eiders. In addition, I investigate the impact of gut contents on the flying capabilities of eiders by comparing the amount of prey present in the gut of both flying and foraging eiders and discuss this in relation to

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wing morphology and takeoff capabilities in this species.

METHODS

Study area.—My study was conducted in Mingan Archipelago National Park on the north shore of the Gulf of St. Lawrence, Québec, Canada. This region is the major wintering area for Common Eiders in the Gulf, containing two-thirds of the total overwintering population of about 155,000 individuals (Bourget et al. 1986). All observations were made on the southeastern portion of Ile à la Chasse (50°40'N, 63°07'W), a remote island where human disturbance is minimal. Common Eiders are highly social birds and, in the Gulf of St. Lawrence, they form groups of up to 17,000 individuals (Bourget et al. 1986).

Sampling procedures.—Eiders were categorized into three groups: flying, feeding and "raft feeding." Specimens were obtained from mid-December through to the end of April during the winters of 1985–1986 and 1987–1988. Eiders were collected using one of two methods: (1) individuals shot over decoys, permitting the collection of flying individuals from small flocks (<30 individuals); (2) individuals shot when foraging on the water, which included individuals from both small (<30) and large flocks (>300). Eiders foraging in small flocks were feeding "normally" in the sense that diving activities were poorly synchronized and were occurring among dispersed flock mates. In addition, when disturbed by a predator or human activities (e.g. during shooting and collection), all individuals took to the air readily. All individuals foraging in large flocks were classified as raft feeding, defined by Campbell (1978) as involving "high intensity synchronized or progressive diving among tight rafts of individuals." In addition, when disturbed, raft-feeding eiders required more time/distance to become airborne as they flapped their wings vigorously on the water in a cohesive manner when dispersing. Following such a disturbance most individuals flew away and only a small proportion (<1%) of the flock did not take flight and were making "panic" dives. I interpreted the latter as indicative of temporary flightlessness, presumably stemming from excessive mass of food in their gut (see Discussion). All flying and foraging eiders were collected during the day, whereas the majority (67%) of eiders classified as raft feeding were shot at dusk, with the remainder collected during the afternoon.

Specimen dissection.—All specimens collected and dissected were of the subspecies *S. mollissima borealis.* Each specimen was weighed and dissected within a few hours of being captured. I determined the mass of esophagus (including proventriculus) and gizzard contents, and preserved them for subsequent analysis. The main prey species eaten by Common Eiders in winter are, in order of decreasing importance: blue mussels (*Mytilus edulis*); green sea urchins (*Strongy-*

locentrotus droebachiensis); and spider crabs (*Hyas araneus*; Guillemette et al. 1992). Only those eiders that had mussels in their stomach were considered in the analysis ($n = 169$). The amount of mussels and water in the intestine was evaluated later in the laboratory by obtaining the total mass of the intestine with its content and then without the contents. Intestine contents were not measured for 42 specimens of the total sample ($n = 169$). The intestine contents of these birds were estimated by fitting a curve of the form:

$$I = 41.409 + 1.541\,S - 0.009\,S^2 \qquad (1)$$

($r^2 = 0.466$, $n = 127$, $P < 0.0001$; SE of linear term 0.195, $P < 0.0001$; SE of quadratic term 0.002, $P < 0.0001$), where S is the mass (in grams) of stomach (esophagus + gizzard) contents and I is the mass (in grams) of the intestine contents.

For 22 other individuals without any trace of prey in the esophagus, gizzard, and intestine, I estimated the residual water content (in grams) of the latter to be 2.1% of the body mass (M_b). This value was subtracted from intestine contents of eiders containing mussels to estimate the amount of prey present in this organ. I calculated the corrected M_b of an eider by subtracting the wet mass of prey in the gut (esophagus + gizzard + intestine) from the fresh M_b. The total prey mass was expressed as a proportion of the corrected M_b. Statistical analyses were done on angular transformed (arcsin of square root) proportions.

