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INTERACTIONS BETWEEN STOMACH STRUCTURE AND DIET CHOICE IN SHOREBIRDS

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ABSTRACT.—Captive Red Knots (*Calidris canutus*) fed soft food pellets developed atrophied stomachs, and were reluctant to eat their usual hard-shelled mollusc prey. An interspecific comparison among shorebirds showed that wild Red Knots and other intact-mollusc-eating species have gizzards with relatively great mass but very small proventriculi. Within six different shorebird species, the heavier individuals usually had the heavier stomachs as well, but in Red Knots and Bar-tailed Godwits (*Limosa lapponica*) we identified heavy pre-migrant individuals with reduced stomach masses, suggesting a reallocation of protein reserves before long-distance flights. In both species reduced stomach mass was associated with a relatively soft diet. We were unable to show that during adjustment of stomachs to hard-shelled prey, such prey are broken down to smaller fragments. We attribute this to the counteractive influence of the pylorus during adjustment. We summarize the suggested stomach/diet interactions as a network of causal relationships and feedback loops involving the type of diet and gizzard mass. We identify two basic modifiers of gizzard mass: one working via endurance training and disuse atrophy; and another involving endocrine and/or neural mechanisms. It is likely that, in the course of their annual cycle, shorebirds are prevented from achieving maximal digestive performance owing to seasonal changes in feeding habitats and diet enforced by their long-distance migrations. Received 28 May 1992, accepted 25 November 1992.

ANIMAL BODIES are dynamic systems showing large changes in composition in relation to season, nutritional condition and diet (e.g. Allison and Wannemacher 1965, King 1972, Goldberg et al. 1974, 1975, Raveling 1979, Cherel et al. 1988, Blem 1990, Gaunt et al. 1990). Variation in the form and mass of stomachs in relation to diet has long attracted the attention of researchers (e.g. Darwin 1885; summary in Ziswiler and Farner 1972), and a series of detailed studies indicates that associations between stomach mass and type of diet often represent species- and individual-specific adaptations (Table 1). For example, eating more fibrous food usually leads to increased gizzard mass (i.e. the muscular part of stomach), as has been shown in experimental as well as in observational studies. Having a particular stomach morphology because of exposure to a particular diet might constrain the ingestion rate, or the digestive yield, of other food types (Moss 1983), at least during the period in which the stomach is adjusting.

Although fiber-eating wildfowl and galliforms are widely recognized as birds with large and muscular stomachs, species with similar stomach types that feed on hard-shelled animal prey ingested whole have escaped detailed attention; only casual remarks on mollusc-eating sea ducks have been made (Bellrose 1976, Barnes

and Thomas 1987, Brown and Frederickson 1987). Some shorebird species, such as Red Knots (*Calidris canutus*), also feed on whole bivalves and gastropods, which they capture by probing in soft intertidal sediments (Prater 1972, Goss-Custard et al. 1977, Boere and Smit 1980b, Piersma 1991, Zwarts and Blomert 1992).

During experimental studies on the feeding behavior of Common Eiders (*Somateria mollissima*; P. Duiven and C. Swennen pers. comm.) and Red Knots, we repeatedly have found that individuals conditioned to soft food pellets did not eat their natural hard-shelled prey for a couple of days. Such observations, and those on Wild Turkeys (*Meleagris gallopavo*) and Surf-birds (*Aphriza virgata*) listed in Table 1, further suggested that gizzard mass may influence diet rather than vice versa. Because most shorebirds show considerable seasonal variation in the types of habitat frequented (e.g. marine intertidal in winter, tundra in summer), and because these shifts coincide with changes in prey type (e.g. hard-shelled molluscs in winter, soft arthropods in summer), we examined the relationship between diet and gizzard morphology in this group of birds.

We first describe some behavioral observations on captive Red Knots that led us to associate diet with stomach mass in shorebirds, both

TABLE 1. Diversity of suggested interactions between diet and stomach mass in birds as documented in modern studies. Mass of the stomach, or its muscular part (gizzard) only, is usually interpreted as measure of strength.

Type ^a	Predator(s)	Food type	Nature of diet/stomach interaction	Reference ^b
B	Wild Turkey (<i>Meleagris gallopavo</i>)	Hickory nuts	Domestic birds used to soft food (less powerful stomach?) refuse to eat hard-shelled nuts	1
B	Surfbird (<i>Aphriza virgata</i>)	Two mussel species (<i>Mytilidae</i>)	Selection for the mussel species that requires least force to break	2
I	Wildfowl (Anatidae)	Invertebrate and plant food	Herbivores and omnivores have heavier gizzards than carnivores eating fiber-free food	3, 4
I	Lorikeets (Psitticidae)	Nectar/pollen vs. seeds/fruits	Species eating soft nectar/pollen have less muscular gizzards than other parrots	5
S	Spruce Grouse (<i>Canachites canadensis</i>)	Leaves and conifer needles	Heaviest gizzard when eating fibrous food (conifer needles in midwinter)	6
S	Bearded Tits (<i>Panurus biarmicus</i>)	Insects vs. seeds	Gizzards in summer (insect diet) weigh only one-half of winter ones (seed diet)	7
S	Ducks (<i>Anas</i>)	Invertebrates and plant material	Gizzards are heaviest in periods of the most fibrous (plant) diet	8–12
S	Geese (Anseridae)	Plant material	Gizzard mass correlated with daily intake	13–15
S	Phainopepla (<i>Phainopepla nitens</i>)	Berries	Change from bulk to single berry feeding coincides with reduction of gizzard by 50%	16
E	Crow/domestic chick (<i>Corvus/Gallus</i>)	Mixed plant/animal food vs. meat	Birds fed pure meat develop small stomachs (only 36% of reference mass)	17, 18
E	Mallard (<i>Anas platyrhynchos</i>)	Corn, variety of food pellets	Fibrous diets lead to heavy gizzards	19, 20

^a Nature of study: (B) behavioral observations; (I) interspecific comparisons; (S) seasonal changes detected in population; (E) experimentally induced changes.

