

Reversible size-changes in stomachs of shorebirds: when, to what extent, and why?

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Abstract. Shorebirds show large interspecific variation in the relative size of the stomach, and especially of the muscular part, the gizzard. Much of this variation can be explained by their diet. Species feeding mainly on hard-shelled prey such as bivalves and gastropods have large stomachs; those feeding on soft-bodied prey such as worms have small stomachs. Within a species, diet- and migration-induced changes in stomach size can occur. Our studies on this intraspecific variation have focused on two mollusc-specialists, the Red Knot *Calidris canutus* and the Great Knot *C. tenuirostris*. Both are renowned for long-range flights between their arctic or sub-arctic alpine breeding grounds and a variety of coastal wetlands. Feeding mainly on shellfish ingested whole, both knot species have large stomachs, but changing diets easily lead to apparently adaptive modifications. In addition, the demands imposed by flights of many thousand kilometres may induce reductions in stomach size. Using ultrasonography we have begun to experimentally disentangle the causal relationships between diet, season and stomach size in Red Knots. A soft diet can induce stomach reductions of 50% within a week, and such changes are reversible. Studies on radiomarked birds in the Wadden Sea emphasize that variations in stomach size are correlated with prey and patch choice in the field.

Key words: diet, migration, stomach, flexible organ size, Red Knot *Calidris canutus*, Great Knot *Calidris tenuirostris*

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INTRODUCTION

It is increasingly clear that the functional significance of some morphological features can only be understood with due reference to behavioural features of the organisms concerned, and vice versa (Wainwright & Reilly 1994, Piersma & Lindström 1997). This is not only true for structures that have reached definitive form and size in adult vertebrate organisms, but even more so for flexible structures, such as the internal body organs. For example, many studies of avian

stomachs have found that changes in diet go hand in hand with changes in stomach size and structure (review in Piersma et al. 1993b).

A summary of the relative mass of stomach and intestine for a range of shorebird species (Fig. 1) shows not only that the size of these two organs is correlated ($r = 0.73$, $n = 12$ species), but also that the species uniquely feeding on hard-shelled prey that are ingested whole (Red Knot *Calidris canutus* and Purple Sandpiper *Calidris maritima*) possess much larger stomach and intestines than species relying mainly on soft

polychaete worms (e.g. Curlew Sandpiper *Calidris ferruginea*, Ringed Plover *Charadrius hiaticula* and Avocet *Recurvirostra avosetta*). That shorebirds crushing ingested molluscs and crustaceans need a relatively large intestine as well as a large stomach may have to do with the fact that the stomach can hardly contribute to the digestive process, unlike species where chemical digestion of soft tissue can start in the glandular stomach or proventriculus, as in Oystercatchers *Haematopus ostralegus* (Kersten & Visser 1996).