Model of ingestion and defecation.—To estimate processing times for the gut, I used a schematic model of ingestion and defecation processes for an eider feeding on mussels (Fig. 1). There are three organs: (1) distensible esophagus where prey stored during ingestion; (2) muscular gizzard where shells crushed; and (3) intestine where nutrients retained. In this model, foraging cycles consist of a feeding bout (FB), during which several dives are made to capture food, and a resting bout (RB), during which no feeding occurs. A meal, the amount of food ingested during one feeding bout, starts with the ingestion of the first prey and continues until the last prey of meal is ingested. A resting bout follows during which resting and preening occur. The resting bout lasts until the amount of food in the gut falls to a (hypothetical) threshold level and then the eider resumes feeding. Evidence from two birds shot at the beginning of a feeding bout suggest that esophagus emptying is a necessary condition for the ingestion of another meal (pers. obs.; see also Worthington 1989). From this, the minimal rate at which the food is passed into the gizzard is given by the length of an average foraging cycle for which an average-sized meal has been processed. Conversely, the maximal gizzard processing rate is obtained assuming that the food is processed only during the resting bout (i.e. there is no handling of prey by gizzard during ingestion).

Because ingestion and digestion (mechanical processing, gastric activity, absorption, and defecation)
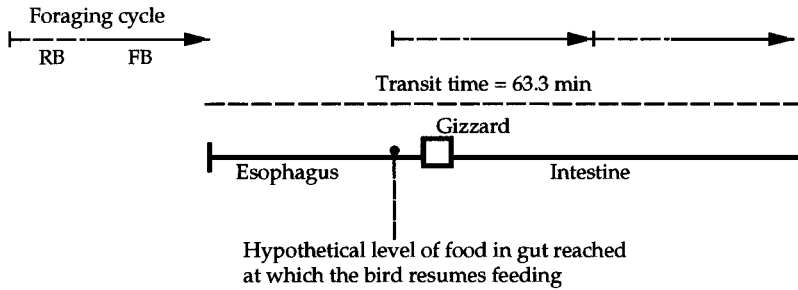
Fig. 1.   Schematic model of ingestion and digestion for an eider feeding on mussels (see Methods). Foraging cycles indicated by arrows consist of a feeding bout (FB = 13.2 min, represented by solid part of arrow) and a resting bout (RB = 8.3 min, represented by dashed part of arrow). Transit time indicated by dashed line, and solid line at bottom shows when food found in esophagus, gizzard (box), and intestine. Drawn on a time scale from left to right.

are consecutive processes, the slower one will determine the rate at which energy is assimilated. Swennen (1976) measured experimentally the rate at which exoskeletons of prey pass through the gut for two nonstarved Common Eiders. He observed that the production of feces was regular and continuous in spite of the frequent interruptions of the intake. From these observations and using the theoretical framework of Penry and Jumars (1987), the esophagus and the intestine of Common Eiders were classified as "plug-flow reactors" rather than "batch reactors." In this type of digestive system, one assumes that the flow pattern is orderly; material is perfectly mixed radially, but mixing or diffusion along the flow path is negligible (Penry and Jumars 1987). Now given the crushing activity of the gizzard, this organ shows probably complete mixing. Therefore, a shell can come out earlier or later than one might expect from a pure plug-flow reactor (P. A. Jumars pers. comm.). In other words, the rank order of a prey determined at ingestion may change in the course of the digestive process. However, since the capacity of the gizzard is four to six times less than the capacity of entire gut in Common Eiders (see Results), this would mean that only a small part of the entire gut content is mixed at any one time. Evidence of an orderly flow pattern in Common Eiders is given by Swennen (1976, pers. comm.), who observed that different prey types were excreted in the rank order they were offered to the experimental birds and also because the changes of prey types at defecation were abrupt. Since transit time is defined as the time interval between ingestion and defecation of a prey item, transit time (under plug-flow model) can be considered as a good estimate of the time to process one gut load. On the basis of color differences of the exoskeltons in the feces, Swennen (1976) determined transit time for Common Eiders feeding on *Mytilus edulis* ($\bar{x}$ = 62.5 min, n = 3), *Cardium edule* ($\bar{x}$ = 67.6 min, n = 3), *Carcinus maenas* ($\bar{x}$ = 63.4 min, n = 5) and *Crangon crangon* ($\bar{x}$ = 58.0

min, n = 2), giving an overall average of 63.3 ± SD of 7.2 min (n = 13).

As parameters of this model, I used the average feeding-bout duration (13.2 min), average resting-bout duration (8.3 min), a meal size of 80 g (Guillemette et al. 1992), and an average transit time of 63.3 min (Swennen 1976). Gut load was estimated by measuring the maximum gut contents of individuals shot when foraging. Because the end result of digestion is the absorption of nutrients and water through the small intestine (and, thus, leaving gut), I used only mussel shells as a common denominator in my comparison of ingestion and defecation rate. For this reason, all rates estimated in this study are reported in terms of shells ingested, processed, and defecated. The mean length of mussels eaten by Common Eiders was 9.7 mm, of which shells constitute 63.4% of the total mass (unpubl. data).