^b References: (1) Schorger 1960; (2) Navarro et al. 1989; (3) Kehoe and Ankney 1985; (4) Barnes and Thomas 1987; (5) Richardson and Wooller 1990; (6) Pendergast and Boag 1973; (7) Spitzer 1972; (8) DuBow 1985; (9) Heitmeyer 1988; (10) Whyte and Bolen 1985; (11) Paulus 1982; (12) Drobney 1984; (13) Ankney 1977; (14) Halse 1985; (15) Hobaugh 1985; (16) Walsberg and Thompson 1990; (17) Oelhafen-Gandolla and Ziswiler 1981; (18) Lenkeit 1934; (19) Kehoe et al. 1988; (20) Miller 1975.

intra- and interspecifically. Although heavier birds of a species usually have heavier stomachs, we describe three cases in free-living Red Knots and Bar-tailed Godwits (*Limosa lapponica*) in which obese premigrant individuals have the lightest stomachs and contained the softest prey. This observation led to an experiment with Red Knots to show the value of a conditioned and, presumably, heavy and strong stomach.

Our central question is whether the large seasonal changes in habitat and diet of shorebirds (e.g. Lange 1968) temporarily constrain the use and, thereby, the intake of certain prey (cf. Diamond and Obst 1988). Most shorebirds are long-distance migrants with tight annual schedules and a great capacity to store and use tissues rapidly (e.g. Drent and Piersma 1990, Evans and Davidson 1990, Piersma and Jukema 1990, Gudmundsson et al. 1991). The muscular stomach might be one of the body components that such migrants can adaptively exploit as a nutrient source (and perhaps even as a nutrient sink).

METHODS

Feeding experiments.—Flocks of 3 to 10 Red Knots were kept in outdoor cages measuring 2.0 by 3.5 m with a height of 2 m. Feeding trials were conducted with individual knots in small cages (0.5 × 0.5 × 0.5 m) in climate rooms at constant temperatures (1.5°, 19.0° or 33.0°C to obtain a range in daily food requirements) and with a 13-h daylight period. Freshwater was always available. In addition, small flocks of foraging birds were studied on an artificial outdoor tidal flat measuring 7 × 7 m. Normally, our captive birds were fed protein-rich, trout-food pellets. In experimental situations we also offered them four bivalve and one gastropod prey, namely the edible mussel (*Mytilus edulis*), edible cockle (*Cerastoderma edule*), Balthic tellin (*Macoma balthica*), and mudsnail (*Hydrobia ulvae*) from the intertidal flats, and the subtidal bivalve *Spisula subtruncata*. The bivalves were collected at a variety of localities near the island of Texel (The Netherlands).

A series of feeding trials was carried out specifically to establish whether a longer exposure to hard-shelled molluscs leads to a stomach with greater muscle mass.

The characteristics of the food (length distribution, length-dependent shell mass and biomass) ingested during a 24-h experimental period were described in detail (see Dekinga and Piersma 1993). Each feeding trial started at 1300 MET with food being placed in the cage. The following morning (at 0900) the remaining food was taken away, leaving the birds 4 h in which to empty their guts before the experiment ended at 1300. The feces were collected, dried to constant mass at 55° to 60°C, weighed, and then sieved through 2-mm, 1-mm, 630- μ m, 500- μ m, 400- μ m, 315- μ m, 200- μ m and 100- μ m mesh sieves. Median feces-fragment size was calculated by plotting on probability paper the cumulative mass retained on the increasingly larger-meshed sieves. We then determined median fragment size at 50% mass. A score for prior experience was calculated as the sum of the relative hardness of the prey ingested during the seven days before the experiment (highest for *Hydrobia*, lowest for food pellets; see below) times a weighting factor for recency (a factor of 7 for day before experiment, 6 for penultimate day, etc.).

Breaking forces required.—A few seconds after experimental Red Knots had ingested bivalve prey, and usually before another prey was taken, we could hear the shell being cracked in the stomach. This suggested that breaking shells between two flat surfaces might provide a reasonable simulation of the cracking process. The force required to crack mollusc prey of variable sizes was measured by slowly increasing the pressure at a constant rate on freshly collected live specimens mounted between a flat metal plate and a flat wooden plate on an electronic balance. The maximum exerted weight (in kg) needed to break the shell was taken as the measure of force (in Newtons, kg/10).

Diet and body composition of wild shorebirds.—Details on the body composition of a large number of shorebird carcasses were accumulated from 1979 to 1991. All birds were accidentally killed during catching operations, by flying against lighthouses, or during mass-starvation incidents during severe winter weather periods in north temperate wintering areas. The sample included individuals originating from the wintering and staging areas in west Africa (see Kersten and Piersma 1983, Piersma and van Brederode 1990, Zwarts et al. 1990), southeastern and northwestern Australia (Piersma and Barter 1991), The Netherlands (Goede et al. 1990, Piersma and Jukema 1990), Germany, Great Britain (Summers et al. 1992), and Iceland (Gudmundsson et al. 1991). After a variable period (up to four years) of storage in deep freezers, carcasses were weighed (though, when possible, body mass at death was used) and dissected. The complete stomach was excised, its contents removed, and the fresh mass taken. The carcasses then were dried to constant mass at 55° to 60°C and the fat extracted in a Soxhlet apparatus, using petroleum ether (boiling traject 40°–60°C) as the solvent.

Throughout this paper “stomach mass” refers to the sum of the mass of the proventriculus (glandular anterior part of stomach) and the mass of the gizzard (muscular posterior part). Note that all sandpipers and plovers examined had small proventriculi relative to their gizzards. We weighed proventriculi and gizzards separately in two Red-necked Stints (*Calidris ruficollis*) and two Red Knots, and found that the proventriculus contributed an average of 6.3% to stomach mass (range 4.3–8.6%). Of the species examined, only the Eurasian Oystercatcher (*Haematopus ostralegus*) had a well-developed glandular stomach, as the proventriculus contributed, on average, 28.0% to stomach mass (range 24.1–31.5%, $n = 3$).

