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Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight?

Theunis Piersma

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Avian long-distance migration involves the storage and expenditure of very large fuel loads. Birds may double in weight before take-off on flights of many 1000 km, and they may lose half their body mass over the subsequent few days that such trips take. Recent studies indicate that in addition to the storage and depletion of fat, the muscles and belly organs also undergo considerable changes in size in the course of such migrations. Such intraindividual and repeatedly reversed changes in stores and organ sizes represent a class of phenotypic plasticity called 'phenotypic flexibility'. Using preliminary comparative data for different populations of Bar-tailed Godwits *Limosa lapponica*, and several other shorebird species adding variation to the migration strategies sampled (Golden Plover *Pluvialis apricaria*, Ruff *Philomachus pugnax*, Red Knot *Calidris canutus* and Bristle-thighed Curlew *Numenius tahitiensis*), the thesis is developed that the size of the organs carried during take-off represent evolutionary compromises between their functions during the storage, flight and post-arrival phases of migration. In all cases fat-free tissue along with fat is deposited during fuel storage, but the proportions vary a great deal between similarly sized species. Just before departure on long-distance flights, exercise organs (pectoral muscle and heart) tend to show hypertrophy and nutritional organs (stomach, intestine and liver) tend to show atrophy. Reductions in nutritional organs appear most pronounced in (sub-) species that are about to overfly barren oceans with few or no opportunities for emergency landings. Migrant birds seem to show a great deal of adaptive flexibility, and the study of this flexibility may shed light on (presently unknown) physiological mechanisms as well as on correlated ecological constraints on bird migration.

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For a long time it was believed that long-distance migrating birds are homeostatic with respect to the non-fat components of their bodies (e.g. Odum 1960, King 1963, Odum et al. 1964, Blem 1976, 1990). Only fat (the optimal fuel for flight, Jenni-Eiermann and Jenni 1998) would fluctuate during the alternating fueling and depletion episodes of a full migration. This old dictum is rapidly being replaced by the idea that migrant birds often show considerable, quite rapid and reversible changes in fat-free mass as a result of changes in the size of (some of) their organs (Piersma 1990, Piersma and Jukema 1990, Lindström and Piersma 1993, Piersma et al. 1993, Klaassen and Biebach 1994,

Hume and Biebach 1996, Klaassen et al. 1996, Weber and Piersma 1996, Piersma and Lindström 1997, and papers cited in Table 1).

Perhaps the most dramatic and best documented example is provided by Eared Grebes *Podiceps nigricollis* in North America (Jehl 1988, 1997, Gaunt et al. 1990). Each year this species undergoes several cycles of atrophy and hypertrophy of particular body parts, the cycle with the largest amplitude occurring during, and at the end of, the autumn staging period, during which flight feathers are replaced. After a period of flightlessness the grebes accumulate fat stores. At this point their nutritional organs show hypertrophy and the pectoral

Table 1. Examples of (phenotypic) flexibility of the exercise and the nutritional organs of birds in relation to long-distance migration based on body composition analyses. The examples are presented in chronological order.

Species	Ecological context	Flexibility in exercise organs	Flexibility in nutritional organs	Authority
Chaffinch <i>Fringilla coelebs</i>	Stopover during southward migration	No information	40–50% mass loss of liver and intestine with increasing fat loads	Dolnik and Blyumental 1967
Greater Snow Goose <i>Anser caerulescens atlanticus</i>	Staging during northward migration	No information	Decrease in gizzard mass during spring stopover	Gauthier et al. 1984
Gray Catbird <i>Dumetella carolinensis</i>	Stopover during southward migration	Increase by ca. 35% of pectoral muscle mass with increase in fat load	No information	Marsh 1984
Dunlin <i>Calidris alpina</i>	Fueling before northward departure from temperate wintering area	Pectoral muscles before departure show increases by 30% relative to winter	No information	Evans et al. 1992
Red Knot <i>Calidris canutus islandica</i>	Northward migration along W. Africa/Europe seaboard	No information	Decrease in stomach mass during with time before northward departure	Piersma et al. 1993
Semipalmated Sandpiper <i>Calidris pusilla</i>	Stopover before transoceanic southward flight	Pectoral muscle and heart show hypertrophy before departure	No information	Driedzic et al. 1993
Eared Grebe <i>Podiceps nigricollis</i>	Before southward departure from moulting area	Pectoral muscle and heart show hypertrophy before departure	Liver, stomach and intestine decrease by more than 50% before departure	Gaunt et al. 1990, Jehl 1997
Red Knot <i>Calidris canutus rogersi</i>	Before northward migration from New Zealand wintering area	Increase in heart and pectoral muscle mass with readiness to migrate	Decrease in stomach and intestine mass with readiness to migrate	Battley and Piersma 1997
Bar-tailed Godwit <i>Limosa lapponica baueri</i>	At departure on trans-Pacific southward flight	Probable increase in size of heart and pectoral muscles before departure	Very small gizzard, liver, kidneys and intestine at departure	Piersma and Gill 1998