Description of wing morphology.—Wing morphology was described for 12 specimens captured in February 1992. I measured wingspan (*b*) and wing area (*S*) of fully extended wings. The wing area was determined by tracing the contour of a wing on a sheet of paper (excluding area between two wings) from which I measured the surface area with a planimeter. Separate measurements were made for each wing and then summed to obtain the total surface area of both wings. I also calculated the wing loading (*Q*) as the ratio of body mass to wing area (m_b/S), and compared these parameters with other species of diving ducks. I used data compiled by Humphrey and Livezey (1982), from which I excluded their value for the Common Eider, and included their results (both sexes separately) for the Flying Steamer-Duck (*Tachyeres patachonicus*). Data gathered by these authors included measurements of body masses and wing areas, representing 22 species of the tribes Aythyini, Mergini, and Oxyurini. Measurements of wingspan were obtained from other sources (Greenewalt 1962, Lowe 1934) and were available for only 12 species of the same tribe. All measures
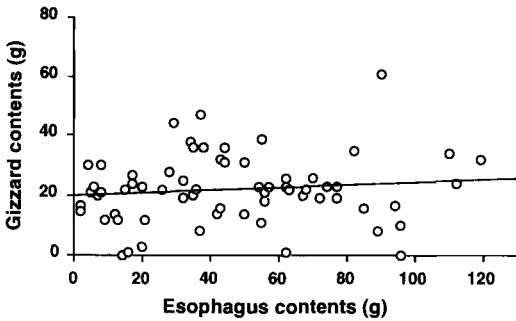
Fig. 2. Common Eider gizzard contents in relation to esophagus contents in winter. Only individuals having prey in their esophagus were included. No significant relationship ($Y = 20.23 + 0.042\ X$, $r = 0.114$, $P = 0.365$ $n = 65$) was found between organ contents.
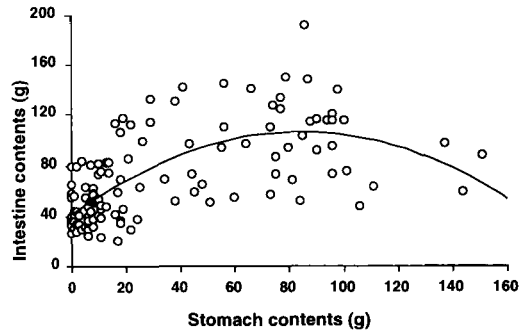

Fig. 3. Relation between stomach (esophagus + gizzard) and intestine contents. Quadratic equation ($Y = 41.409 + 1.541X - 0.009X^2$, $r = 0.683$, $P < 0.0001$, $n = 127$) was best descriptor of data.

were transformed using natural logarithm, and power functions were fitted to the data using geometric-mean functional regressions (Ricker 1973), with body mass (M_b) as the abscissa. Wingspan, wing area, and wing loading increase in an allometric fashion with body mass in diving ducks as indicated by:

$$b = 9.830 M_b^{0.309} \qquad (2)$$

($n = 12$, $R^2 = 0.827$),

$$S = 6.044 M_b^{0.678} \qquad (3)$$

($n = 23$, $R^2 = 0.859$), and

$$Q = 0.071 M_b^{0.447} \qquad (4)$$

($n = 23$, $R^2 = 0.667$). These regressions were significant ($P < 0.001$) and considered to be representative of the "standard diving duck." I determined if the mean observed values of eider wing morphology fell within 95% confidence intervals of these equations using the expression of variance given by Ricker (1973:414, eq. 18).

RESULTS

Relationship between contents of different organs.—I found no significant relationship ($r = 0.114$, $n = 65$, $P = 0.365$) between the mass of gizzard and esophagus contents (Fig. 2). As the quantity of prey in the esophagus increased there was no concomitant increase of prey in the gizzard, indicating that the former functions as a storage organ.