Stomach contents were stored in 90% ethanol for later examination. Reconstructions of the spring diet of Red Knots from Mauritania and Bar-tailed Godwits from The Netherlands were made on the basis of preserved samples. We used published (Zwarts 1988, Zwarts and Esselink 1989, Dekinga and Piersma 1993) and unpublished (L. Zwarts pers. comm., Piersma pers. observ.) sources to estimate the proportional composition in terms of wet mass.

RESULTS

How hard are hard-shelled prey?—In all four mollusc species examined, breaking force scaled to shell length with an exponent of about 3 (Fig. 1), indicating that breaking force scales linearly to shell mass. This confirms the findings of Currey (1979) and Vermeij and Currey (1980). Navarro et al. (1989), however, found breaking force to scale with the much lower exponents of 1.53 to 1.70 on shell length in two mussel species.

During the feeding trials, Red Knots ingested tiny *Hydrobia* snails or small *Mytilus* (up to 15 mm long), *Cerastoderma* (up to 12 mm) or *Macoma* (up to 16 mm). The size ranges taken relative to the required breaking forces of the different species (Fig. 1) imply that their gizzards had to generate forces similar to those exerted by us between two flat plates (i.e. up to 0.4 N). Within the size ranges of prey taken, we ranked *Hydrobia* as the hardest prey to crack, with *Mytilus*, *Cerastoderma*, *Macoma* and pellets being successively easier.

Knots used to soft food dislike hard-shelled prey.—Captive Red Knots took several days to adjust to a novel food type, especially if it was a hard-shelled bivalve such as *Spisula* (Table 2). Red Knots always immediately began feeding on familiar (and soft) food pellets and required about a day before starting to feed on familiar shellfish, such as *Mytilus* (Table 2). Why are

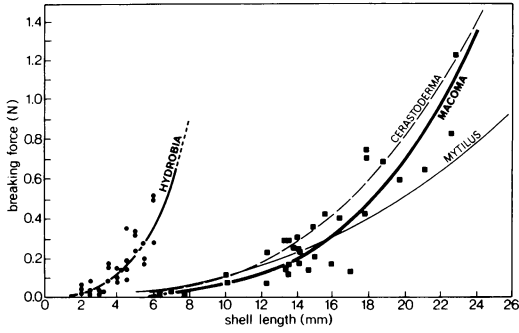


Fig. 1. Scaling of force (F, in Newtons) required to break mollusc prey of varying sizes and species on shell length (SL, in mm). Only data points for *Hydrobia ulvae* (dots) and *Macoma balthica* (squares) shown in addition to calculated regression lines for these two species plus *Cerastoderma edule* and *Mytilus edulis*. Relevant details of log-log regression equations are for: *Hydrobia*, $F = 0.001979SL^{2.897}$, $r^2 = 0.73$, $n = 29$; *Macoma*, $F = 0.000018SL^{3.527}$, $r^2 = 0.86$, $n = 32$; *Cerastoderma*, $F = 0.000101SL^{2.994}$, $r^2 = 0.89$, $n = 37$; *Mytilus*, $F = 0.000446SL^{2.351}$, $r^2 = 0.96$, $n = 50$.

captive, but clearly hungry, birds reluctant to feed on their natural hard-shelled prey?

Figure 2 shows that free-living Red Knots, even if they have starved to death in midwinter, have heavier stomachs than captive birds (cf. Moss 1972). The average wet masses of the stomach and the body of well fed and starved birds from the wild were respectively ($\bar{x} \pm SD$): stomach, well fed, 8.8 ± 2.3 ($n = 67$); stomach, starved, 7.2 ± 1.5 ($n = 5$); body, well fed, 141.1 ± 26.1 ; body, starved, 87.9 ± 3.3 g. Stomach and

TABLE 2. Time delay ($\bar{x} \pm SD$) in accepting a new food type by Red Knots kept in captivity. Differences between time delays before accepting a soft after a hard food type and the reverse treatment are significant, both when new food is novel as when it is not (Student's *t*-test, $P < 0.05$). Daily energy requirements during these experiments were similar, since experiments were carried out in enclosed cages at air temperatures between 15° and 25°C.

Type of change	Delay in days	n ^a
Pellets to <i>Spisula</i> ^b	4.5 ± 1.7	4
Molluscs ^c to pellets ^b	1.1 ± 0.4	8
Pellets to <i>Mytilus</i>	2.0 ± 0.6	5
<i>Mytilus</i> to pellets	0.0	25
<i>Spisula</i> to pellets	0.0	4

^a Number of individual diet changes in which delays were properly recorded.

^b Probable novel food type.

^c "Molluscs" refers to unspecified mollusc prey taken in field before exposure to food pellets in captivity.

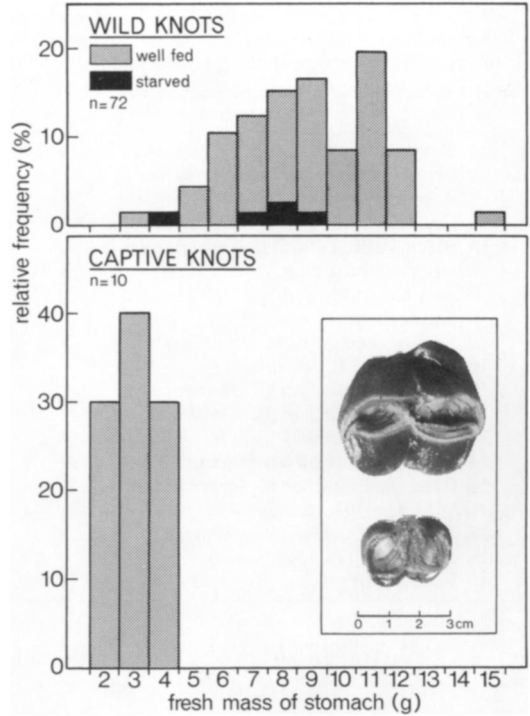


Fig. 2. Red Knots in wild (top) have much heavier stomachs than those in captivity (bottom), even if former have starved to death in severe weather in winter. Inset in bottom panel shows typical examples of gizzards (cross-sectioned through thickest part of muscle wall) of a 130-g wild (top) and a 125-g captive (bottom) Red Knot.