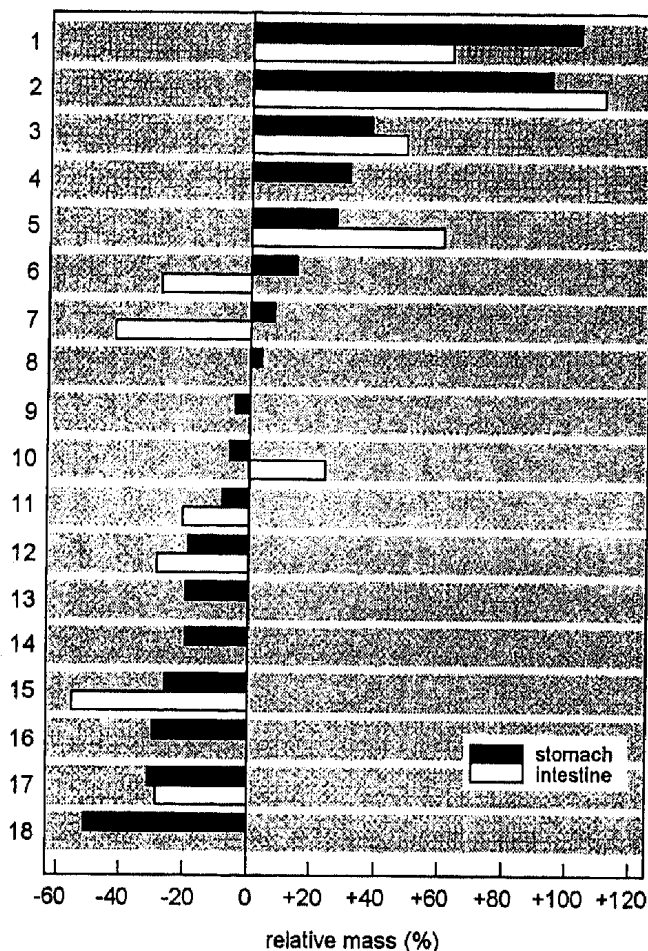


Fig. 1. Relative mass of stomach and intestine of 18 European shorebird species. Relative mass of each organ was calculated as the absolute deviation of the predicted fresh organ mass on a doubly-logarithmic plot of organ mass on body mass (allometric scaling) divided by the predicted organ mass.

1. *Calidris canutus*, 2. *C. maritima*, 3. *Numenius arquata*, 4. *Numenius phaeopus*, 5. *Calidris alpina*, 6. *Pluvialis squatarola*, 7. *Limosa limosa*, 8. *Crocethia alba*, 9. *Charadrius alexandrinus*, 10. *Haematopus ostralegus*, 11. *Calidris minuta*, 12. *Pluvialis apricaria*, 13. *Tringa totanus*, 14. *Arenaria interpres*, 15. *Calidris ferruginea*, 16. *Charadrius hiaticula*, 17. *Limosa lapponica*, 18. *Recurvirostra avosetta*.

In this review we aim to summarize our findings on the functional significance of variation in stomach size based on our ongoing studies of two closely related large sandpiper species, the Red Knot and the Great Knot *Calidris tenuirostris*. In the nonbreeding season, both species mainly eat molluscs (bivalves and gastropods) and sometimes crustaceans, prey that they find on intertidal soft sediments (Piersma et al. 1996). On their breeding grounds — high arctic and alpine tundra — they tend to rely on rather more soft-bodied spiders and insects, although Great Knots seem to some extent feed on berries, and have even been found to eat nuts (Tomkovich 1996).

CAUSALITY IN STOMACH/DIET INTERACTIONS

Earlier studies have provided ample demonstration that stomach size is correlated with diet type, but the directions of the causal arrows in these relationships are far from clear (Piersma et al. 1993b). Whereas stomach size may influence diet and thereby feeding site, a choice for a certain diet as a consequence of a choice for a certain feeding site may also feed back to the size of the stomach (Fig. 2). Season, or phase of the annual cycle, may influence stomach size in more direct ways (Dietz et al. 1999b), for example in relation to necessary stomach weight reduction before take-off on long dis-

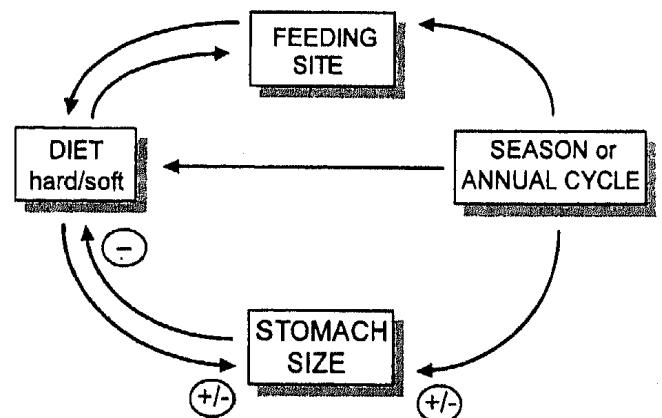


Fig. 2. Stomach size as a function of diet, feeding site and time of the year.

tance flights (Piersma 1998, Piersma & Gill 1998, Piersma et al. 1999), special diet requirements in relation to migratory events (Bairlein & Gwinner 1994), and feeding site selection (Piersma et al. 1994, Yong et

al. 1998). Thus, we are presented with a series of chicken-or-egg problems. To get a handle on these issues, 'directional' experiments are required. But first we shall examine how stomach mass changes in parallel with very drastic changes in body mass, i.e. before and during long-distance migration flights.