muscles shrink. When they regain flight in the few days preceding southward departure, not only do Eared Grebes lose as much as 1/3 of their fat deposits, they also decrease the size of the nutritional organs by more than half, while building their pectoral muscles and heart (Jehl 1997).

Because it is now clear that organs of long-distance migrants may indeed reversibly vary in size (Table 1), we may ask: (1) how widespread this condition is, and (2) which organs should show hypertrophy and atrophy in relation to migration, and to what degree. Do atrophy/hypertrophy cycles represent general ecological adaptations at the species level, or does such migration-related *phenotypic flexibility* (representing *reversible* forms of phenotypic plasticity; see Karasov 1996, Piersma and Lindström 1997) vary within species in accordance with the specifics of particular migration schedules (Ens et al. 1994)? Could such physiological adjustments be the result of evolutionary fine-tuning to the demands of specific migratory flight strategies? An insightful way to look at such questions is the comparative one (Feder et al. 1987). Based on intra- and interspecific comparisons of the relative organ sizes of shorebirds with varying flight prospects and ecological characteristics, I will develop the thesis that the sizes of organs carried during take-off represent evolutionarily informed compromises between their functions during the storage, flight and post-arrival phases of migration.

Material and methods

Origin of samples

This study is based on shorebird samples from staging grounds in the Netherlands (Golden Plover *Pluvialis apricaria*, Ruff *Philomachus pugnax* and Bar-tailed Godwit *Limosa lapponica lapponica*), Iceland (Red Knot), Alaska (Bar-tailed Godwit *Limosa lapponica baueri*) and the Hawaiian Islands (Bristle-thighed Curlew *Numenius tahitiensis*). The birds from the Netherlands were all captured with 'wilsternets' (Koopman and Hulscher 1979), and consisted of catching casualties accumulated during intensive ringing programmes over the period 1984–1997 (e.g. Jukema and Piersma 1987, Jukema 1991, Jukema et al. 1995, Piersma and Jukema 1990, 1993, Piersma et al. 1996b). Staging Red Knots *Calidris canutus islandica* were collected in south-west Iceland in 1994 (Gudmundsson et al. unpubl. data, Piersma et al. 1996c). They included a sample of individuals arriving from Britain or the Wadden Sea on 3 May, further samples during the stopover period, and one at the peak of departures on 27 May. The Alaska sample of Bar-tailed Godwits consisted of nine birds that collided with a spotlight radar dome on the Alaska Peninsula on 19 October 1987 (Piersma and Gill 1998). These birds most probably had just departed

from nearby staging areas and were en route to their New Zealand wintering grounds. Three Bristle-thighed Curlews were collected on Laysan Island in late April–early May 1991 and three additional birds on Midway Atoll in late April 1992 (Marks and Redmond 1994). These curlews were very close to spring departure and probably carried maximum fat stores.

The samples of Alaska Bar-tailed Godwits and Bristle-thighed Curlews consisted of individuals clearly about to depart, all of which were incorporated in the analyses that follow. To achieve consistency with regard to sample selection and sample size of birds upon departure, for the five remaining (sub-) species I took the five heaviest birds from the last date(s) for the determination of body condition in birds departing on long-distance flights. For comparison, the five lightest birds from the earliest date(s) were selected to provide information on body condition on arrival. In no case was there any evidence for bias with respect to particularly small or large sized birds (cf. Lindström and Piersma 1993). Except for the birds from Alaska, which were juveniles (see Piersma and Gill 1998 for discussion), individuals for which data are presented were aged as adults.

