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GUTS DON'T FLY: SMALL DIGESTIVE ORGANS IN OBESE BAR-TAILED GODWITS

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ABSTRACT.—We documented fat loads and abdominal organ sizes of Bar-tailed Godwits (*Limosa lapponica baueri*) that died after colliding against a radar dome on the Alaska Peninsula, most likely just after takeoff on a trans-Pacific flight of 11,000 km, and of birds of the same subspecies just before northward departure from New Zealand. We compared these data with data on body composition of godwits of the smaller *lapponica* subspecies obtained during a northward stopover in The Netherlands. As a consequence of high amounts of subcutaneous and intraperitoneal fat, and very small fat-free mass, Bar-tailed Godwits from Alaska had relative fat loads that are among the highest ever recorded in birds (ca. 55% of fresh body mass). Compared with northbound godwits from New Zealand, the Alaskan birds had very small gizzards, livers, kidneys, and guts. This suggests that upon departure, long-distance migrants dispense with parts of their "metabolic machinery" that are not directly necessary during flight, and rebuild these organs upon arrival at the migratory destination. *Received 19 February 1997, accepted 9 June 1997.*

SHOREBIRDS include some of the most impressive long-distance avian migrants. They cross the world's largest stretches of ocean nonstop, during which they may fly from one climatic extreme to another (Johnson et al. 1989, Williams and Williams 1990, Marks and Redmond 1994, Wiersma and Piersma 1994). Not surprisingly, shorebirds have the ability to rapidly store and use up large amounts of fat (e.g. Zwarts et al. 1990, Jehl 1997a). There is increasing awareness, however, that during long-distance migration, birds undergo many physiological changes other than the storage and depletion of fat (Marsh 1981; Lundgren and Kiessling 1985, 1986; Piersma 1990; Ramenofsky 1990; Jenni-Eiermann and Jenni 1992; Driedzic et al. 1993; Ramenofsky et al. 1995; Piersma et al. 1996b). Recent studies indicate that in the course of a migratory cycle, skeletal muscles as well as organs may undergo considerable change in size and capacity (Piersma and Jukema 1990, Lindström and Piersma 1993, Piersma et al. 1993, Van der Meer and Piersma 1994, Hume and Biebach 1996, Weber and Piersma 1996, Jehl 1997b, Klaassen et al. 1997, Piersma and Lindström 1997).

Here, we present comparative data on body composition of the largest of the three recognized subspecies of Bar-tailed Godwit (*Limosa lapponica baueri*) at different stages of their spectacular life cycle. A sample of juvenile males was obtained at the time of their southward departure from the Alaska Peninsula, a major postbreeding staging area. We compare their composition with that of adult males obtained during northward departure from northernmost New Zealand, a major nonbreeding area. Band returns and sightings of marked birds (Barter 1989, Gill unpubl. data) have linked populations from the two regions, which are separated by 11,000 km (great circle) of mostly open ocean. Furthermore, Barter (1989) suggested that northbound *baueri* may transit virtually nonstop from eastern Australasia to Siberia/Alaska, despite the enormous distance. Barter and Hou (1990) reviewed evidence supporting single northward flights of at least 8,000 km between Australia and China. Evidence for such flights during southward migration is less clear, but it suggests that birds are capable of extended single flights similar to or exceeding those made during northward migration (see below; Gill unpubl. data). However, the occurrence of godwits, albeit in small

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numbers, in Kiribati and Tuvalu in October, and in somewhat larger numbers closer to New Zealand in Fiji and the Kermadec Islands (Higgins and Davies 1996), indicates that although the southward flight may be direct from Alaska, a certain proportion of the population cannot reach the nonbreeding grounds without one or more stopovers.