MIGRATION-RELATED CHANGES

Many shorebird species migrate over very long distances, often doubling body mass at stopover sites before take-off on nonstop flights that may last several days, sometimes perhaps even more than a week. The two focal species of knots both carry out nonstop flights of several thousand kilometers. The only study of what happens during such long flights was carried out on northward migrating Great Knots that leave the coast of northwest Australia for a direct flight of 5 400 km over the South China Sea to stopover areas along the China coast, from Shanghai northwards (unpublished data of P. F. Battley et al.). In late March Great Knots leave northwest Australia with body masses of about 240–260 g, arriving in China about four days later with masses of about 125 g. Much of this mass reduction is due to the loss of fat (from about 90 g to 11 g), but there are also significant reductions in all body organs other than the brain and the lungs (data of P. F. Battley et al.). Among the organs, both the stomach and the intestine show strong reductions in size between departure from northwest Australia and arrival in coastal China (Fig. 3). The digestive tract thus contributes to the minimum requirement for proteins during starvation (Jenni & Jenni-Eiermann 1998), although the functional significance of these in-flight size reductions may also extend to weight-savings and reduced flight costs (Pennycuik 1998). At present we do not know whether the relatively small stomach and intestine are built up again during stopover in China. The flight to the breeding grounds for Great Knots from northern China is still > 4000 km, so substantial fuelling will be required. However, there is some evidence that stomach mass on the alpine tundra breeding grounds is even smaller than that upon arrival in coastal China (Fig. 3). Therefore, with respect to requirements during the breeding season the stomach may perhaps not need to be restored to full size and capacity during the China-stopover.

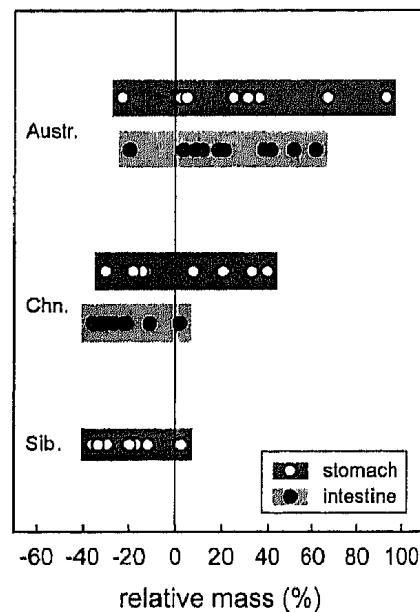


Fig. 3. Masses of stomach and intestine (relative to the overall average) of Great Knots before departure from the northwest Australian nonbreeding grounds (Austr.), upon arrival in coastal China (Chn.), and on the breeding grounds in the Siberia (Sib.). Each dot represents one sampled individual; sexes are combined.

Such design-conflicts stemming from a requirement for large stomach size during the refuelling phase and small stomach size during flight towards and on the breeding grounds may perhaps explain a recurrent pattern of change in stomach masses of Red Knots (Fig. 4, and see Battley & Piersma 1997 for Red Knots in New Zealand). We have studied compositional changes of Red Knots at two comparable stopover sites, in southwest Iceland (Piersma et al. 1999) and at Delaware Bay, U.S.A. (T. Piersma et al. unpubl. data). In both areas Red Knots make a stopover before 2000–3000 km long flights into the arctic breeding areas in northern Greenland and Canada at the end of May. Birds refuelling in southwest Iceland arrive after a 2500 km long flight from the British estuaries and the Wadden Sea. Birds in Delaware Bay arrive after much longer nonstop flights, as long as 5000 km if they took off in northern Brazil and perhaps 8000 km if they took off in southern Brazil (Harrington 1996). This difference in length of the previous flight may be reflected by the much more depleted state with which Red Knots arrive in Delaware Bay compared to Iceland (body mass upon arrival close to 100 g, and over 140 g, respectively; Fig. 4). Another important difference between the two sites is the nature of the food. In southwest Iceland the diet consists entirely of hard-shelled