Laboratory methods

All carcasses (except for three of the six Bristle-thighed Curlews that were kept in formalin before analyses, J. Marks pers. comm.) were stored frozen and transported to the laboratory of the Netherlands Institute for Sea Research, Texel (Golden Plovers, Ruffs, Red Knots and Dutch Bar-tailed Godwits) or the University of Missouri Experiment Station Chemical Laboratory (Alaska Bar-tailed Godwits and Bristle-thighed Curlews) for compositional analysis. The birds were weighed to the nearest 1 or 5 g and measurements taken of their external dimensions. Birds were sexed by gonadal inspection. At the Texel laboratory the various muscle blocks (pectoral muscles, including *musculus pectoralis* and *m. supracoracoideus*, and leg muscles from both sides of the body) and organs (heart, liver, stomach, intestines, kidneys, lungs) were cut out (see Piersma et al. 1996a, Battley and Piersma 1997). After taking their wet weights (empty in the case of stomach and intestine), each separate component was dried to constant mass at 55–60°C and reweighed. The parts were packed separately in filter paper to extract fat in a Soxhlet apparatus using petroleum-ether (boiling at 40–60°C) as the solvent. The defatted parts were dried at 55–60°C and reweighed. Loss of dry mass during fat extraction was taken as the extracted fat mass. In the Missouri laboratory, the right pectoral muscles, heart, gizzard, liver, left kidney, and intestine were removed and weighed wet. For compositional analysis, the entire carcass including all internal organs but excluding gut

Table 2. Body composition at arrival and departure, and estimates of the magnitude and fat content (F_{fat} , stored) of the mass gains of four shorebird species with different ecologies and flight prospects. In all cases sample size is $n = 5$; M = male and F = female. For the body mass values averages are given, with standard deviations in parentheses. Relative body mass gains were computed in respect to body mass at arrival.

Species	Sex	Stopover area	Time of year	Body mass at arrival (g)	Body mass at departure (g)	Interval (d)	Body mass gain (g/d)	Relative body mass gain (%/d)	Fat gain (g/d)	Fat-free mass gain (g/d)	F_{fat} stored
Golden Plover	M+F	Friesland, Netherlands	April	188 (7)	234 (6)	8	5.6	3.0	1.9	3.6	0.35
Ruff	M	Friesland, Netherlands	March–April	189 (6)	260 (5)	36	2.0	1.1	1.2	0.8	0.59
Bar-tailed Godwit	M	Wadden Sea, Netherlands	May	203 (17)	389 (22)	23	8.1	4.0	4.7	3.4	0.58
Red Knot	M+F	Iceland	May	138 (3)	225 (5)	24	3.6	3.6	2.6	1.0	0.72

contents was ground to a homogenate by passing the body through a commercial food grinder several times (see Austin and Fredrickson 1987, Brown and Fredrickson 1987). A random sample was removed and frozen 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.

The fat loads reported as a percentage of total body mass thus represent minima, because body mass values were not corrected for mass of stomach and intestinal contents since: (1) gut content was very small and never amounted to more than 10 g wet mass, and (2) body mass values that are commonly reported for live birds include the mass of stomach and intestinal content. The ratios calculated for the Alaska Bar-tailed Godwits and the Bristle-thighed Curlews refer to wet masses of the relevant body parts; the ratios calculated for all other birds were based on fat free dry-mass values.

Cautionary notes: data selection and treatment

The dataset assembled so far is preliminary and represents six different shorebird migrations. With such a small sample there is little point in trying to statistically account for any phylogenetic bias (Feder et al. 1987, Harvey and Pagel 1991). In the absence of detailed situation-specific analyses of the migratory status of the compositionally-analysed individuals with reference to other field data (arrival and departure times in different years; evidence for catching bias, etc.; see e.g. Piersma and Jukema 1990), my examples are necessarily based on a rather brief and uniform data analysis; some parameter estimates are based on mass and composition data of selected early and late individuals (as in Tables 2 and 3 and Fig. 3). A full analysis of the various data sets would be far outside the scope of this exploratory paper. As I try to explore biological trends rather than to firmly establish the suggested patterns, I hope that the reader will bear with me.