body masses in the sample of 10 captive birds averaged 3.5 ± 0.7 g and 109.0 ± 10.0 g, respectively. The change in stomach mass in captivity is expressed in a large decrease in the cross-sectional area of the gizzard of captives fed only with soft food pellets (Fig. 2 inset). The captives' apparent reluctance to eat hard-shelled prey, along with their small stomach mass, suggests that wild birds have stomachs that are adjusted to crack hard-shelled molluscs with heavy muscular gizzards. Given these findings, we asked whether wild Red Knots have heavy stomachs in comparison with other shorebird species, including those with softer diets.

Allometry of stomach mass in shorebirds.—An analysis of a sample of 135 stomachs of five species (Greater Golden-Plover, *Pluvialis apricaria*; Red Knot; Red-necked Stint; Purple Sandpiper, *Calidris maritima*; and Bar-tailed Godwit) showed that the excised stomachs consisted of

TABLE 3. Average wet masses ($\bar{x} \pm \text{SD}$) of body and stomach (proventriculus + gizzard) in 19 species of shorebirds (Charadrii). Includes only apparently healthy birds from nonbreeding season (usually inadvertently killed during catching operations).

Species	n	Body mass (g)	Stomach mass (g)
1 Eurasian Oystercatcher (<i>Haematopus ostralegus</i>)	3	546.67 \pm 30.71	15.60 \pm 0.54
2 Ringed Plover (<i>Charadrius hiaticula</i>)	6	53.40 \pm 8.21	1.18 \pm 0.25
3 Snowy Plover (<i>C. alexandrinus</i>)	2	41.75 \pm 0.25	1.25 \pm 0.35
4 Greater Golden-Plover (<i>Pluvialis apricaria</i>)	80	217.85 \pm 19.19	5.43 \pm 1.15
5 Black-bellied Plover (<i>P. squatarola</i>)	2	234.50 \pm 9.50	8.21 \pm 2.01
6 Great Knot (<i>Calidris tenuirostris</i>)	5	195.86 \pm 36.99	9.34 \pm 2.98
7 Red Knot (<i>C. canutus</i>)	67	141.36 \pm 26.13	8.82 \pm 2.25
8 Sanderling (<i>C. alba</i>)	1	56.00	1.80
9 Red-necked Stint (<i>C. ruficollis</i>)	157	26.93 \pm 1.87	1.08 \pm 0.18
10 Little Stint (<i>C. minuta</i>)	14	26.01 \pm 3.52	0.74 \pm 0.10
11 Curlew Sandpiper (<i>C. ferruginea</i>)	1	65.00	1.50
12 Purple Sandpiper (<i>C. maritima</i>)	6	65.63 \pm 5.21	3.95 \pm 0.55
13 Dunlin (<i>C. alpina</i>)	55	49.96 \pm 9.62	1.97 \pm 0.51
14 Black-tailed Godwit (<i>Limosa limosa</i>)	3	317.77 \pm 52.95	10.41 \pm 0.41
15 Bar-tailed Godwit (<i>L. lapponica</i>)	84	320.30 \pm 69.52	8.98 \pm 3.06
16 Whimbrel (<i>Numenius phaeopus</i>)	3	510.00 \pm 40.82	20.13 \pm 4.28
17 Eurasian Curlew (<i>N. arquata</i>)	3	870.83 \pm 72.28	35.95 \pm 4.47
18 Redshank (<i>Tringa totanus</i>)	3	154.33 \pm 16.01	3.83 \pm 1.38
19 Ruddy Turnstone (<i>Arenaria interpres</i>)	6	102.67 \pm 7.36	2.55 \pm 0.72

9.1 \pm 6.2% fat (range 0.0–29.6), 27.2 \pm 3.6% other dry matter (15.5–43.1) and 63.7 \pm 6.0% water (47.6–81.9). The percentage of fat of the wet stomach mass was positively correlated with the

fat index of the entire body (i.e. 100 [fat mass/body mass]), with a linear regression of $Y = 0.74 + 0.64X$ ($r^2 = 0.59$, $P < 0.05$).

Stomach mass in shorebird species (data listed in Table 3) is isometric with body mass (i.e. an exponent of 1; see Fig. 3). The allometric regressions yielded an exponent of 1.026 (not significantly different from one) across all species, with a slightly higher value for the sandpipers (1.066) than for plovers (1.029). A covariance analysis showed that neither the slopes nor the intercepts differed significantly between sandpipers and plovers. However, some sandpiper species had relatively heavy stomachs, with particularly high values being recorded in Red Knot (89% heavier than average), Purple Sandpiper (84% heavier), and Great Knot (44% heavier). The diet of these species consists in large part of held-shelled molluscs which are ingested whole (Cramp and Simmons 1983, Lane 1987, Summers et al. 1990), thus supporting the suggested interspecific association between a diet of shellfish and a heavy stomach.