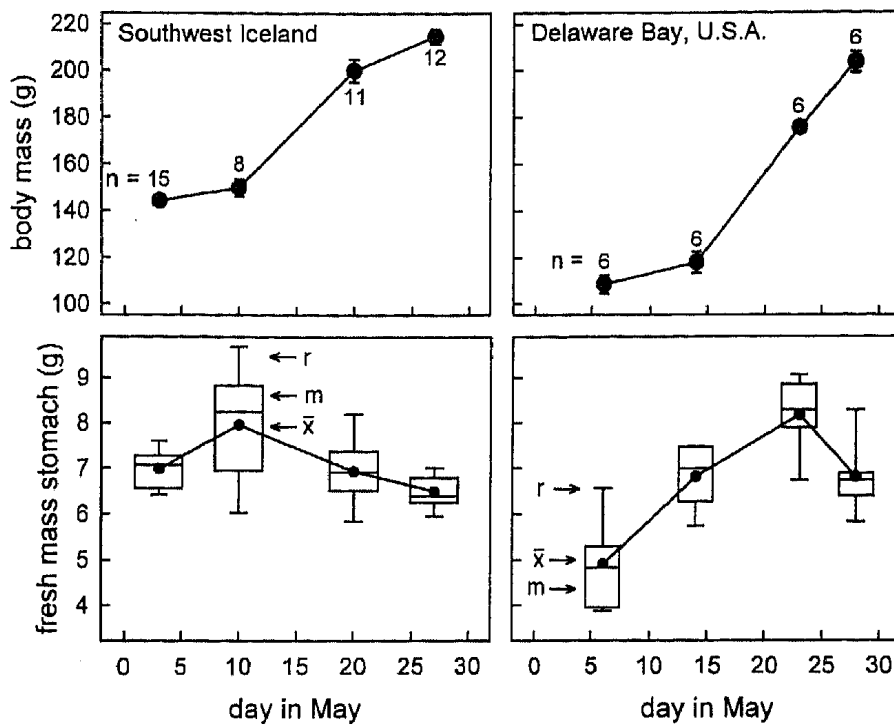


Fig. 4. Changes in body and stomach mass of two species of Red Knots staging in southwest Iceland (c.t. *islandica*) and in Delaware Bay, U.S.A. (c.t. *rufa*). Mean body masses are plotted ± 1 SEM, and stomach masses are presented as box-plots: the box encloses 50% of the data points; *r* — the total range, *m* — the median, \bar{x} — the average value. The data for males and females were lumped (see Piersma et al. 1999).

molluscs, i.e. mussels and periwinkles (Piersma et al. 1999), whereas in Delaware Bay the birds rely totally on the small eggs of horseshoe crabs *Limulus polyphemus* that abundantly occur on some beaches (Harrington 1996, Tsipoura & Burger 1999). The molluscs require a crushing action of the stomach; the horseshoe crab eggs require grinding. Indeed, only in the stomachs of Red Knots from Delaware Bay did we find many small stones that may help the grinding.

Despite the considerable differences in previous flight performance and in prey type at the Iceland and Delaware Bay staging sites, the pattern of change in stomach size is remarkably similar. At both sites an initial increase in size is followed by a subsequent decrease, and peak stomach masses of about 8 g occur approximately at stages during which refuelling rates are highest. Nevertheless, in Red Knots in Iceland the decrease in stomach size starts surprisingly early, which may relate to an imminent diet change (from molluscs to tundra arthropods) requiring early preparation (Piersma et al. 1999). The knots in Delaware Bay may be more time-stressed and a change from a diet of invertebrate eggs to tundra

arthropods may not require as many modifications. In both cases Red Knots show the seemingly strategic reductions in parts of the digestive tracts that are also known for other species before take-off on long nonstop flights (Piersma 1998, Piersma & Gill 1998). The fact that stomach size changes occur in rapidly refuelling and hard-working birds suggest that there is much more to the regulation of stomach size than training effects. But training effects obviously do play a role.

DIET DETERMINES STOMACH SIZE

Red Knots in captivity that were maintained on a diet of soft trout food-pellets (brandname "Trouvit") developed very small stomachs and were reluctant to eat their natural hard-shelled prey (Piersma et al. 1993b). We studied stomach size changes in Red Knots fed alternately on mussels and soft food-pellets (Fig. 5) using the novel technical tool of ultrasonography to estimate the size of stomachs in live birds (Dietz et al. 1999a), We