To account for differences in body size, both within and between species, dimensionless parameters are required. Multivariate statistical analyses of the size of different organ groups in shorebirds (Piersma et al. 1996a), generally show statistical independence between the 'exercise' organs (notably pectoral muscles and heart) and the 'nutritional' organs (stomach, intestine, liver, and sometimes kidneys). A review of the sort of changes in these organ groups in relation to long-distance migration (Table 1) confirms that the two categories 'behave' differently

during fat storage. The exercise organs tend to increase in size before take-off (as indicated by large pectoral muscles in birds with large fat loads), at a time when the nutritional organs show strong atrophy. The ratio of the mass of nutritional to exercise organs may therefore be a sensitive indicator of the degree to which nutritional organs show atrophy with an increasing propensity of their owners to migrate.

Such a ratio is conveniently dimensionless, but it assumes isometry between the different organ groups among species. At least one nutritional organ – the gizzard – does not necessarily scale isometrically with the other organs in interspecific comparisons. Hard-shelled-mollusk-eating specialists such as Red Knots have stomach mass values almost twice as large as that predicted on the basis of body mass (Piersma et al. 1993). Such relatively heavy stomachs would affect the ratio of nutritional to exercise organ mass. I have therefore computed a second dimensionless parameter based on the ratio of liver mass and pectoral muscle mass. A second drawback of a ratio is that it obscures information on specific changes in either the nutritional organs or the exercise organs. In the presented cases these changes tended to be fully complementary as expected on the basis of Table 1.

Results

Nutritional organ ratios during fat storage

In four of the six examples of organ sizes and fat stores at departure on long-distance flights, it was possible to derive estimates of the overall composition of the mass gains during stopover (Table 2). The fat-fraction of stored mass is highly variable, ranging from 0.35 to 0.72 between shorebird species, but confirm Lindström and Piersma's (1993) conclusion that fat-fractions of mass gains before long-distance flights are usually lower than 1. It is reassuring that the value for Bar-tailed Godwits from the Wadden Sea ($F_{\text{fat}} = 0.58$) is close to the earlier estimate of 0.64 based on the ratio of the calculated slopes of fat-free and total body mass on date, computed for a smaller but overlapping sample (Lindström and Piersma 1993). The Bar-tailed Godwits from the Wadden Sea seem to hold the middle ground in respect to the relative contribution of fat to body mass gains (Table 2). The data for Red Knot in Iceland suggest that the selection of the five earliest and lightest and the five latest and heaviest birds did not necessarily lead to heavily biased results. A full and refined analysis based on larger samples (T. Piersma, G. A. Gudmundsson and K. Lilliendahl unpubl.), showed an average body mass increase of 3.0 g/d (rather than the 3.6 g/d reported in Table 2) and a F_{fat} stored of 0.78 (rather than 0.72 in Table 2).

Not only do fat-fractions of mass stored before take-off vary between species (Table 2, Lindström and Piersma 1993), the temporal patterns in relative size of nutritional and exercise organs during refueling show large differences among species as well. This can be illustrated with a comparison between the storage patterns of Ruffs and Bar-tailed Godwits, both showing fat-fractions of stored mass that are slightly less than 0.6 (Table 2). Male Bar-tailed Godwits show a linear mass increase of about 4% of arrival mass per day (Table 2, Fig. 1A), the sampled birds closely following the population average trend. The ratio between liver and pectoral muscle size, however, varies a great deal over the refueling period. Arriving godwits show very low ratios, and so do birds that are about to depart (Fig. 1B; note that the two earliest data points were obtained from godwits that got killed when captured during actual arrival from West Africa at a location just south of the Wadden Sea). During the middle of the refueling period the ratio is about twice as high, with relative liver sizes averaging 0.25–0.30 times pectoral muscle mass.