MATERIALS AND METHODS

The key sample was collected near the distal end of the Alaska Peninsula on 19 October 1987, at about 2330 ADT, when a flock of godwits collided with a lighted Minimally Attended Radar dome 6.5 km northwest of Cold Bay (55°15'N, 162°46'W). Nine juvenile males were salvaged; two died upon impact and seven were held for 10 h without food or water before being euthanized due to their injuries. On 7 March 1992, about 40 godwits were confiscated from a poacher (and probably had been shot that day; R. J. Pierce pers. comm.) near Great Exhibition Bay, Northland, New Zealand (34°45'S, 173°08'E). The analyzed sample consisted of 26 adult males (the main material for comparison) and 9 adult females.

Further comparative material was available from the Wadden Sea (53°N, 05°E), a staging area in The Netherlands used by the small *lapponica* subspecies when underway from wintering areas in West Africa to breeding grounds in central Siberian arctic (Drent and Piersma 1990, Piersma and Jukema 1990). Godwits that stage in the Wadden Sea in May have been studied intensively since 1984 (Piersma and Jukema 1990, 1993; Ramenofsky et al. 1995; Piersma et al. 1996b). Of several thousand birds captured for banding and weighing during this study, we include here 93 that died in the process and subsequently were analyzed for body composition.

Alaskan godwits were weighed (± 5 g) immediately after death using a Pesola spring scale. The length of the flattened wing was measured to the nearest 1.0 mm; this may underestimate wing length (2 to 4%) compared with the godwits in the other samples for which wings were measured flat and stretched. Exposed culmen and diagonal tarsus length were measured to the nearest 0.1 mm with calipers. All carcasses were packed in airtight plastic bags and stored at −20°C before being shipped to Anchorage, Alaska, where they were aged, repackaged, and then transported frozen to the University of Missouri Experiment Station Chemical Laboratory for compositional analysis. Subsequent analyses (see beyond) revealed no differences in body composition between birds that died on impact and ones that lived an additional 10 h. Birds were sexed by gonadal inspection. The right breast muscles (including m. pectoralis and m. supracoracoideus), heart, gizzard, liver, left kidney, and gut were removed and weighed wet to the nearest 0.01 g. The length of the gut from gizzard to cloaca was stretched and measured to the nearest 1.0 mm before being emptied. The few shell fragments that remained in the gizzard were removed before weighing. For compositional analysis, the entire carcass, including all internal organs but excluding gut contents, was ground to a homogenate in a commercial food grinder by passing the body through the grinder several times (see Austin and Fredrickson 1987, Brown and Fredrickson 1987). A random sample was removed and refrozen for later analysis. Compositional analysis procedures followed Horwitz (1970) and involved petroleum-ether Soxhlet extraction of fats after the water content of the samples had been determined by drying them in a vacuum oven for about 15 h. The results, initially expressed as proportions of total fresh body mass, were calculated back to total fat, water, and fat-free dry masses.

Godwits from New Zealand were stored at −20°C, transported frozen to The Netherlands, and analyzed there in January 1996. After storage and thawing, the New Zealand and Dutch birds were weighed to the nearest 1.0 g and measurements taken of the external dimensions to the nearest 0.1 mm (culmen, tarsus) or 1 mm (wing). Birds were sexed by gonadal inspection. Various muscles, organs, and the intraperitoneal fat layer in the abdomen (i.e. abdominal fat) were excised, emptied in the case of gizzard, and their wet masses measured immediately (± 0.1 g; see Piersma et al. 1996a, Battley and Piersma 1997). Guts were disentangled, stretched, and their lengths measured to the nearest 0.5 cm before also being emptied. Each component was dried separately to constant mass at 55 to 60°C and reweighed. They were then individually packed in filter paper so that fat could be extracted in a Soxhlet apparatus using petroleum ether (boiling at 40 to 60°C) as a solvent for 8 to 24 h, depending on the size of the component. These in turn were dried at 55 to 60°C and reweighed. The loss of dry mass during fat extraction was taken as the extracted fat mass. In the comparisons that follow, body parts were matched to those distinguished at the University of Missouri laboratory. Because the complete stomach was taken, rather than the gizzard as in the Alaskan birds, stomach mass was reduced to gizzard mass by subtracting the predicted mass of the proventriculus (mean 6.3% of overall wet mass of stomach; Piersma et al. 1993). The fat loads reported as a percentage of total body mass are minima, because body-mass values were not corrected for mass of gut contents for two reasons: (1) gut contents were very small and never amounted to more than 10 g wet mass, and (2) body-mass values commonly reported for live birds include mass of the gut contents.