Do the allometric relationships, with exponents close to 1, also hold within species? In the six species we examined, stomach mass was positively correlated with body mass, though the exponents varied widely from 0.28 in Red Knots to 1.39 in Greater Golden-Plovers (Fig. 4). The low slopes in Red Knots and Bar-tailed Godwits were due to a few particularly heavy individuals with light stomachs (Fig. 4). These

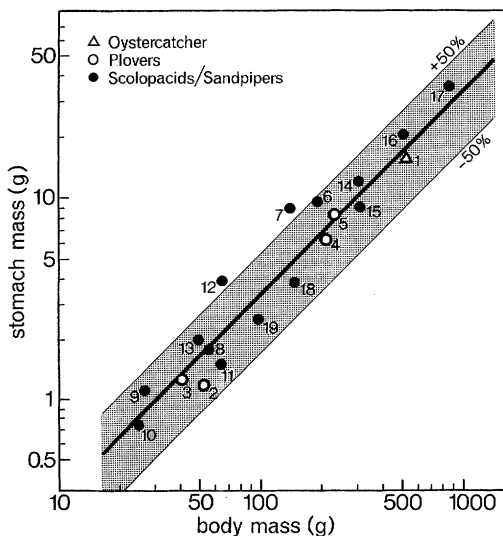


Fig. 3. Allometry of stomach mass and body mass in sample of 19 species of shorebirds of three families: (1) oystercatchers (Haematopodidae; $n = 1$, open square); (2) plovers (Charadriidae; $n = 4$, open circles); and sandpipers (Scolopacidae; $n = 14$, closed dots). Allometric relationship for all 19 data points is $Y = 0.0295X^{1.026}$ ($r^2 = 0.93$). Equations for individual families: plovers, $Y = 0.0193X^{1.077}$ ($r^2 = 0.96$); sandpipers (including Ruddy Turnstone), $Y = 0.0311X^{1.029}$ ($r^2 = 0.92$). Numbers refer to species listed in Table 3.

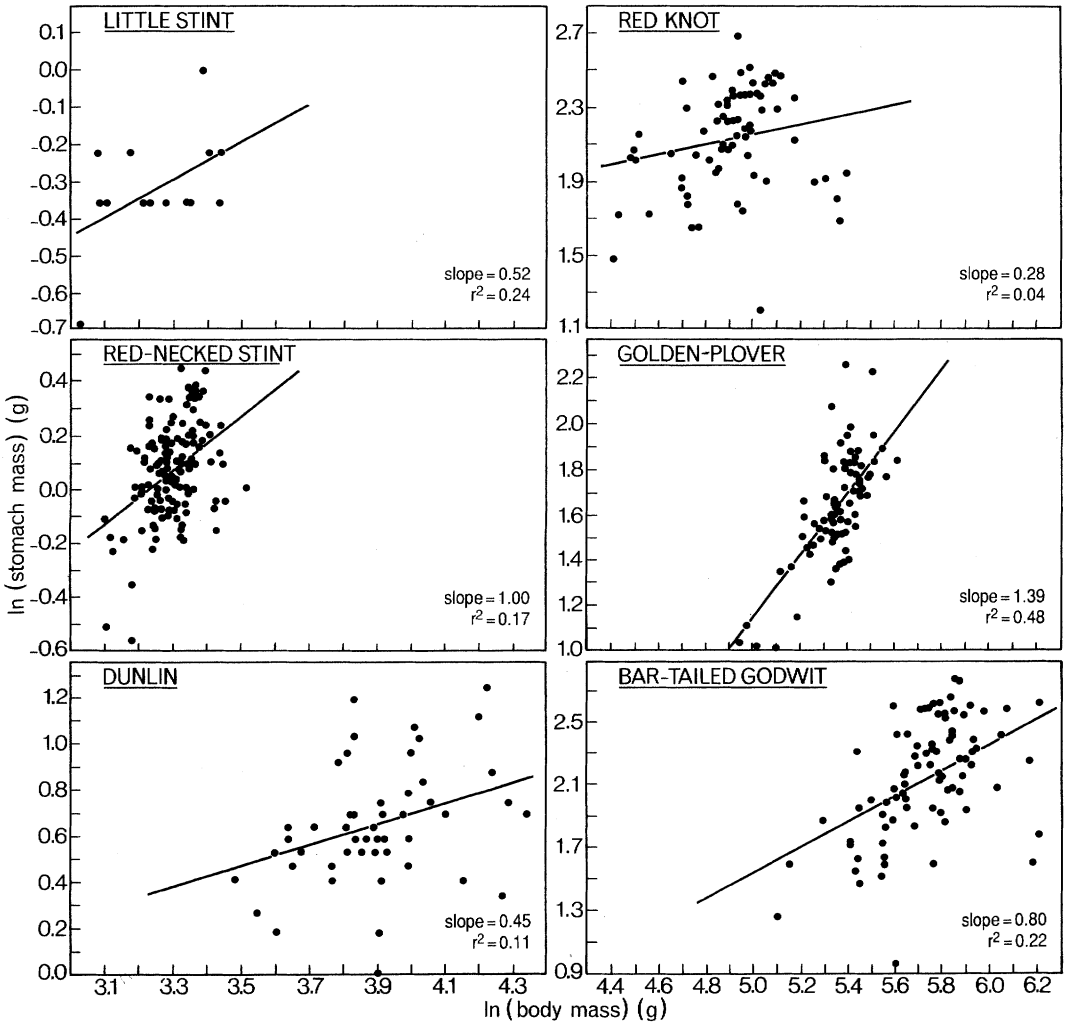


Fig. 4. Allometry of stomach mass and body mass in Little Stint ($n = 14$), Red-necked Stint ($n = 157$), Dunlin ($n = 55$), Red Knot ($n = 72$), Greater Golden-Plover ($n = 85$), and Bar-tailed Godwit ($n = 84$). Sample sizes are slightly bigger than those in Table 3 because information for starved wild birds also included here. All regression coefficients significantly different from zero at 5% level.

heavy birds contained large fat loads (pers. observ.) and were sampled shortly before departure on a long-distance migration to the arctic breeding grounds (Piersma and Jukema 1990). This observation raises the question whether stomach masses change in relation to the migratory cycle.