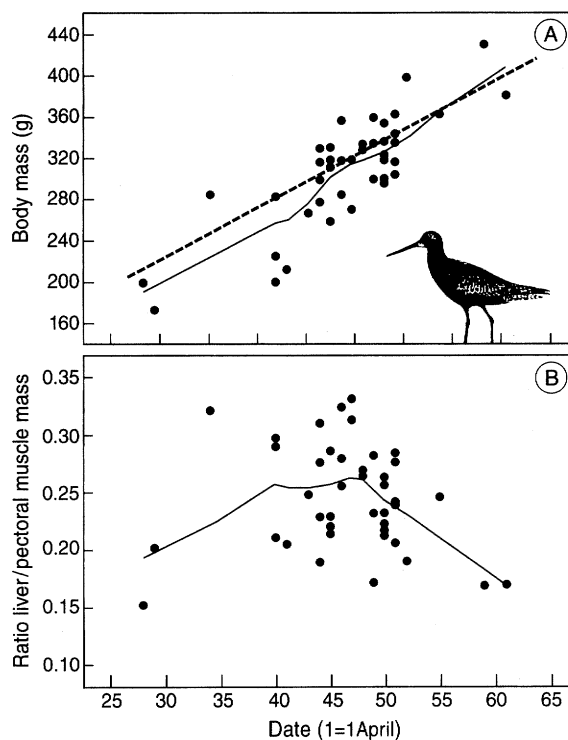


Fig. 1. Increase in body mass (A) and the ratio of liver to pectoral muscle mass (B) of adult male Bar-tailed Godwits staging in the Dutch Wadden Sea in May. The dashed straight line in the top panel indicates the average population mass increase (linear regression) in 1984–1988 based on 570 recorded body masses (from Piersma and Jukema 1990: Table 3). The trend lines were calculated with the LOWESS routine of SYSTAT (tension = 0.75).

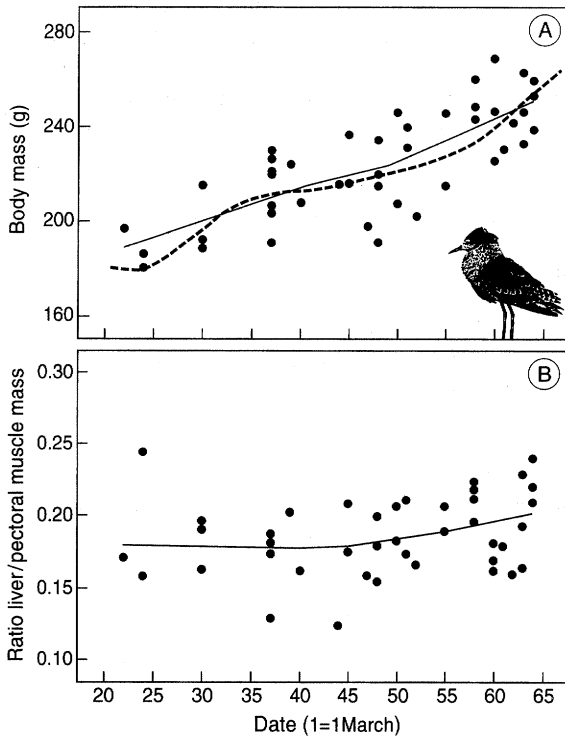


Fig. 2. Increase in body mass (A) and the ratio of liver to pectoral muscle mass (B) of adult male Ruffs staging in the province of Friesland, the Netherlands in March–May. The dashed line in the top panel indicates the average population mass increase in 1993 and 1994 based on 390 recorded body masses (from Jukema et al. 1995: Fig. 5). The trend lines were calculated with the LOWESS routine of SYSTAT (tension = 0.75).

The latter pattern is very different for male Ruffs. These birds also show a linear mass increase, albeit, with about 1% of arrival mass per day, of a much smaller magnitude than that of the godwits (Table 2, Fig. 2A). Again, the sampled birds follow the average population trend. With ratios of liver mass over pectoral muscle mass (Fig. 2B) that are generally lower than those of the godwits (Fig. 1B), relative organ sizes of Ruffs fail to show any marked changes over time. Arriving, refueling and departing birds have very similar nutritional to exercise organ ratios, even though arriving and departing birds (evidence based on absence/presence in the study area and the absence of active body moult, J. Jukema pers. comm.) are clearly represented in the samples.

Fat stores and organ size at take-off

The fat-fraction of departure mass varies between 0.11 in the Golden Plover and 0.55 in the Alaska Bar-tailed Godwits (Table 3). Much of this variation seems attributable to the length of the ensuing flights, which is

lowest in the Golden Plovers and longest in the Alaska Bar-tailed Godwits (Fig. 3A).