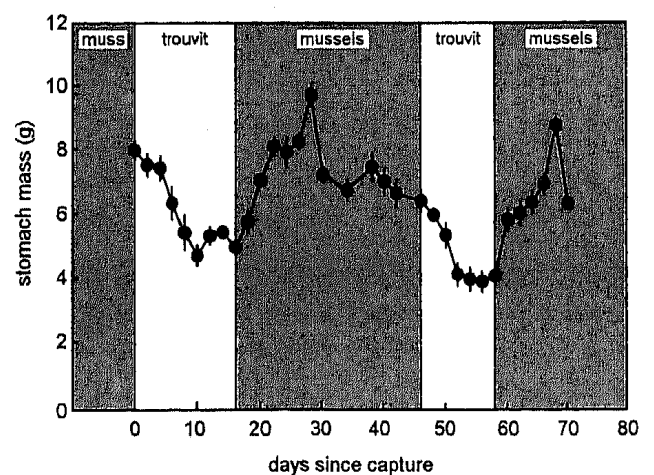


Fig. 5. Changes in mean stomach mass in a group of 10 Red Knots maintained in an outdoor aviary on a diet that alternately consisted of Hard-shelled Mussels *Mytilus edulis* and soft trout-food pellets "Trouvit". Stomach diameters were measured every other day. Mean stomach masses ± 1 SEM are given.

started off with freshly captured Red Knots that had been feeding on bivalves in the field. The group of 10 birds showed (Fig. 5) a rapid reduction in stomach size to about half the initial mass within 10 days after the diet change. When the birds were shifted back to hard-shelled molluscs, their stomachs returned to initial mass within a week. In the experiment this was followed by a slow decrease in stomach mass, perhaps due to the fact that by necessity the birds had to be fed with increasingly smaller-sized mussels (which are easier to crack; Piersma et al. 1993b). Nevertheless, a repeated switch to soft pellets and then back to mussels yielded a replay of the earlier pattern, a pattern that was also repeated independently in two other groups of birds (A. Dekinga et al.

ern Wadden Sea (see Piersma et al. 1993a, van Gils & Piersma 1999), birds of which stomach size had been determined upon capture and tagging using ultrasonography. Not only were we able to locate the radio-tagged individuals on the feeding sites, we were also able to determine the diet of these feeding flocks based on droppings collected at the feeding sites (Dekinga & Piersma 1993). In August 1997 there was a clear relation (Fig. 6) between estimated stomach size of radio-tagged Red Knots and the extent to which the flocks in which they occurred fed on cockles *Cerastoderma edule* rather than bivalve prey that are easier to swallow and to crack, such as *Macoma balthica* and *Mya arenaria* (see Zwarts & Blomert 1992). No other phenotypic variable of the ra-

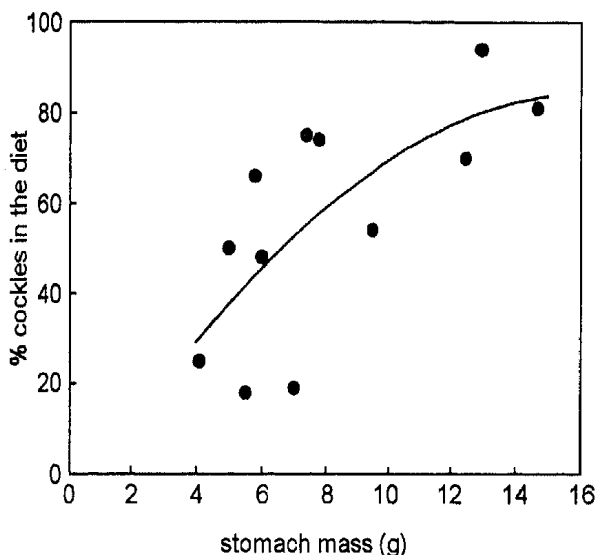


Fig. 6. Variation in the relative proportions of cockles in the diet of flocks containing radio-tagged Red Knots in the western Wadden Sea in August 1997. Quadratic function ($Y = -11.55 + 11.60X - 0.35X^2$)

unpubl. data). Thus, Red Knots that are forced to accept a drastic change in diet, even at possibly inappropriate times of their annual cycle, can still double stomach size in about a week, and reduce it by half in about a week. Diet clearly determines stomach size.

