

 Open access • Journal Article • DOI:10.1098/RSPB.2000.0986

## Empirical evidence for differential organ reductions during trans-oceanic bird flight

— [Source link](#) 

Phil F. Battley, Theunis Piersma, Maurine W. Dietz, Sixian Tang ...+2 more authors

**Institutions:** Griffith University, East China Normal University

**Published on:** 22 Jan 2000 - Proceedings of The Royal Society B: Biological Sciences (The Royal Society)

**Topics:** Bird flight

Related papers:

- [Rapid Changes in the Size of Different Functional Organ and Muscle Groups during Refueling in a Long-Distance Migrating Shorebird](#)
- [Fuel supply and metabolic constraints in migrating birds](#)
- [Guts Don't Fly: Small Digestive Organs in Obese Bar-Tailed Godwits](#)
- [Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight?](#)
- [Rapid reversible changes in organ size as a component of adaptive behaviour](#)

Share this paper:    

View more about this paper here: <https://typeset.io/papers/empirical-evidence-for-differential-organ-reductions-during-1fdt0k4d8a>

University of Groningen

## Empirical evidence for differential organ reductions during trans-oceanic bird flight

Battley, PF; Piersma, T; Dietz, MW; Tang, SX; Dekinga, A; Hulsman, K

*Published in:*

Proceedings of the Royal Society of London. Series B, Biological Sciences

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*

Publisher's PDF, also known as Version of record

*Publication date:*

2000

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Battley, PF., Piersma, T., Dietz, MW., Tang, SX., Dekinga, A., & Hulsman, K. (2000). Empirical evidence for differential organ reductions during trans-oceanic bird flight. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, 267(1439), 191-195.

### Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

### Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

*Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.*

# Empirical evidence for differential organ reductions during trans-oceanic bird flight

Phil F. Battley<sup>1\*</sup>, Theunis Piersma<sup>2,3</sup>, Maurine W. Dietz<sup>3</sup>, Sixian Tang<sup>4</sup>, Anne Dekinga<sup>2</sup> and Kees Hulsman<sup>1</sup>

<sup>1</sup>*Australian School of Environmental Studies, Griffith University, Nathan, Queensland 4111, Australia*

<sup>2</sup>*Netherlands Institute for Sea Research (NIOZ), PO Box 59, 1790 AB Den Burg, Texel, The Netherlands*

<sup>3</sup>*Centre for Ecological and Evolutionary Studies, Zoological Laboratory, University of Groningen, PO Box 14, 9750 AA Haren, The Netherlands*

<sup>4</sup>*Department of Biology, East China Normal University, Shanghai 200062, China*

Since the early 1960s it has been held that migrating birds deposit and use only fat as fuel during migratory flight, with the non-fat portion of the body remaining homeostatic. Recent evidence from field studies has shown large changes in organ sizes in fuelling birds, and theory on fuel use suggests protein may be a necessary fuel during flight. However, an absence of information on the body condition of migrants before and after a long flight has hampered understanding of the dynamics of organs during sustained flight. We studied body condition in a medium-sized shorebird, the great knot (*Calidris tenuirostris*), before and after a flight of 5400 km from Australia to China during northward migration. Not only did these birds show the expected large reduction in fat content after migration, there was also a decrease in lean tissue mass, with significant decreases in seven organs. The reduction in functional components is reflected in a lowering of the basal metabolic rate by 46%. Recent flight models have tried to separate the 'flexible' part of the body from the constant portion. Our results suggest that apart from brains and lungs no organs are homeostatic during long-distance flight. Such organ reductions may be a crucial adaptation for long-distance flight in birds.