The maximum organ capacity observed in eiders was approximately 6.0, 3.0, and 6.0% of M_b for the esophagus, gizzard and intestine, respectively. If each organ could be filled to its maximum capacity simultaneously, eiders would

transport 15.0% of M_b in prey, although the maximum observed was 11% of M_b (see below). Moreover, the relationship between stomach (esophagus + gizzard) and intestinal contents is best described by a quadratic equation (Fig. 3), indicating that when the stomach content is maximum (150 g) the intestine contains much less than its maximum capacity (and vice versa).

Ingestion and processing rate.—Assuming that a meal is processed in the gizzard during both the feeding and the resting bout, I divided meal size (50.7 g of shells) by an average foraging cycle (21.5 min), estimating the minimum working capacity of the gizzard to be 2.4 g·min⁻¹, which is low compared to the rate prey are ingested (3.8 g·min⁻¹). However, mussels may be stored first in the esophagus during ingestion and then crushed during the resting bout (Fig. 2). Assuming now that the resting bout is the only time food is processed, the maximum gizzard processing rate is 6.1 g·min⁻¹, 2.3 g·min⁻¹ higher than the rate at which mussels are ingested (3.8 g·min⁻¹).

In order to compare ingestion and defecation rates, I estimated that maximum gut contents were 104.7 g (total mass = 165 g) and 145 g of shells (total mass = 229 g) for feeding and raft-feeding eiders, respectively. Division of this mass of ingesta by the transit time ($\bar{x} = 63.3$ min; Swennen 1976) results in a defecation rate lying between 1.7 and 2.3 g·min⁻¹, which is lower than the ingestion rate.

Effect of season on gut contents.—A two-factor ANOVA was conducted on total gut contents (angular-transformed proportions); the first factor was season, of which there were three groups (December–January, February–March, and
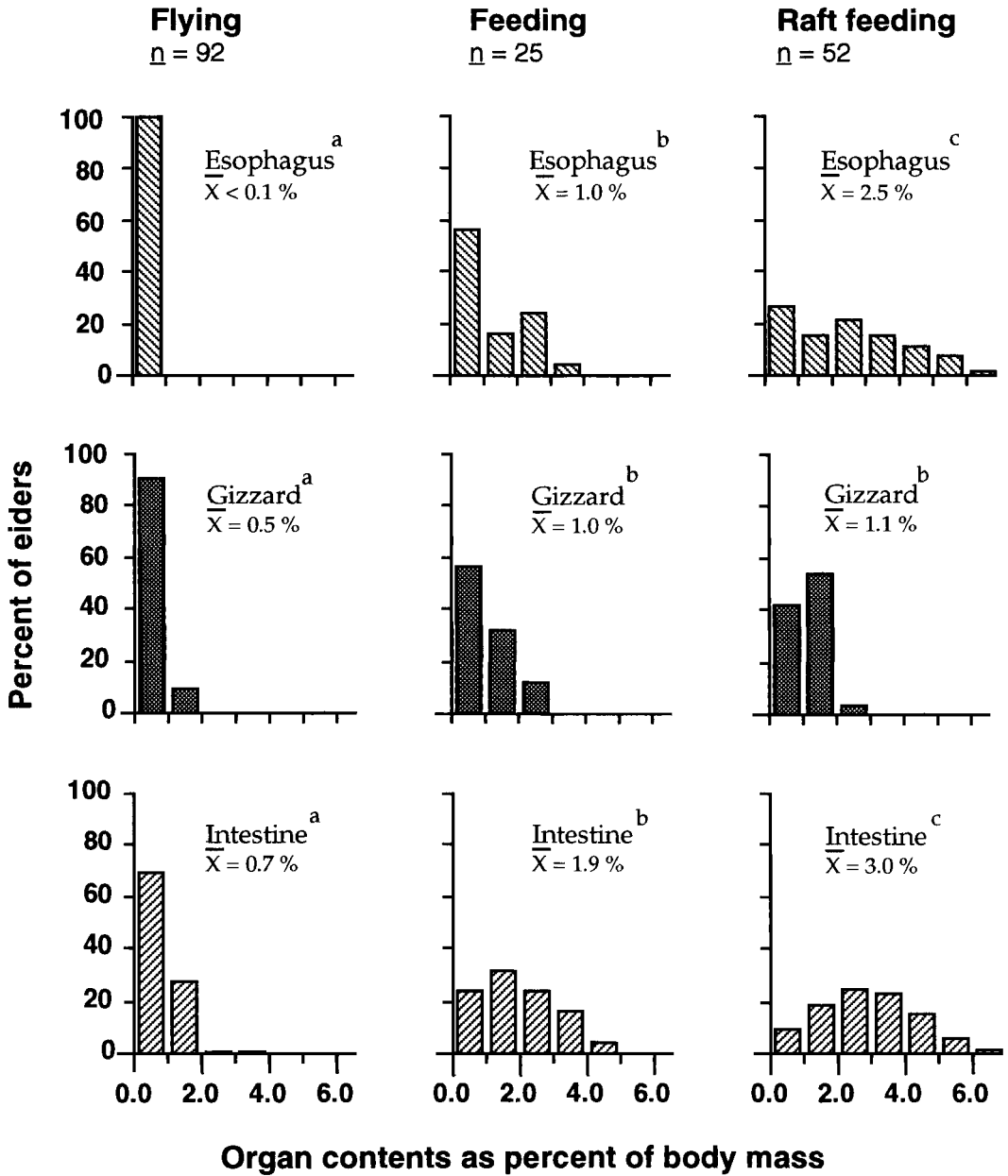
Flying
n = 92