STOMACH SIZE DETERMINES DIET

That the causal arrow between diet type and stomach size may also be directed in the direction of diet type is suggested by some intriguing findings from the field. For two seasons we have now been able to follow the feeding movements of radio-tagged Red Knots in the west-

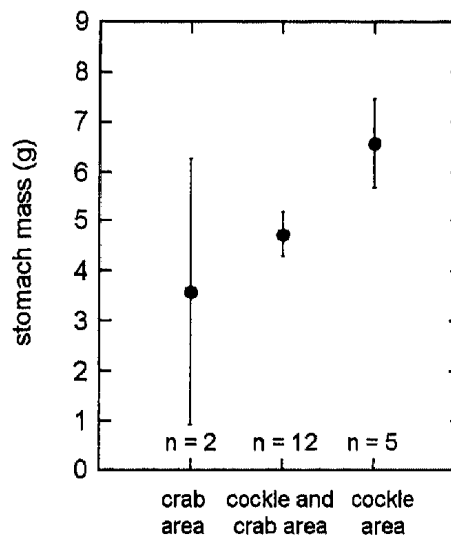


Fig. 7. Occurrence of radiomarked Red Knots at cockle, crab/cockle and crab areas in August 1998 on the intertidal flats west of Griend in the Dutch Wadden Sea. Means \pm SEM.

ern Wadden Sea (see Piersma et al. 1993a, van Gils & Piersma 1999), birds of which stomach size had been determined upon capture and tagging using ultrasonography. Not only were we able to locate the radio-tagged individuals on the feeding sites, we were also able to determine the diet of these feeding flocks based on droppings collected at the feeding sites (Dekinga & Piersma 1993). In August 1997 there was a clear relation (Fig. 6) between estimated stomach size of radio-tagged Red Knots and the extent to which the flocks in which they occurred fed on cockles *Cerastoderma edule* rather than bivalve prey that are easier to swallow and to crack, such as *Macoma balthica* and *Mya arenaria* (see Zwarts & Blomert 1992). No other phenotypic variable of the ra-

dio-tagged individuals (sex, age, bill length, wing length, tarsus length, body mass) could explain these differences in diet. In August–September 1998 on the intertidal study areas west of the islet of Griend, Red Knots fed at two sites, one where small shorecrabs *Carcinus maenas* were abundant and dominated the diet, and another where cockles were both abundant and fed upon. Shorecrabs are much softer shelled and easier to crack than cockles. Radio-tagged Red Knots encountered only at the shorecrab site had significant smaller stomachs upon capture than Red Knots found only at the cockle site (Fig. 7). Red Knots feeding on small cockles at intertidal flat sites where these prey were abundant, contained radio-tagged individuals with significantly larger stom-

achs than individuals in flocks that fed on small shore-crabs in areas where these crabs were very abundant. Individual Red Knots that were encountered in either of these sites had intermediate stomach sizes as estimated with ultrasonography upon capture a few weeks earlier. This suggests that the size of the stomach that a Red Knot "decides" to carry around during autumn in the Wadden Sea, determines both prey type and feeding site.

PERSPECTIVE

We have shown that the stomachs of mollusc-eating shorebird species such as Red Knots and Great Knots are highly flexible with regard to size. Indeed, the stomachs and other parts of the digestive tract may be flexible with regard to specific functions as well, but this requires morphological studies at another level (e.g. using histological techniques). It is clear that diet determines stomach size, but it is equally clear the interaction between stomach size and diet is a dynamic one, with causal arrows pointing both ways. It is also probable that there is an endogenous component to the regulation of stomach size and function (Dietz et al. 1999b, Piersma et al. 1999). The functional morphology and ecology of mollusc-eating shorebirds (and their digestive tracts) thus provides a rich and accessible field for biological discovery. But what further "discoveries" can we expect?

In flying animals like birds, weight-saving must be a strong selective force on form and function. We would thus expect knots to be built in ways where large organs such as stomachs are always kept at minimal size. Building from this assumption, and with further information on the energetic pay-offs of variations in size (i. e. what costs are involved in building and maintaining large stomachs, what benefits are gained by having a large stomach in terms of potential intake rate and digestive efficiency), it may be possible to carry out true cost-benefit analyses of stomach size in different natural contexts. Such studies on the "behavioural ecology" of organs (see Piersma & Lindström 1997) will not only enrich our understanding of the design of organisms in general, it will also help understanding of the constraints on diet and habitat selection in birds that roam the globe at great speed. In a world where humankind leaves fewer and fewer space and resources untouched, such

information may be actually critical to help safeguarding the fantastic phenomena of shorebird migrations (Piersma & Baker in press).

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STRESZCZENIE

[Odwracalność zmian wielkości żołądka ptaków brodzących: kiedy, w jakim stopniu i dlaczego?]