TABLE 1. Mass, size, and composition of male Bar-tailed Godwits at or just before departure (southbound from Alaska, northbound from New Zealand) on flights over the Pacific Ocean.

	Alaska juveniles (n = 9)			New Zealand adults (n = 26)			Ratio[a] AK/NZ
Variable	Mean	SD	Range	Mean	SD	Range	
Body mass (g)[b]	366.9	25.1	325–400	445.8	31.6	377–503	0.82
Total fat mass (g)	201.40	19.24	172.3–225.6	190.51	21.30	147.6–236.5	1.06
Total fat-free dry mass (g)	49.91	3.33	43.3–56.8	93.69	8.38	76.0–108.4	0.53
Fat (fraction of body mass)	0.548	0.027	0.51–0.58	0.427	0.029	0.36–0.49	—
Water (fraction of fat-free mass)	0.685	0.016	0.66–0.71	0.633	0.016	0.61–0.68	—
Wing length (mm)	215.6	4.0	209–220	229.4	6.2	217–240	0.94
Culmen length (mm)	71.94	6.45	61.7–81.5	83.51	6.21	71.1–97.4	0.86
Tarsus length (mm)[c]	52.99	1.09	51.5–55.3	54.99	2.60	49.8–56.7	0.96
Intraperitoneal fat (g)	28.02	9.06	6.6–36.6	21.07	3.91	11.5–28.9	1.33
Right breast muscle (g)	27.18	1.77	24.9–30.1	30.82	2.37	27.0–35.1	0.88
Heart mass (g)	3.50	0.50	2.8–4.3	4.09	0.47	3.2–5.3	0.86
Empty gizzard mass (g)	4.47	0.76	3.2–5.6	8.65	1.87	5.4–14.3	0.52
Liver mass (g)	6.85	0.87	5.5–8.1	10.65	1.28	8.0–12.7	0.64
Left kidney mass (g)	1.53	0.24	1.1–1.8	2.15	0.30	1.6–2.6	0.71
Gut length (mm)	75.5	4.7	66–83	82.8	7.7	59–95	0.91

[a] Mean value for juveniles from Alaska Peninsula divided by mean value of adults from New Zealand.
[b] Not corrected for variation in water content of fat-free mass as a result of dehydration (Piersma and Jukema 1990).
[c] Measured in only 22 of the 26 birds from New Zealand.

RESULTS

With an average total body mass of about 367 g and an extracted fat mass of 201 g (Table 1), the juvenile Bar-tailed Godwits from Alaska consisted of more than half fat (55%). The sample of adult *baueri* males before northward departure from New Zealand (average total body mass 446 g) also consisted of very fat birds (average 43%; Table 1), but still showed no overlap in fat content with the Alaskan birds. Thus, despite the fact that the New Zealand carcasses appeared slightly dehydrated (63.3% water of fat-free mass rather than the more normal value of 69%; see Piersma and Van Brederode 1990, Ellis and Jehl 1991), the juvenile male godwits from Alaska were much lighter. They also were somewhat smaller (Table 1); among the linear dimensions, the bill of the juveniles was relatively smallest, tarsus and wing almost having reached adult size. The Alaskan birds, nevertheless, contained larger absolute amounts of fat, especially in their intraperitoneal fat depots (33% larger in Alaskan males). This is a fat-storage site that seems to be filled last (Piersma 1984, Battley and Piersma 1997).

With a total fat-free dry mass of only half that of the New Zealand males (Table 1), not surprisingly the Alaskan birds also had small organs. However, a considerable and biologically significant difference existed between the two "exercise" organs (i.e. breast muscle and heart; see Piersma et al. 1996a) and the three "nutritional" organs (i.e. gizzard, liver, and kidney) of the two groups. Whereas the wet mass of the exercise organs roughly paralleled body mass (ratio Alaska/New Zealand was 0.86 to 0.88), the nutritional organs were smaller than predicted from body mass (ratios of 0.52 to 0.71). This may be true also for the gut, which was 9% shorter in the Alaskan sample. If gut thickness follows gut length, then gut mass (a cubic measure) of the Alaskan birds would be 0.75 (i.e. 0.91^3) times that of the New Zealand birds.