**Keywords:** migration; physiology; phenotypic flexibility; birds; waders; *Calidris tenuirostris*

## 1. INTRODUCTION

Migrating birds make the longest single flights in the animal kingdom, during which no nutrients are ingested and all energy is derived from stored fuel. This fuel was long held to be exclusively fat, with the non-fat component of the body remaining unchanged (Odum *et al.* 1964). This 'aircraft refuelling paradigm' treated birds like aeroplanes, having a constant structural mass and filling and emptying only the fuel tanks. Gradually, evidence began to accumulate showing that fuelling birds may add mass to their exercise muscles before migration (Fry *et al.* 1972; McLandress & Raveling 1981; Lindström & Piersma 1993; Piersma 1998; Piersma *et al.* 1999), and even reduce the mass of nutritional organs (presumably to keep body mass during flight low) (Piersma *et al.* 1993, 1999; Piersma 1998). At the same time, theory on fuel use suggested that protein may be a necessary supplement to fat during flight (Jenni & Jenni-Eiermann 1998).

Field data of the body condition of migrating birds caught before and after a long flight have been few, so it has been difficult to determine whether, in these actively exercising animals, organs are catabolized during flight and if so, how uniformly. European robins (*Erithacus rubecula*) in Sweden had lower total lean tissue content, flight muscle mass and liver mass after a long flight than after shorter flights (Åkesson *et al.* 1992). Garden warblers (*Sylvia borin*) were shown to be likely to reduce pectoral, stomach and leg muscles during migration (but other organs were not tested) (Biebach 1998). Blackcaps (*Sylvia*

*atricapilla*), upon arrival in southern Israel after migration across the Negev desert, appear to deposit substantial amounts of lean tissue, implying that lean tissue as well as fat had been catabolized during flight (Karasov & Pinshow 1998). Experiments with fasting blackcaps suggested that the nutritional organs might be disproportionately involved in lean tissue catabolism (Karasov & Pinshow 1998). No study has yet examined changes in organ mass across the whole suite of organs in migrating birds on a flight of known length.

We capitalized on a unique situation in which a medium-sized shorebird, the great knot (*Calidris tenuirostris*), could be caught before and after migration on a well-documented long-distance flight of over 5000 km. By comparing the body composition of birds before departure from Australia and after arrival in China, we aimed to determine whether lean tissue is broken down during flight and if so, in what organs. We also measured basal metabolic rate (BMR) before and after migration to assess the metabolic consequences of such a long flight. This is the first time birds have been assessed for such changes within a season, where departure and arrival sites are known.

## 2. MATERIAL AND METHODS

### (a) General

Great knots breed in the eastern Siberian mountains and most spend the non-breeding season in northern Australia. In March or early April they migrate north in a single flight to eastern Asia, especially eastern China and Korea (figure 1), with the majority launching off from north-west Australia. We

\* Author for correspondence (p.battley@mailbox.gu.edu.au).

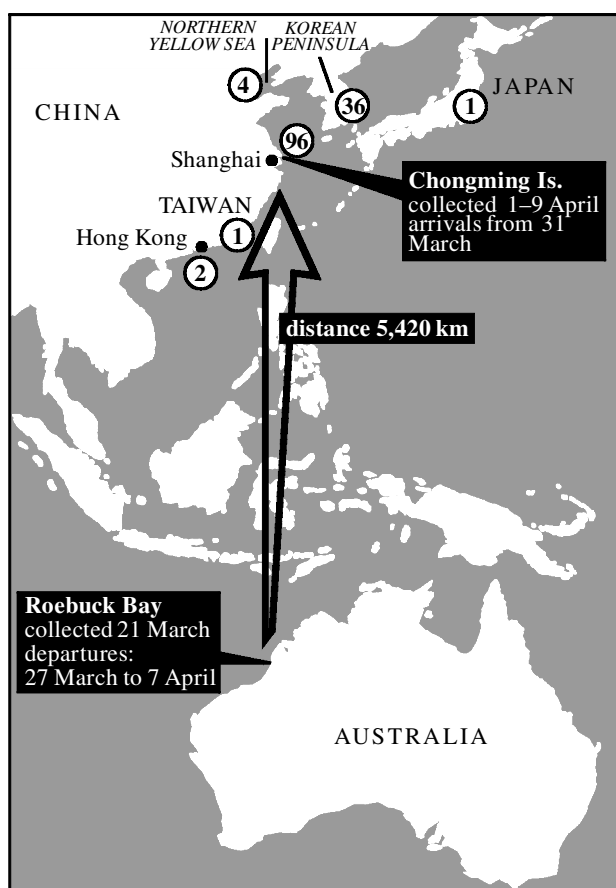


Figure 1. Flight route between Roebuck Bay, north-west Australia, and the Yangtze River estuary in China. Numbers in circles represent band recoveries or leg-flag sightings of great knots banded in north-west Australia.