However, this relationship between fat content and presumed flight distance hides the interesting patterns in relative organ sizes. The Bristle-thighed Curlews and the Alaska Bar-tailed Godwits, both underway on a trans-Pacific flight without stopover possibilities, have nutritional/exercise organ ratios (ratio-1, Table 3) close to 0.3, whereas all other examples show ratios of 0.4 and more. The same holds for the ratio of liver over pectoral muscle (ratio-2), where the trans-Pacific migrants show values close to 0.13 and all others show ratios of 0.19 or more. A possible negative trend in the relationship between ratio-2 and migration distance (Fig. 3B) is mainly due to the small values for the transoceanic flyers. This trend may represent a biologically significant pattern, but note that at shorter migration distances the variation in liver/pectoral muscle ratios is large. Thus, most strikingly, birds able to make additional stopovers en route have higher ratios than birds that will find it very hard to make any stopovers after departure (Fig. 3B).

Discussion

Mass storage before take-off: fattening or fueling?

This study confirms that increases in body mass before departure on long-distance flights consist of fat only to a certain extent (Lindström and Piersma 1993). The present data suggest that attempts to predict, on the basis of body mass, the relative contributions of energy-rich fat and energy-poor fat-free tissue to mass changes (Lindström and Piersma 1993), are bound to be very unreliable. Even within a group of shorebirds of comparable body sizes, considerable variation exists in the fat-fraction of stored mass (Table 2). Mass increases before take-off are thus better described by the term 'fueling' than by the term 'fattening'. Given the large variation between similarly sized and closely related species, the variable contributions of fat and non-fat necessitate measurement in every detailed study of the energetics of avian fuel storage.

Length of flight, stopover possibilities and relative organ size

The data for the two subspecies of Bar-tailed Godwit, one (*L. l. lapponica*) embarking from the Dutch Wadden Sea on mostly an overland flight of about 4,500 km towards the arctic breeding grounds in central Siberia, and the other (juvenile *L. l. baueri*) underway from the Alaska Peninsula on a 11,000 km long, and potentially direct, flight over the Pacific to the New Zealand win-

Table 3. Body mass, fat content and relative organ size in shorebird species embarking on long-distance flights. The species were arranged in order of an increasing fat-fraction of total (wet) body mass at departure (F_{fat}). Average values are given, with standard deviations in parentheses (see Table 2 for additional information). Except for the Bar-tailed Godwits from the Alaska Peninsula ($n = 9$; Piersma and Gill 1998) and the Bristle-thighed Curlew ($n = 6$; Marks and Redmond 1994), sample size is always $n = 5$. M = male and F = female. Ratio-1 indicates the sum of gizzard, intestine and liver mass divided by the sum of pectoral muscle and heart mass. Ratio-2 indicates the ratio of liver to pectoral muscle mass. See Methods section for further details.

Species	Sex	Area of departure	Flight towards?	Destination	Length of migration (km)	Stopover possibilities?	Body mass (g)	Fat mass (g)	F_{fat}	Ratio-1	Ratio-2
1. Golden Plover	M + F	Friesland, Netherlands	North	N. Finland & Russia	1,500–3,000	Yes	234 (6)	25.7 (7.5)	0.11	0.393 (0.041)	0.212 (0.018)
2. Ruff,	M,	Friesland, Netherlands	North	N. Russia	1,500–5,000	Yes	260 (5)	57.9 (3.5)	0.22	0.405 (0.014)	0.213 (0.027)
3. Bar-tailed Godwit	M	Wadden Sea, Netherlands	North	Siberia	4,500	Yes	389 (22)	116.6 (14.0)	0.30	0.471 (0.045)	0.189 (0.023)
4. Red Knot	M + F	Iceland	North	High arctic Canada	2,000–3,000	Yes	225 (5)	81.9 (2.9)	0.36	0.567 (0.063)	0.267 (0.051)
5. Bristle-thighed Curlew	M + F	Hawaiian Islands	North	Alaska	4,000	No	675 (122)	287.8 (66.2)	0.43	0.322 (0.048)	0.138 (0.021)
6. Bar-tailed Godwit	M	Alaska Peninsula	South	New Zealand	11,000	Minimal	367 (25)	201.4 (19.2)	0.55	0.306 (0.033)	0.126 (0.017)