Ptaki brodzące charakteryzują się dużą zmiennością międzygatunkową względnej wielkości żołądka, w szczególności zaś jego części mięśniowej (Fig. 1). Większość tej zmienności można tłumaczyć zróżnicowaniem diety. Gatunki odżywiające się głównie ofiarami otoczonymi twardym pancerzem, takimi jak małże i ślimaki, posiadają duże żołądki mięśniowe. U ptaków żerujących na miękkiej zdobyczy, na przykład nicieniach są one znacznie mniejsze. Indukowane rodzajem pokarmu bądź migracją zmiany wielkości żołądków mogą również zachodzić na poziomie wewnątrzgatunkowym. W prezentowanych badaniach nad tego typu zmiennością skupiono się na dwóch gatunkach specjalizujących się w odżywianiu mięczakami — biegusem rdzawym *Calidris canutus* i biegusem wielkim *Calidris tenuirostris*. Obydwa ptaki słyną z dokonywania długodystansowych lotów między arktycznymi lub subarktycznymi łęgówiskami, a różnorodnymi obszarami nadbrzeżnych mokradeł. Duże żołądki służą im do odżywiania się połykanymi w całości mięczakami, jednak zmiana diety doprowadza do ich modyfikacji o najwyraźniej dostosowawczym charakterze (Fig. 3, 4). Poza tym redukcja wielkości żołądka może być wymuszana ograniczeniami związanymi z przelotami na dystansie wielu tysięcy kilometrów. Stosując metody ultrasonograficzne podjęto próbę eksperymentalnego wyjaśnienia zależności przyczynowych łączących rodzaj zjadanego pokarmu i sezon, z wielkością żołądka u biegusa rdzawego. Łatwo strawna dieta w ciągu tygodnia może u tego ptaka wywołać 50%, odwracalne zmniejszenie masy żołądka. Wyniki badań telemetrycznych prowadzonych nad biegusami na wybrzeżu Waddensee dowodzą, że w warunkach naturalnych zróżnicowanie wielkości żołądków jest skorelowane z wyborem pokarmu i żerowisk (Fig. 6, 7).

INTERNATIONAL SYMPOSIUM
"ECOLOGY AND CONSERVATION
OF EUROPEAN WOOD OWLS"
(12-15 October 2000, Harz, Germany)

Organizer of the Symposium is German owl working group "AG Eulen". The symposium will be held at the "International House Sonnenberg/St. Andreasberg" in the central Harz mountains (about 100 km SE of Hannover) from 12 through 15 October 2000.

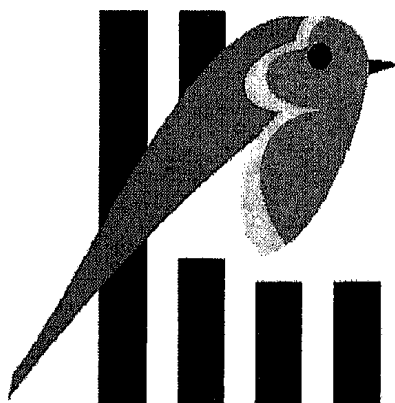
The scientific programme of the symposium will include the main topics: effects of forest-structure and forest fragmentation, population dynamics and limiting factors, dynamics of species distribution, interspecific relationship, species conservation and owls and humans. Papers, posters and other contributions like films, videos and slides are welcome on any aspects of biology and ecology of woodland owls centered on the main topics: What does woodland offer to owls? How owls use woodland resources? Contributions should be restricted to the species: Eagle, Hawk, Pygmy, Tawny, Ural, Great Grey, Long-eared and Tengmalm's owl.

Spoken papers and plenary lectures are scheduled to last 20 to 30 minutes, plus 5 minutes for questions. Contributions to the symposium and to the symposium volume should be in English or in German. Abstracts for oral papers should be submitted by 31 January 2000, preferred in an electronic format. Before and after the owl symposium there will be the opportunity to visit the Expo 2000 in Hannover and the highest mountain of northern Germany, the "Brocken". Booking forms and all relevant information for the symposium like Programme and Travel and Accommodation details will be available in spring 2000, also via the internet.

For further details, guidance notes for abstract submission and registration please contact: Dr. Otwin Schwerdtfeger, AG Eulen, Quellenweg 4, D-37520 Osterode am Harz, GERMANY, e-mail: o.schwerdtfeger@gmx.de, tel: 05522/5184.

SECOND MEETING OF THE EUROPEAN ORNITHOLOGISTS' UNION

Gdańsk, 15–18 September 1999



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