Feeding
n = 25

Raft feeding
n = 52

Esophagus[a]
$\overline{X} < 0.1\%$

Esophagus[b]
$\overline{X} = 1.0\%$

Esophagus[c]
$\overline{X} = 2.5\%$

Gizzard[a]
$\overline{X} = 0.5\%$

Gizzard[b]
$\overline{X} = 1.0\%$

Gizzard[b]
$\overline{X} = 1.1\%$

Intestine[a]
$\overline{X} = 0.7\%$

Intestine[b]
$\overline{X} = 1.9\%$

Intestine[c]
$\overline{X} = 3.0\%$

Percent of eiders

Organ contents as percent of body mass

Fig. 4. Frequency distribution of organ contents expressed as percent (%) of body mass for three categories of wintering eiders. Esophagus ($F = 144.0$), gizzard ($F = 28.1$), and intestine ($F = 55.5$) contents differ significantly among categories (ANOVA on angular-transformed proportion, df = 2 and 166, $P < 0.0001$ in all cases). Superscripts denote a Scheffé *a posteriori* comparison and organs with a similar letter do not differ significantly ($P > 0.05$) among categories; otherwise they do ($P < 0.01$).

April); the second factor involved whether the bird was flying, feeding, or raft feeding. No effect of season was found (ANOVA; $F = 0.52$, df = 2 and 160, $P = 0.60$), but the effect of collection categories was highly significant (F = 95.35, df = 2 and 160, $P < 0.0001$). No interaction was found between the two factors ($F = 0.67$, df = 4 and 160, $P = 0.62$), and I concluded from this that season did not influence gut contents in wintering Common Eiders.

Amount of prey vs. category of collection.—Almost no food was found in the esophagus or the gizzard of flying eiders, and few prey were left in the intestine of these birds (Fig. 4). This suggests that they had ceased feeding some time before flying. Foraging eiders had a greater amount of food present in the digestive system (Fig. 5). Feeding eiders had significantly more food in their esophagus, gizzard and intestine than flying eiders ($P < 0.01$ in all cases). Similarly, when compared with feeding eiders (Fig. 4), raft-feeding eiders had a greater amount of prey in their esophagus ($P < 0.01$) and intestine ($P < 0.01$), but not in the gizzard ($P > 0.05$). Consequently, feeding eiders possessed significantly more food in the entire gut than flying eiders ($P < 0.01$), and raft-feeding eiders possessed more food than feeding eiders ($P < 0.01$; Fig. 5).

I plotted the cumulative frequency of the observed gut contents of foraging eiders as a percentage of body mass, and I assumed that the last 20% of this cumulative distribution corresponded to individuals that had essentially finished their ingestion period. Eiders feeding normally stopped feeding when the food in their gut represented 6 to 9% of M_b, whereas raft-feeding eiders stopped somewhere between 8 to 11% of M_b. Therefore, these results support the contention that temporary flightlessness in raft-feeding eiders could arise because of the excessive mass of ingested prey. For example, an apparently flightless female eider was followed for a short time with a kayak, during which she attempted to takeoff two times without success. After several panic dives, this female was shot and its gut was inspected. The gut contained 203 g (10% M_b) of mussels, of which 110 g was found in its esophagus.