Stomach mass and long-distance migration.—Red Knots of the subspecies *islandica* winter in Europe and breed in the High Arctic of Greenland and Canada (Davidson and Wilson 1992; for review of subspecies, see Piersma and Davidson 1992). They are represented by an early spring

sample (March) from Dutch and German parts of the Wadden Sea, and a sample from late May of birds ready to leave from Iceland (see Gudmundsson et al. 1991). Birds staging in the Wadden Sea in early spring had a significantly greater stomach mass than individuals just before their departure to the arctic breeding grounds captured later in spring in Iceland (Fig. 5, top), even though the former group had a much lower body mass (135 ± 13 g) than the latter (208 ± 11 g). A decreasing stomach mass during the period of premigratory body-mass gain was also evident in Red Knots of the subspecies *canutus*

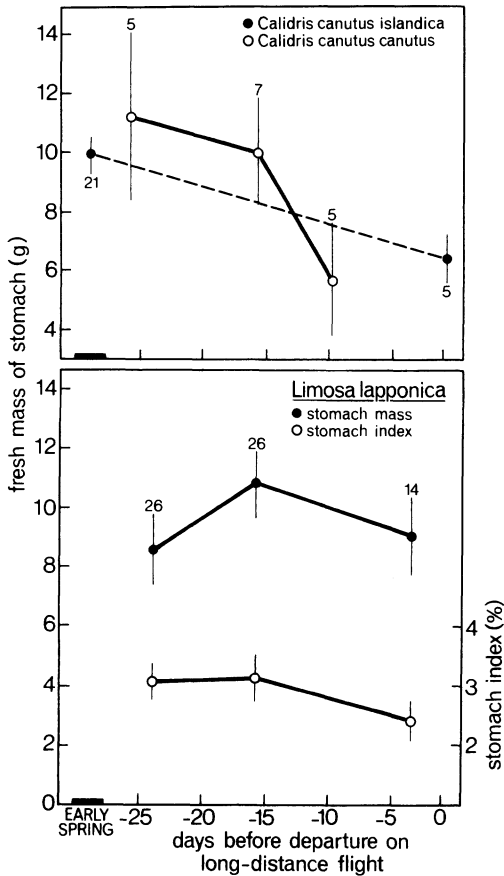


Fig. 5. Decreases in stomach mass prior to long-distance migration in two populations of Red Knot (top) and in Bar-tailed Godwits (bottom). Averages with 95% confidence intervals and sample sizes are shown. Analyses of variance indicated that between-sample variation to be larger than the within-sample variation in all three examined cases (*islandica* Knots, $F = 32.2$, $P < 0.001$; *canutus* Knots, $F = 11.4$, $P = 0.001$; Bar-tailed Godwits, stomach mass, $F = 4.4$, $P = 0.016$; Bar-tailed Godwits, stomach index, $F = 3.93$, $P = 0.025$).

(migrating between West Africa and Siberia; see Piersma et al. 1992) on the Banc d'Arguin, Mauritania (Fig. 5, top).

The Bar-tailed Godwits staging in May in The Netherlands are of a population migrating from the West African wintering grounds to the Siberian breeding areas (see Drent and Piersma 1990, Piersma and Jukema 1990, 1993). A similar pattern as in Red Knots was detected in the stomach masses of staging Bar-tailed Godwits (Fig. 5, bottom). Having arrived after a 4,300-km flight (ca. 25 days before next departure), the birds had depleted their nutrient reserves

(Piersma and Jukema 1990, Lindström and Piersma 1993), which apparently also negatively affected their stomach mass. As a consequence of the initially depleted state, the pattern is best reflected by the changes in stomach index ($100[\text{stomach mass}/\text{body mass}]$). During the staging period when body mass increased (with both fat and proteins being stored; Lindström and Piersma 1993), relative stomach mass decreased.

In the Red Knots from Mauritania the pre-departure decrease in stomach mass was associated with a decrease in the incidence of hard-shelled prey remains in the stomachs. There were on average, respectively, 46 ± 10 , 29 ± 20 and 14 ± 12 mollusc fragments in the stomachs of the three successive groups of birds depicted in Figure 5.

Diet and stomach structure in Bar-tailed Godwits.—Bar-tailed Godwits have a particularly variable diet in the Wadden Sea during spring staging. They feed both on hard-shelled molluscs and on soft-bodied polychaete worms (Boere and Smit 1980a), and on insect larvae and lumbricid worms in the adjacent fields (pers. observ.). Is the highly variable diet of Bar-tailed Godwits also associated with stomach mass (Fig. 5, below), as in the Red Knots from Mauritania?

Of the 55 analyzed stomachs of Bar-tailed Godwits, 16 contained leatherjackets only. Of the 14 godwits with the remains of soft-bodied polychaete worms (*Nereis diversicolor*) only one also contained leatherjackets, whereas of the 25 godwit stomachs with the remains of marine molluscs (usually *Macoma balthica*), 12 contained leatherjackets too. The proportion of *Nereis*-eating birds additionally containing leatherjackets is significantly smaller than the proportion of mollusc eaters ($X^2 = 10.1$, $df = 1$, $P < 0.01$). Leatherjackets have no hard parts but, as their common name implies, they are rather strong-skinned. Their well preserved state in the stomach indicates that they are hard to wear down. The diet of the godwits, therefore, consisted either of: (1) soft and easily digested prey (*Nereis*); or (2) hard-shelled (*Macoma*) and/or tough-skinned (leatherjacket) prey.

Godwits feeding on soft prey were heavier but had lighter stomachs than those feeding on other prey types, and their stomachs contained fewer stones but more grit (Table 4). The high average body mass of *Nereis* eaters indicates the presence of heavy premigrating godwits in the sample, but is also due to a higher percentage

TABLE 4. Body, stomach and relative stomach masses ($\bar{x} \pm SD$) and their dry-grit content in Bar-tailed Godwits containing either hard-shelled molluscs and leatherjackets (tipulid larvae), or soft-bodied polychaete worms (*Nereis diversicolor*) as prey remains. Birds were accidentally collected in May 1984–1989 on their spring staging area in the Dutch Wadden Sea.