By further comparing the Alaska and New Zealand samples with data from male and female *lapponica* at refueling sites in The Netherlands and northbound adult females from New Zealand (Fig. 1), we underscore the conclusion that the Alaskan godwits were very fat (55%). Fat stores of northbound females from New Zealand averaged 42% of fresh mass (Fig. 1). In addition to being very fat, the Alaskan godwits also were much lighter with regard to fat-free mass (Fig. 1A). Among the five groups examined, average fat-free dry mass was lowest in the southbound birds from Alaska. Even though all of the different organs of the Alaskan males were the smallest measured, the *relative sizes* (with respect to total fat-free mass) of the *exercise* organs (breast muscle and heart) were largest (Figs. 1B,C). In contrast, the relative sizes of the nutritional organs were either

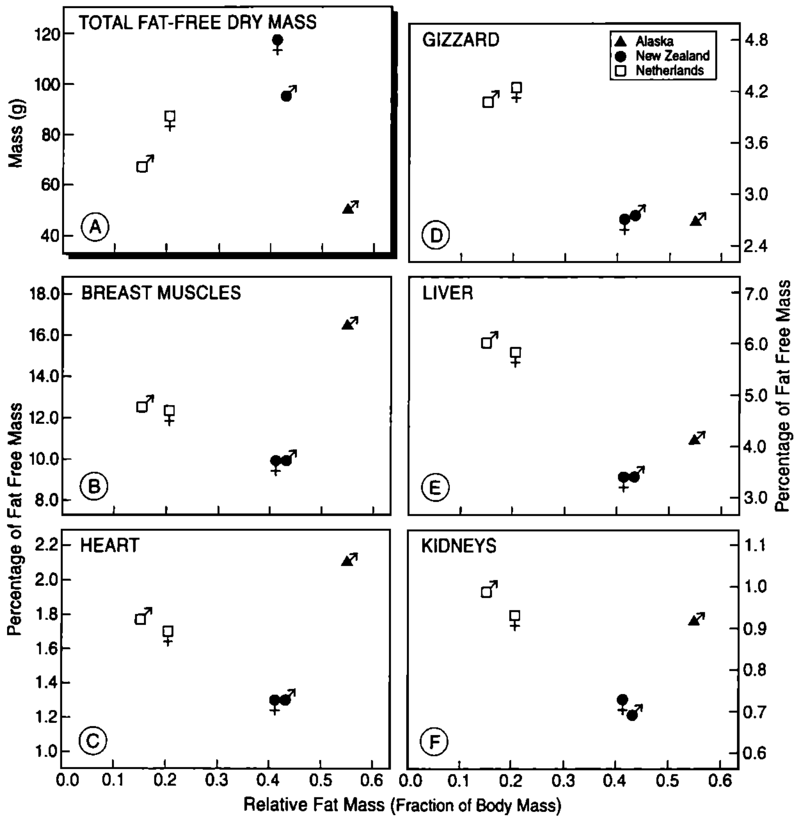

FIG. 1. Comparison of the total fat-free dry mass (A) and the relative sizes of two "exercise organs" (B: breast muscles and C: heart) and three "nutritional organs" (D: gizzard, E: liver and F: kidneys) in relation to fat content in different groups of Bar-tailed Godwits. Average values per sex and origin are presented, based on 9 juvenile *baueri* males from Alaska (filled triangles); 26 adult *baueri* males and 9 females (filled dots) from New Zealand; and 52 adult *lapponica* males and 41 females from The Netherlands (open squares). Averages of males from Alaska and New Zealand (values presented in Table 1) are connected by a dotted line. Organ masses were corrected for "size" by dividing by total fat-free mass (i.e. total fat-free dry mass divided by an average dry-matter content coefficient of 0.3; Piersma unpubl. data).

smallest (gizzard; Fig. 1D), small (liver; Fig. 1E), or average (kidney; Fig. 1F). Nutritional organs were relatively largest in *lapponica* from The Netherlands, establishing the point that nutritional organs are needed most during refueling. The sizes of the breast muscles and heart were well correlated with body mass (r = 0.88 and 0.81, respectively; Figs. 2A,B).