Wing loading and morphology.—Wing loading in the Common Eider averages 2.03 g·cm^{-2} in males and 1.96 g·cm^{-2} in females (Table 1); the sexes were not statistically different from each other (*t*-test, $P > 0.05$). When sexes are pooled, wing loading in this species averages 2.0 g·cm^{-2}, which is not significantly different ($P > 0.05$) from that predicted for a standard diving duck of equal mass. Although Common Eiders tend to have shorter wings (9%) and lower wing area (5%) than predicted (Table 1), no significant differences were found ($P > 0.05$ in both cases) for these parameters. Also, large pectoral muscles average 304.8 ± SD of 5.8 g in this species (both sexes included, $n = 12$), which is very
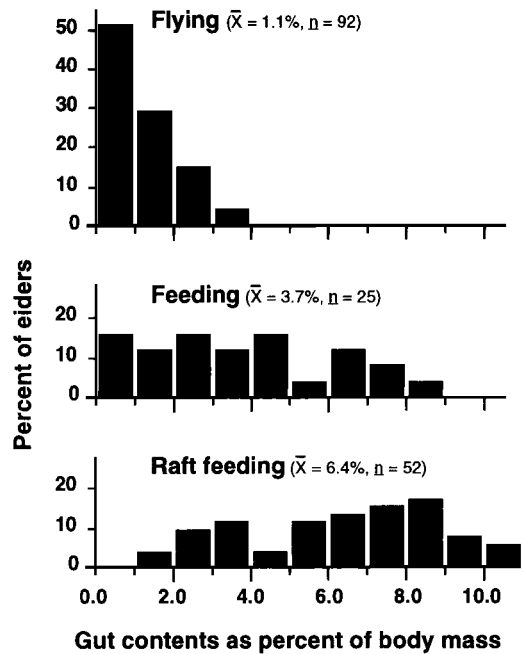

Fig. 5. Frequency distribution of gut contents expressed as percent (%) of body mass for three different categories of wintering eiders. Gut contents differ significantly among categories (ANOVA on angular-transformed proportion, $F = 119.9$, $P < 0.0001$, df = 2 and 166, $n = 169$), and Sheffé *a posteriori* comparisons indicate that gut contents of flying and feeding eiders differ significantly ($P < 0.05$), as do gut contents of feeding and overfeeding eiders ($P < 0.01$).

close to the value of 312 g generated from the equation furnished by Greenewalt (1975) for 15 species of ducks.

DISCUSSION

Digestive-rate constraint.—The simple observation that a bird has a large amount of food in its esophagus or a similar organ could be an indication that the ingestion rate is higher than the digestion rate. Because a full gizzard contains about 20 g (Fig. 2) and meal size lies between 60 and 100 g in the Common Eider (Guillemette et al. 1992), it follows that the gizzard must be emptied and filled about four times to process one meal. Mussel shells are crushed into fine material (1–4 mm), and it probably takes a certain amount of time before the mechanical digestion of a meal is completed. The digestive strategy of many species ingesting prey with nondigestible, possibly dangerous material consists of regurgitating pieces of food or pel-

TABLE 1. Percent difference between predicted and mean observed measures describing wing morphology in female and male Common Eiders in winter. No significant differences ($P > 0.05$) between predicted and observed values were found (see Methods).

	Body mass (g)	Wingspan (cm)	Wing area (cm)	Wing loading (g·cm)
Females				
Predicted (confidence interval[a])	—	100.6 (85.0–119.1)	994 (435–2,268)	2.05 (1.49–2.82)
Observed (range)	1,849 (1,672–1,949)	90.9 (87.5–94.0)	948 (880–1,035)	1.96 (1.7–2.2)
Percent difference	—	9.6	4.6	4.4
Males				
Predicted (confidence interval[a])	—	103.4 (87.2–122.6)	1,055 (458–2,248)	2.13 (1.53–2.95)
Observed (range)	2,019 (1,867–2,087)	94.1 (90.5–97.5)	995 (926–1,053)	2.03 (1.68–2.18)
Percent difference	—	9.0	5.6	4.7

[a] At 95% level.

lets (e.g. raptors [Kirkwood 1979] and frugivores [Worthington 1989]). Neither prey nor parts thereof are regurgitated in the Common Eider. Thus, the rate at which the gizzard crushes the prey may be the first constraint imposed on the foraging activities of the Common Eider. However, I estimate that the working capacity of the gizzard varied between 2.4 and 6.1 g·min^{-1} in the Common Eider. The rate at which prey is ingested (3.8 g·min^{-1}) lies between these two values; thus, it cannot be concluded that crushing activity of the gizzard constrains energy assimilation in this species. This is because it is not known whether food is processed in the gizzard throughout a foraging cycle, or if food is processed by the gizzard only during the resting bout. Prey may be ingested first and then processed only during the resting bout as in hummingbirds (Hainsworth and Wolf 1972).