Variable	Prey category		t-value ^a
	Molluscs and/or leatherjackets (n = 41)	<i>Nereis</i> (n = 14)	
Body mass (g)	314.7 ± 56.7	392.9 ± 91.0	3.02**
Stomach mass (g)	10.0 ± 3.1	7.5 ± 1.9	3.62***
Stomach index ^b (%)	3.2 ± 0.8	2.3 ± 0.6	4.16***
Stones (grit) (g)	1.0 ± 1.08	0.3 ± 0.3	3.40***
Shell grit (g)	0.1 ± 0.2	0.4 ± 0.4	2.37*

^a Indicates whether values of two categories differ significantly from zero (two-sided Student's t-tests). *, P < 0.05; **, P < 0.01; ***, P < 0.005.

^b 100(stomach mass/body mass).

of females (the larger sex) in the *Nereis*-eating sample (57%) than in the mollusc/leatherjacket sample (27%). The significantly smaller stomach index of the category of birds feeding on soft prey, nevertheless, indicates an association between stomach mass and diet in migrant Bar-tailed Godwits. Relatively heavy stomachs occurred in birds feeding either on hard-shelled prey or on tough-skinned prey that require the grinding action of stones for proper digestion. Light stomachs were found in birds feeding on worms.

Do trained stomachs crack better?—Why do birds feeding on hard-shelled prey have heavier stomachs? Do large stomachs crack better, or would lighter stomachs become exhausted too soon when they have to deal with large numbers of hard-shelled prey? On the assumption that a better cracking performance by the stomach would reveal itself in the droppings in shells fragmented to smaller pieces, the hypothesis that trained and heavy stomachs crack better was tested by examining median fecal-fragment size produced by Red Knots fed on a particular prey type with different recent diet experiences. We assumed that training effects would be evident within a week (Goldberg et al. 1975, Piersma 1988, Mufti and Qureshi 1989). The attempt to correlate fecal-fragment size of birds fed with *Mytilus* and *Hydrobia* against a score for prior experience was complicated because

TABLE 5. Results of two stepwise multiple regressions to estimate median fragment size in feces in which prey size (shell length, SL), daily intake (dry mass ingested during a 24-h experimental period, DI) and prior experience (hardness score weighted for number of days before, PE) are consecutively entered as independent variables.

Independent variable	Multiple-regression parameters		
	Standardized coefficient (β)	T-value	P-value
<i>Mytilus</i> (n = 58)^a			
Shell length	0.50	5.47	<0.001
Daily intake	0.34	3.00	0.004
Prior experience	0.24	2.16	0.035
<i>Hydrobia</i> (n = 16)^b			
Shell length	0.11	0.33	0.746
Daily intake	0.22	0.79	0.445
Prior experience	0.18	0.55	0.594

^a Equation: Y = 44.9SL + 3.1DI + 2.6PE + 49.9 (r² = 0.55, P < 0.05).

^b No equation (r² = 0.12, P > 0.05).

several variables other than recent prior experience with hard-shelled prey appeared to be highly correlated with fecal-fragment size. Birds eating larger *Mytilus* produced larger fecal fragments as did birds eating more *Mytilus* (Table 5). Taking these two effects into account statistically, we came to the surprising conclusion that conditioned birds produced larger fecal fragments (Table 5). The results for *Hydrobia*, although not statistically significant, were similar. We, thus, must reject our hypothesis that trained stomachs lead to more fragmented prey remains.

DISCUSSION

Pyloric complications.—The pylorus is the structure that determines how long food items remain in the stomach and are subject to its forces. The pyloric region is the muscular complex around the exit from the stomach to the small intestine. The pylorus ensures that only properly degraded particles enter the intestine (Stevens 1988). It is likely that the pylorus becomes increasingly “relaxed” and allows hard particles to enter the intestine sooner upon prolonged exposure to hard shell fragments (see Levey and Duke 1992). Because retention and, therefore, fragmentation times in the gizzard will become shorter, increasingly large fragments would be found in the feces. A strong modifying effect of the pylorus on stomach re-

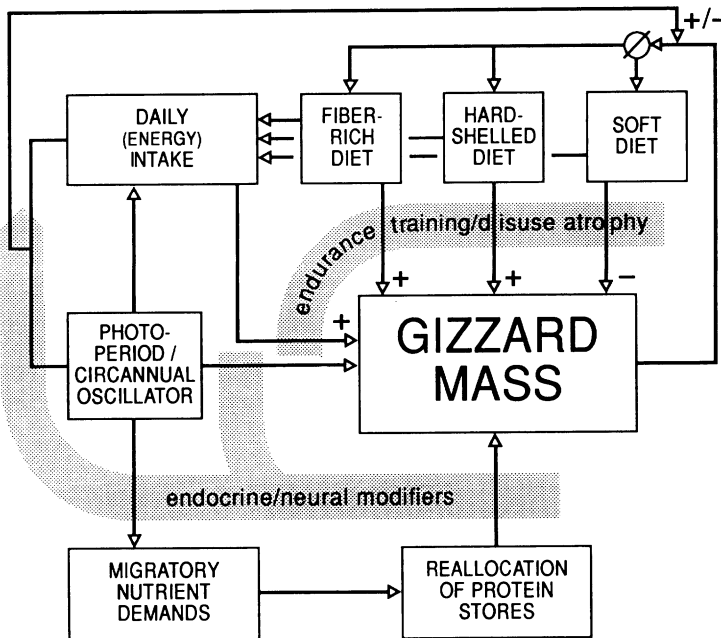


Fig. 6. Scheme outlining a set of hypotheses about feedback loops between food type and gizzard mass, and about points of interaction of other identified influences on gizzard mass, based on our findings for shorebirds and those reported for other species (see Table 1 and text).

tention times, and a change in its “admission criteria,” would account for the observed decreases in median mussel-fragment size upon exposure to a hard-shelled diet. The only disadvantage of passing large shell fragments is potential tissue damage to the intestines. If both pylorus and intestines can adjust to passing larger fragments the birds may benefit because the processing rate would increase.