DISCUSSION

Blem (1976, 1980) suggested that the fat load carried by migrating birds never is much higher than 50% of total body mass. In a review based on 132 taxa discussed by Lindström (1986), Alerstam and Lindström (1990) indeed showed that fat loads in shorebirds and passerines never exceed 50% of total body mass. The maxima based on hard (i.e fat extraction) data were values of 50% in a Reed Warbler (*Acrocephalus scirpaceus*; Fogden 1972) and a Bobolink (*Dolichonyx oryzivorus*; Odum 1960a), and 52% in a Scarlet Tanager (*Piranga olivacea*; Odum 1960b). Two other estimates came close (57%), but are not definitive because they were based on peak body-mass values from which predicted lean mass was subtracted. Thus, despite their larger body size, based on which they should carry relatively small proportional fuel loads (Pennycuick 1975, Hedenström and Alerstam 1992), the average fat load (55%) in the Alaskan godwits is greater than any other

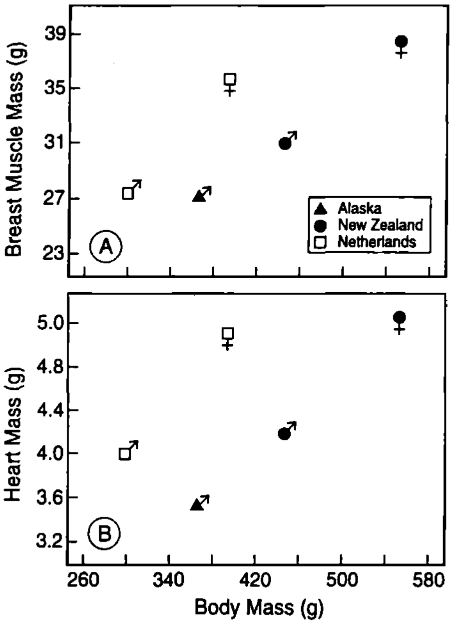

FIG. 2. Fresh mass of the breast muscles (A) and heart (B) are linearly correlated with fresh body mass; comparison of average values of different groups of Bar-tailed Godwits (see Fig. 1 for sample sizes and symbols).

estimate demonstrated by fat extraction. Nonetheless, their fuel loads are within the theoretical limits calculated by Hedenström and Alerstam (1992:figure 1). Although some Wilson's Phalaropes (*Phalaropus tricolor*) were almost as fat as the godwits, these individuals were unable to fly (Jehl 1997a).

The two samples of male *baueri* from Alaska and New Zealand consisted of very fat birds, but there were considerable differences as well. The Alaskan birds not only contained more fat with larger intraperitoneal fat deposits, they also had smaller muscles and viscera. Should this difference be attributed to the fact that the godwits from Alaska were juveniles and southbound, whereas the New Zealand males were adults and northbound? Are fat content and muscle/organ size somehow inversely related for functional reasons, and are the small organs of the Alaskan birds a consequence or correlate of their enormous fat load? Or, were the increased fat and decreased viscera of the Alaska birds a function of their migratory state; i.e. had birds already begun their migration when they collided with the radar facility? Below, we outline why we think that the high fat load and the small size of the abdominal organs are functionally related, and why this relationship represents the typical physiological state of birds that have just started on an energetically extreme long-distance flight.