studied great knots at Roebuck Bay, Broome, north-west Australia ( $18^{\circ}00' S$ ,  $122^{\circ}22' E$ ) and Chongming Island, Yangtze River, China ( $30^{\circ}48' N$ ,  $121^{\circ}27' E$ ). Banding records, timing of departures and arrivals, and bird counts all indicate that knots fly direct from Australia to eastern Asia. Band records show that Chongming Island is heavily used by birds from north-west Australia. Although the recovery rate for western-Australian-banded knots is slightly higher than for eastern-banded birds during northward migration, probably because of uneven field-work in Asia (146 recovered out of 8651 banded in western Australia, 20 recovered out of 1995 in eastern Australia;  $\chi^2 = 4.89$ , d.f. = 1,  $p < 0.05$ ), western-Australian-banded birds account for the large majority of the east Chinese records (94 out of 100 records;  $\chi^2 = 10.66$ , d.f. = 1,  $p < 0.005$ ). There are also eight same-season recoveries of great knots in China of birds banded in north-west Australia, one recorded seven days and one 12 days after banding. Dates of departure from north-west Australia and arrival in China are very close, indicating that birds do not use intermediate stop-over sites. In 1998, the first departures at Roebuck Bay were seen on 27 March, and in China, hunters at Chongming Island recorded the first arrivals on 31 March. Furthermore, even though the great knot is the second most abundant shorebird in Australia, nowhere in south-east Asia does it occur in large numbers, indicating a direct flight to east Asia (Higgins & Davies 1996). These observations give us faith that birds arriving in eastern China are Australian, most from north-west Australia. Upon arrival in China, many birds are caught almost immediately by local hunters, which

enables assessment of changes of body composition occurring during a 5400 km flight.

### (b) Samples

We collected ten birds at Roebuck Bay on 21 March 1998, and ten birds on Chongming Island from 1–9 April 1998. As departures from Australia are not fully synchronized, to ensure birds collected were as close to departure as possible we selected (by visual assessment in the field) birds with the most advanced alternate plumage development and plumpness. Collected knots weighed on average 9.3 g more than 23 other adults caught (collected mean  $\pm$  s.d., corrected for mass loss after capture,  $239.4 \pm 14.3$  g; other birds,  $230.1 \pm 17.9$  g; Student's *t*-test,  $t_{31} = 1.44$ ,  $p = 0.16$ ). The collected birds were not significantly different in bill ( $43.9 \pm 2.1$  versus  $45.0 \pm 0.9$  mm,  $t_{19} = -1.58$ ,  $p = 0.13$ ) and total head length ( $75.4 \pm 2.4$  versus  $76.2 \pm 1.8$  mm;  $t_{29} = -1.00$ ,  $p = 0.32$ ), and mean wing-length was actually slightly shorter ( $187.9 \pm 3.6$  versus  $191.7 \pm 4.6$  mm,  $t_{31} = -2.34$ ,  $p = 0.026$ ). We did not inadvertently collect larger birds. Chinese birds were similar in mass to knots caught in eastern China in previous years: mean masses were  $126.97 \pm 17.7$  g in 1982–1986 ( $n = 116$ ) (Wang & Qian 1988);  $120.5$  g in 1989 ( $n = 112$ ) (Barter *et al.* 1997);  $128.9 \pm 13.5$  g in 1996 ( $n = 144$ ) (M. Barter, personal communication);  $125.6 \pm 11.8$  g in 1998 ( $n = 17$ , this study; includes seven birds weighed and released). Our results would be compromised if we caught only the lightest birds, with heavy birds carrying on to the Korean peninsula or the northern Yellow Sea. In that case, birds using eastern China should be heavier in years when bad weather forces large numbers of birds down than years in which few birds use the region. This was not the case: few birds used Chongming Island during this study, yet the mean mass of birds handled in 1998 was no different than in 1996 ( $t_{159} = -1.05$ ,  $p > 0.2$ ), a year in which large numbers of great knots used Chongming Island and nearby Jiduansha (Barter *et al.* 1997). Furthermore, most birds were not nutritionally stressed, retaining substantial amounts of fat (see §3). In addition to these samples, two great knots were collected at Roebuck Bay on 20 February, nine on 6 March and one on 12 March.