The low apparent assimilation efficiency (39%) of horseshoe crab (*Limulus polyphemus*) eggs ingested by Sanderlings is a consequence of the majority of eggs passing through the digestive tract intact (Castro et al. 1989). It is likely that the small egg diameter (1 mm) allows horseshoe crab eggs to pass rapidly through the pylorus, thereby foregoing grinding by the gizzard. Shorebirds consuming horseshoe crab eggs in Delaware Bay during spring migration (Myers 1986) might benefit from a pyloric filter system, such as the pyloric feather plug of grebes (Podicipedidae; Piersma and van Eerden 1989).

Diet/stomach interactions.—Shorebirds appear to exhibit almost all the relationships between stomach mass/structure and diet that are known in other birds (Table 1): (1) experimental exposure to soft food leads to light gizzards; (2) individuals with atrophied gizzards initially re-

fuse to ingest hard-shelled prey; (3) shorebird species that feed on molluscs have relatively the heaviest stomachs; (4) light and thin-walled stomachs are associated with diets of soft prey. The indication that Red Knots and Bar-tailed Godwits show stomach atrophy during general body hypertrophy before long-distance flights is paralleled by a similar observation of an unaccountable decrease in stomach mass of pre-migratory fattening Greater Snow Geese (*Chen caerulescens atlanticus*; Gauthier et al. 1984); in the case of the geese, there was no change in diet.

The diet/stomach relationship is dynamic and reciprocal. On the basis of the literature summarized in Table 1 and our own findings, we have tried to integrate the (causal) interactions that may be involved in Figure 6. The crux of the problem of whether gizzard mass influences diet is the position of the valve in the upper right corner, allowing a fully hard-shelled or fiber-rich diet, or not. Assuming that it is the gizzard part of the stomach that critically influences diet choice, we suggest that the mass of this organ is influenced by direct (endurance) training and by atrophy through disuse (caused by changes in ingested volume or characteristics of prey), as well as through the effects of

endocrine or neural modifiers. The latter mechanism may be involved in a possible reallocation of protein reserves prior to long-distance flights, as in Bar-tailed Godwits. A direct endocrine or neural mechanism was also implied by Spitzer (1972) in his study of the dramatic changes in stomach structure and mass of Bearded Tits (*Panurus biarmicus*), changes that occurred independently of migratory events. Spitzer suggested that a photosensitive circannual oscillator caused the seasonal changes in stomach mass, which in turn were associated with changes from seed to invertebrate diets.

Two different diet types apparently lead to heavy muscular stomachs, and they involve two different functional requirements. Tough-skinned prey (such as leatherjackets) and fiber-rich food probably require long gizzard retention times during which the food is ground and worn down, usually with the help of stones (see studies of herbivores summarized in Table 1, and Table 4). Hard-shelled prey, which can be cracked singly or against each other instead of being ground slowly with the help of grit, require a strong muscular gizzard as well, but probably involve much shorter stomach retention times. Such a dichotomy in diet and retention times in birds with muscular stomachs might suggest correlated differences in the relative contribution of the stomach to the chemical breakdown of food. Since no chemical action can be carried out in the proventriculus where prey are intact, and since little digestive work can occur during the short stage in the muscular gizzard, we suggest that the intestines of birds feeding on hard-shelled prey play a larger role in digestion than they do in either birds feeding on fiber-rich food, in which part of the chemical breakdown is carried out in the stomach, or in birds feeding on soft food, in which the glandular stomach begins the process of the chemical breakdown. Alternatively, the meat contained in hard-shelled prey might generally be so easy to digest that "lack of stomach digestion" and "ease of digestion" could cancel each other out.

A number of issues remain. Does a long-term exposure in the field to soft food always lead to reduced gizzard mass? It may fail to do so if endocrine/neural modifiers interfere (Fig. 6). Does the presence of a weak gizzard constrain the dietary options, and for how long? The only, admittedly weak, evidence that gizzards do temporarily constrain diets is supplied by the

fact that Bar-tailed Godwits with light stomachs and worm diets were particularly prominent among fat pre-migratory females, in spite of the fact that *Nereis* worms are abundantly available on the feeding grounds all through the godwits' staging period (Zwarts 1988); *Nereis* might not be the preferred prey and is only taken when stomach structure prevents a focus on hard or tough prey.

The time course of such constraints was not resolved, but clinical studies of muscle hypertrophy show rapid effects of training, with over one-half of the muscle usually being built up within a week (Goldberg et al. 1975, Mufti and Qureshi 1989). The significance of this finding is that, if a summer season on the tundra with a diet of relatively soft terrestrial invertebrates results in reduced stomach mass in arctic-breeding shorebirds, we might expect them to require time to adjust to a diet of hard-shelled mollusc prey on their return to the nonbreeding grounds. If shorebirds try to maximize the speed of migration (Alerstam and Lindström 1990, Gudmundsson et al. 1991) and if periods of only one week matter (Piersma 1987), the diet/stomach interaction described here may have considerable relevance to birds in the wild. Indeed, this was recently implicated by Klaassen and Biebach (in press) in their study of fattening and starvation in migrant Garden Warblers (*Sylvia borin*). After a period of starvation, which mimicked the use of nutrient reserves during a long-distance flight, Garden Warblers had submaximal intake rates for several days, which the authors attributed to limitations imposed by a reduced digestive tract. The increase in staging time for refattening induced by suboptimal feeding contrasts with the rest of the metabolic adaptations of Garden Warblers, which can all be interpreted as being designed to speed up migration.

Diet-, activity-, or season-induced changes in the digestive tract, thus, may affect a host of behavioral and ecological phenomena displayed by birds. Further study will undoubtedly yield more quantitative insight into the ways in which the digestive physiology of birds constrains their behavioral performance.

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