tering grounds, provide the most informative contrast within the available data-set (Table 3). The Alaskan godwits combine large absolute amounts of fat with reductions in overall fat-free mass relative to the Wadden Sea birds, leading to unprecedented measured values of relative fat content (Piersma and Gill 1998). The reductions in lean mass are due to much smaller nutritional organs, reductions that are only partly compensated by increases in the (relative) sizes of the exercise organs (Piersma and Gill 1998, Table 3). Although the godwits from the Wadden Sea do reduce the nutritional/exercise organ ratio before take-off (see Fig. 1), this does not result in ratios that come even close to those of the Alaskan godwits (Table 3). The godwits from the Wadden Sea were adults en route to the breeding grounds, whereas the godwits from Alaska were juveniles en route to the wintering grounds. As argued by Piersma and Gill (1998), rather than reflecting age and breeding/nonbreeding destination, the patterns are consistent with the following interpretation based on flight distance and stopover possibilities.

The Wadden Sea-Siberia flight is mostly overland and the godwits come across at least one suitable stopover site halfway (i.e. the eastern shores of the White Sea, M. Poot et al. pers. comm.). For most of the route birds are close to habitats that may not be rich in food but where they can make an emergency stopover; once underway, these godwits still have the option to make landings. In contrast, the Alaskan godwits embark on a flight over plain open ocean. When they have crossed the equator, after 5,000 km or more away from Alaska, a few island archipelagos may provide emergency landing sites in the southwestern quarter of the Pacific, but most of these places are not very hospitable to Bar-tailed Godwits (J. R. Jehl pers. comm.). Even though some Bar-tailed Godwits turn up in Kiribati and Tuvalu in October, and in somewhat larger numbers closer to New Zealand in Fiji and the Kermadec Islands, many of them may reach the food-rich estuaries of New Zealand in one flight (Higgins and Davies 1996).

That the godwits apparently discard so much of the nutritional organs before these arduous flights, demonstrates that these body parts are not strictly necessary during or after such flights. Godwits arriving in New Zealand no doubt incur a time cost to build up the machinery needed for digestion, and it would be interesting to study temporal changes in food and feeding of arriving individuals. That the godwits departing from the Wadden Sea maintain so much nutritional organ tissue means that they: (1) are wasteful, (2) get rid of any superfluous nutritional organ tissue during flight (cf. Hume and Biebach 1996, Biebach 1998), (3) might need the organs during eventual additional (emergency) stopovers, or (4) need the organs upon arrival. Arguments from natural selection make it hard to accept explanation (1). The jury is out.

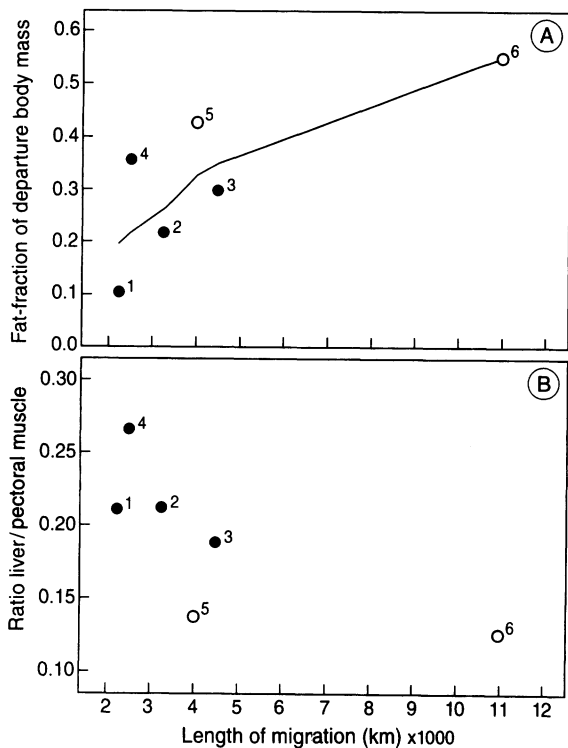


Fig. 3. Comparison of fat loads (A) and relative organ sizes (B) before departure on long-distance flights in six shorebird examples. The data are from Table 3, with the numbers indicating the particular (sub-)species. Closed circles indicate (sub-)species that would be able to make (emergency) stopovers during the migratory flight, open circles indicate species that could not. The trend line in (A) is calculated with the LOWESS routine of SYSTAT (tension 0.75).