### (c) Body composition

We analysed the body composition of all 20 birds collected to determine fat content and fat-free dry organ masses of birds before and after migration. After dissection, organs were dried at  $60^{\circ} C$  to constant mass (three to five days, but longer for fatty tissues such as the skin) to remove water, and the fat was extracted in a Soxhlet apparatus using petroleum ether. In the results, pectoral muscles refer to the mass of pectoral and supra-coracoideus muscles combined. To ensure that organ mass differences do not simply reflect structural size variation between individuals, a principal components analysis was performed on 11 structural measurements (bill, total head, tarsus, tarsus plus mid-toe, and wing lengths, plus six sternum measurements) for all birds collected in 1998 ( $n = 32$ ). An index of structural size was generated for each bird based on the PC1 scores applied to the individual's measurements. The ratio of this index to the average index for all individuals was used to correct the organ masses. This index was also used to test for size differences between the birds from Roebuck Bay and China: a Student's *t*-test showed no difference in size between sites for both all birds and males only (see below): all birds,  $t_{18} = -0.04$ ,  $p = 0.97$ ; males only,  $t_{11} = -0.98$ ,  $p = 0.35$ .

Preliminary analyses indicated several significant sex by site interaction effects on organ sizes (females were the heaviest

birds in Australia yet the lightest in China). Because we caught fewer females than males (three females in Australia, four in China) and are unable to assess whether this sex difference is real or a sampling artefact, we present analyses from only male birds, unless stated otherwise. The seven male birds in Australia weighed on average  $233.4 \pm 12.2$  g, and the six Chinese males  $125.0 \pm 7.5$  g.

#### (d) Basal metabolic rate

To get a measure of the immediate energetic consequences of organ reductions, we also determined BMR in five birds during the fuelling period in Australia (one from 20 February, two from 6 March and two from 21 March; BMR was not related to date so we treat these values as representative of all pre-migratory birds; Pearson's  $r = 0.021$ ,  $p = 0.974$ ), and five birds caught in China (two caught on 3 April, one on 6 April and two on 9 April, the latter pair being measured on 10 April, having been maintained on a fish diet in the interim). BMR was measured during the night with a portable two-channel open-flow respirometry unit (Servomex Oxygen Analyser A570, Servomex BV, Zoetermeer, The Netherlands). Most measurements (after calibration) were started from 18.53 to 00.58 local time, and stopped between 06.25 and 08.00 the following morning. Total duration of measurement varied between 332 and 637 min. Flows were adjusted so that the oxygen consumption was between 0.5 and 1% ( $200\text{--}850$  ml  $\text{min}^{-1}$ , Brooks Massflowmeters 5860S, Brooks Instruments, Hatfield, PA, USA). The oxygen analyser was calibrated before and after the measurement. The unit switched automatically between the two channels (each time sampled for 10 min) and reference air (sampled hourly for 10 min). Chamber temperatures were within the expected thermoneutral zone for a great knot: mean  $30.8^\circ\text{C}$  in Australia (ambient temperature) and  $23.3^\circ\text{C}$  in China (heated). Metabolic rates were calculated according to Hill (1972). Data from the first half of the measurement period, and the first 2 min of each 10-min block were discarded. Calculated values represent the mean of the lowest two consecutive 10-min periods in the latter half of the measurement period.