Breast muscles and heart show high positive correlations with total body mass (Fig. 2), and these body parts appear to be fine-tuned to the energy demand for keeping bodies of different masses aloft during long-distance migratory flights. A second point is that the small gizzards reported in the Alaskan birds are unlikely to be the result of disuse atrophy due to a previous diet consisting of soft foods only (Piersma et al. 1993). The analyzed godwits had empty stomachs apart from a few shell fragments, but at Nelson Lagoon, the most likely point of departure of these birds (see below), Bar-tailed Godwits are known to feed mainly on hard-shelled bivalves (*Macoma* spp.; 95% of 421 items, $n = 8$ stomachs) that are ingested whole (Gill unpubl. data).

Thus, as has recently been suggested for different (re-) fueling populations of Red Knots (*Calidris canutus*; Battley and Piersma 1997, Piersma, Gudmundsson, and Lilliendahl unpubl. data), the present comparative data are in agreement with the idea that before departure on transoceanic flights, long-distance migrants reduce the size of their digestive apparatus and at the same time increase the size of their flight machinery (Piersma and Lindström 1997). Our findings corroborate "field" observations of reduced stomachs in waterfowl, shorebirds, and grebes before migratory flights (see Piersma et al. 1993, Jehl 1997b), and of increased breast-muscle sizes in grebes, geese, shorebirds, and passerines (Marsh 1981, Gaunt et al. 1990, Lindström and Piersma 1993, Jehl 1997b), as well as similar observations in captive passerines experimentally undergoing migration-related body-mass cycles (Klaassen and Biebach 1994, Hume and Biebach 1996, Klaassen et al. 1997).

Several lines of evidence support our contention that the Alaskan birds died during the early stage of their lengthy southward migration. A six-month study (July to November 1993) of shorebird use of estuaries adjacent to the Cold Bay radar facility revealed virtually no use by *baueri* godwits (Tibbitts and Gill unpubl. data). Hence, it is very unlikely that the birds in question were local and died while, for instance, transiting between feeding areas. Where, then, did these birds originate? The most distant staging area occurs on the Yukon-Kuskokwim Delta (Gill and Handel 1990, Gill 1996), only 450 km north-northwest of Cold Bay. However, between the Yukon Delta and Cold Bay are several other estuaries used by staging godwits, including Nelson Lagoon, only 140 km to the northeast, where concentrations of more than 10,000 godwits regularly occur (Gill and Jorgensen 1979, Gill et al. 1981, Gill 1996). As recently as September 1996, *baueri* birds were observed departing en masse from Nelson Lagoon in the general direction of Cold Bay on their southward migration. The weather conditions at that time, including strong northwest-northeast winds from a 976-mb low-pressure system 550 km south of Cold Bay, were almost identical to conditions at Cold Bay during the late evening of 19 October 1987 (Gill unpubl. data; see Gill et al. 1997).

Furthermore, the 1996 departure occurred in the late afternoon when the local tide was high. In 1987, the tide at Nelson Lagoon also was high in the early evening but low at Cold Bay at the time of the collision. These observations are consistent with evidence that shorebirds usually depart on long-distance flights before sunset in the late afternoon/early evening, and that they are least likely to depart from tidal areas during the lowest part of the tide (Alerstam et al. 1990, Piersma et al. 1990, Tulp et al. 1994). Thus, we believe it highly likely that the juvenile Bar-tailed Godwits that flew into the radar facility at Cold Bay just before midnight on 19 October 1987 came from Nelson Lagoon, where they had departed around high tide that evening. It is predicted that exactly such departing individuals, rather than those that still reside on the (re-) fueling site, should show the most extreme compositional adjustments for long-distance flights. As far as we are aware, our Alaskan sample is unique in that it likely represents individual shorebirds taken just *after* takeoff on a long-distance migratory flight.

In summary, the small size of the nutritional organs of extremely fat Bar-tailed Godwits that likely had died just as they embarked on a trans-Pacific flight, is consistent with the suggestion that it is unprofitable and energetically too expensive to carry a digestive machinery over thousands of kilometers of open ocean (Piersma and Lindström 1997). It seems better to get rid of such tissue even before takeoff, and to rebuild the strategically discarded body parts upon arrival at the destination, even though firm proof remains to be collected by sequential sampling.

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