The data for the other species (Table 3) are congruent with the above interpretation based on Bar-tailed Godwits. In particular, the finding that the nutritional/exercise organ ratios of Bristle-thighed Curlews before a 4,000 km long flight (adults en route to the breeding grounds) are similar to the ones of the Alaska Bar-tailed Godwits emphasizes the fact that it is the lack of stopover possibilities (they are absent between Hawaii and Alaska) that matters in regard to organ savings. The relatively high nutritional/organ size ratios for the Red Knots in Iceland (Fig. 3), birds that embark on flights across the Iceland Strait and the Greenland Inland-ice (Gudmundsson et al. 1991), is somewhat surprising. The potential for additional stopovers en route may have been underestimated (cf. Alerstam et al. 1990, Gudmundsson et al. 1991). Alternatively, Red Knots cannot accept any delays (caused by the time necessary for organ build-ups) upon arrival in the Arctic because they face severe time-pressures, and/or immediately need to process sufficient food to maintain energy balance under severe weather conditions and the concomitant high energy expenditures.

Adaptive design: how much is enough but not too much?

'Overdesigned' (i.e. overdimensioned) structures cost energy and space (Diamond 1991, 1993), and this problem is particularly pressing when structures have to be carried aloft for long distances. Therefore, when there are no rebuilding costs (time, energy, nutrients), any structure that is dispensable should be dispensed with before or shortly after take-off. Not only may particular organs be important especially for fuel storage (digestion and metabolic processing) or for flight (pectoral muscles for mechanical power, lungs for oxygen uptake and heart for pumping the blood around), the conditions at staging areas may also influence the optimal size of an organ. For example, at sites where the risk of predation is large, birds may benefit from powerful (large) pectoral muscles and mass savings by reductions in the belly organs, in order to be able to evade attacking raptors (e.g. Hedenström 1992).

It is easy to see why the stomach and intestine should be reduced just before take-off. If no stops are made and no food would be eaten, the presence of an active alimentary canal is just a waste of energy for maintenance and transport in flight (cf. Secor et al. 1994). In contrast, hypertrophy of the pectoral muscles with increases in body mass is predicted by aerodynamic theory (Pennycuick 1975, Hedenström and Alerstam 1992, Pennycuick 1998, and see example of Marsh and Storer 1981).

But the story appears more problematic with an organ like the liver. The liver plays a critical role as a fuel-processing engine, and contributes to waste disposal (Sturkie 1986). At first sight one would expect that a powerful liver would be needed as much during the flight phase as during the fueling phase of a migration. Indeed, the suggested avian-specific alternative pathway to efficiently supply free-fatty acids to the working muscle during endurance flights (Jenni-Eiermann and Jenni 1992) alleviates the necessity to increase blood flow or to increase blood albumin concentration, but requires the liver to re-esterify free-fatty acids to very-low-density-lipoproteins (VLDL) for quick transport to hard-working muscle tissue. The decrease in liver size before migratory flights documented here, and previously in passerine migrants (Dolnik and Blyumental 1967), is therefore not understood, and calls for sophisticated physiological studies on liver function and performance in avian migrants.

Outlook

The striking patterns of changes in relative organ size in respect to migration distance and stopover possibilities suggest that much will be learned by careful and more quantitative comparisons of physiological characteris-

tics at the organ level and required performance of migrating birds. Not only will the interpretation of organ sizes in an ecological context enhance the understanding of organ function and its constraints, deviations from expected physiological patterns may lead the search for critical ecological parameters. Thus, bird migration research not only needs more details of flight routes and migration itineraries of cohorts and individuals, it also requires a much greater understanding of physiological processes at the organ level and the ecological factors at play at staging areas (food types, presence of predators), as well as integrations of this empirical knowledge.

Compensatory changes in the size and capacity of organs seem to represent short-term solutions to conflicting selection pressures in organisms with physiologically highly variable and demanding lifestyles. Phenotypic flexibility thus adds another layer of complexity (see Schluter et al. 1991) to the many life history trade-off equations that natural selection continually solves.

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