A better means of demonstrating that energy assimilation is constrained by the rate of digestion in the Common Eider is obtained when defecation rate is estimated. Based on the average transit time in the Common Eider, I estimated that ingestion rate is about two times faster than the defecation rate. Some studies have indicated that transit time could be related to the amount of food present in the gut (i.e. a larger meal size may reduce transit time; Worthington 1989). However, it is unlikely that transit time used in this study would reduce sufficiently the estimation of defecation rate and change the conclusion that digestion is slower than ingestion rate. This is because it would need a transit time of 28 to 38 min to equate the rate at which prey are ingested. In 13 trials, Swennen (1976) showed that transit time for two nonstarved Common Eiders ranged from 51 to 75 min among four types of prey. Thus, comparison of ingestion rate of shells (3.8 g·min^{-1}) with defecation rate (1.7–2.3 g·min^{-1}) in my study indicates that the rate of digestion is a major constraint of energy assimilation for eiders foraging during winter. Digestive-rate constraints in birds have been demonstrated in herbivores (Kenward and Sibly 1977), frugivores (Worthington 1989, Levey and Duke 1992), and nectarivores (Karasov et al. 1986). However, most models of diet selection (Schoener 1987) assume that animals maximize their rate of ingestion when foraging. If digestion rate is limiting, the rate at which the prey are ingested no longer determines the assimilation of energy.

Physical regulation of feeding.—Digestive constraint in Common Eiders results in an accumulation of prey in their gut as a feeding bout progresses. Thus, it is likely that the initiation and the termination of an ingestion period is related to the amount of food present in the gut. One could argue that eiders stop ingesting prey because some maximum gut capacity is reached. By summing maximum organ contents separately, I determined that the maximum gut capacity was 15.0% M_b, much higher than the maximum of 11% M_b measured in raft-feeding individuals. This suggests that eiders stop feeding before the maximum capacity of the entire gut is attained. Wolf and Hainsworth (1977) observed that hummingbirds do not fill their crop during a feeding bout, and hypothesized that increased meal size may impose some costs to the flying animal. However, gut capacity must regulate feeding activities to some extent in wintering eiders because no more prey can be added once the esophagus is filled to the max-

imum, even if the intestine is empty (although the reverse is not true). Nevertheless, I hypothesize that meal size and feeding-bout duration in Common Eiders are regulated around a certain proportion of their total body mass. Because the net result of both ingesting and defecating prey is the accumulation of food in the gut, the body mass of an eider will increase during ingestion. Eventually, the eider will stop feeding at some critical threshold because the added mass of a meal on body mass will impose some severe costs (see below). Body mass will then start to decrease as a result of defecation of prey during a resting bout. Depending on the type of defecation rate (linear or exponential), the rate of body-mass increase may or may not fall toward the end of an ingestion bout. Defecation rate typically follows a negative exponential curve (e.g. Sibly 1981). Such an exponential model could be highly advantageous because increased meal size would add little surplus time for digestion (Wolf and Hainsworth 1977).

Gut contents and mass minimization.—Data described here (Fig. 5) suggest that eiders tend to fly when the mass of food in their gut is minimal, although it is possible that defecation during flight may reduce gut contents to some degree in flying individuals. However, the latter is unlikely because wintering eiders spend less than 2% of the daylight hours flying and average flight duration is about 75 s (unpubl. data). In addition, Bustnes and Erikstad (1990) observed that the most frequent size of mussels (from 7 to 23 mm) eaten by Common Eider in Norway correspond to the highest flesh : shell ratio and showed that, when larger than 25 mm, the quantity of mussels required daily increases the shell intake by about 1 kg. I am not aware of documented examples of other bird species that behave so as to minimize the mass of food before flying. In flying mammals, Gunderson (1976) reported that blood-feeding bats may dramatically increase their mass while feeding, stating that individuals begin to urinate copiously shortly after they begin feeding.

One advantage of minimizing the mass of food in the gut before flying is to reduce the energy cost of flight. Gessaman and Nagy (1988) found that radio-transmitter loads as small as 2.5% of M_b affected flight speed and metabolism of homing pigeons (*Columbia livia*), although the effect of drag from transmitters was not partitioned. Most foraging eiders exceed this value (Fig. 5) with their gut containing as much as 6

to 11% of M_b in prey at the end of an ingestion period. Using the empirical model of Masman and Klaassen (1987), I estimated flight costs in the Common Eider to be 14 × BMR (basic metabolic rate in winter; Jenssen et al. 1989). Although body mass of eiders (Table 1) far exceeds those used in the predictive model (maximum M_b = 1,000 g), this fairly high estimate of flight costs is in accordance with aerodynamics. Low wing loadings are usually associated with low flight costs in flying animals (Greenewalt 1975, Norberg 1990). In contrast, diving ducks, including *Somateria*, have short pointed wings and some of the highest wing loading observed in birds (Greenewalt 1975, Livezey and Humphrey 1986, Norberg 1990).

Compared to other bird species, takeoff capabilities are reduced in diving ducks as they need high-speed taxiing runs to become airborne (Norberg 1990). Thus, it is probable that controlling food mass may also reduce the risk of predation. Avian predators of wintering Common Eiders are numerous and include, by increasing order of importance, the Snowy Owl (*Nycta scandiaca*), Gyrfalcon (*Falco rusticolus*), and Bald Eagle (*Haliaeetus leucocephalus*; pers. obs.). A surplus load (see below) might increase takeoff distance and probably would increase the probability of being caught by Gyrfalcons, which prey on flying or perched individuals. In addition, a small proportion of raft-feeding eiders do not take wing, but make panic dives that may increase their vulnerability to Bald Eagles, which can secure their prey from the water (pers. obs.). Supportive evidence for this is scarce, although Kenward (1978) reported that Northern Goshawks (*Accipiter gentilis*) increased their capture success when hunting Common Wood-Pigeons (*Columba palumbus*) filling their gut at dusk.

Gut contents and temporary flightlessness.— Common Eiders are characterized by one of the highest wing loadings (2.00 g·cm⁻²) observed in birds capable of flight. Other species with similar wing loadings are Common Murres (*Uria aalge*; 2.06 g·cm⁻²), Razorbills (*Alca torda*; 2.04 g·cm⁻²), and other species of eiders (*S. spectabilis* and *S. fischeri*; 2.06 and 2.03 g·cm⁻², respectively; Meunier 1951, Greenewalt 1962, Humphrey and Livezey 1982). The only other known flighted species with higher wing loadings are the Flying Steamer-Duck (Humphrey and Livezey 1982) and the Common Loon (*Gavia immer*; Livezey 1993). With these two exceptions, these

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values were based on few individuals and presumably body masses were not adjusted for gut contents as in my study. Adding gut contents increases wing loading in the Common Eider well over 2.0 $g \cdot cm^{-2}$, based on observed gut contents varying from a few grams to 229 g (up to 11% M_b). Humphrey and Livezey (1982) suggested that gut contents of steamer-ducks could make them flightless as the added mass could increase wing loadings to a point nearing the flightlessness threshold of 2.5 $g \cdot cm^{-2}$. Adding maximum gut contents to the average wing loading of the Common Eider gives a value of 2.24 $g \cdot cm^{-2}$, which is still below the threshold of 2.5 $g \cdot cm^{-2}$.

So why would flightlessness arise in raft-feeding eiders? There are three potential explanations for this phenomenon. The first one questions the validity of the flightlessness threshold. Humphrey and Livezey (1982) found that the threshold proposed by Meunier (1951) was applicable for *Tachyeres*, but they did not give Meunier's rationale behind such a value. The second reason is that I considered only average values of body mass for Common Eiders in estimating the effect of gut contents on wing loading. Body masses of raft-feeding eiders varied between 1,665 to 2,301 g, and it is possible that temporary flightlessness occurred in the heavier individuals only because wing loading in diving ducks increases in an allometric fashion with body mass both among and within species (Livezey and Humphrey 1986). Finally, feeding and raft-feeding eiders differed in their esophagus contents, which could have an impact on takeoff capabilities because this organ can contain as much as 5 to 7% of M_b in raft-feeding eiders. Such a mass of food could move the center of gravity forward on the body and make takeoff especially arduous.

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