### 3. RESULTS

#### (a) Body composition

In addition to having used most of the fat stores in the body, the fat-free dry masses of most organs were lower in China than in Australia (figure 2). For organs which did not reach statistical significance, a negative trend was present in all except the brain and lungs (leg muscles become significant if the outlier is removed,  $p < 0.001$ ; the heart becomes almost significant,  $p = 0.059$ ). The fat content of migrated birds was only 15.7% of that of pre-departure birds. This underestimates true fat use as departures did not start for a further six days, giving time for further fattening in the Australian sample. For non-fat tissue, the proportionately largest significant differences were in the skin, salt glands, intestine, liver and kidneys. Of the total reduction of 5.74 g of non-fat tissue, most was accounted for by the skin (26.4%), pectoral muscles (25.8%), and the remainder of the carcass (15.8%). As a measure of overall condition, total fat-free dry mass (sum of all organs excluding feathers) was much lower in China (84.2% of the Australian average). Australian and Chinese birds did not differ structurally, so the differences found do not simply reflect body size effects. Nor was

there extreme depletion of nutrient reserves in arriving birds (out of the six males collected in China, five had 11.4–17.5 g of fat remaining, whilst the final bird had 6.6 g), and birds in this study were not unusually light compared with other years.

#### (b) Basal metabolic rate

The reduced lean body mass upon arrival was reflected in much lower BMR values in China than Australia (figure 3). Total BMR was 46% lower after migration (sexes combined, 1.59 W in Australia and 0.89 W in China,  $n = 5$  for both samples;  $t_8 = -3.16$ ,  $p = 0.013$ ). Compared with the birds from China, the Australian birds had large fat stores, and as fat contributes little to overall metabolic rate, we calculated mass-specific metabolic rates per kilogram lean fresh tissue (equal to lean dry tissue/0.3). Mass-specific BMR was 40% lower in China ( $164.4$  W  $\text{kg}^{-1}$  in Australia and  $99.1$  W  $\text{kg}^{-1}$  in China;  $t_8 = -2.72$ ,  $p = 0.026$ ).

### 4. DISCUSSION

These organ reductions are evidence that protein as well as fat is catabolized during flight, and show that few organs are homeostatic. In fact, the brain may be the only truly homeostatic organ in these birds. There were no differences in brain size between all 20 birds in this study, 12 birds collected in Broome earlier in the fuelling period in 1998, and accidental catching casualties from north-west Australia (five in 1990 and five in 1996). Even the lungs, which appeared to remain constant in these birds, have been suggested to decrease during flight as physical demands lessen (Pennycuik 1998).

In contrast, many other organs are far more dynamic. Field studies have revealed changes in stomach size during fuelling episodes (Lindström & Piersma 1993; Piersma 1998; Piersma *et al.* 1999), and laboratory studies have shown considerable diet-related flexibility in nutritional organ size (Starck 1999). Particularly, red knots in Iceland reduced their nutritional organs substantially before migration (Piersma *et al.* 1999). If this occurred in great knots, then some of the changes may be overestimated. In the pre-departure sample of male great knots from Australia, stomach mass did not appear to reduce before migration (cf. Piersma *et al.* 1993): there was no relationship between stomach mass and fat mass (a measure of migratory preparation) (Pearson's  $r = -0.097$ ,  $p = 0.836$ ,  $n = 7$ ). A negative trend against fat mass was present for kidneys, liver and intestine, though scatter was high and no organs approached significance (Pearson's  $r = -0.445$ ,  $p = 0.317$  for liver;  $r = -0.191$ ,  $p = 0.682$  for kidneys;  $r = -0.450$ ,  $p = 0.311$  for intestine). The time delay between sampling and departures could also lead to underestimates of changes in exercise organs such as the pectoral muscles and heart if these continued to increase over the intervening period.

The males in the pre-departure sample did, however, have similar amounts of fat to the females (Student's  $t$ -test,  $t_8 = -1.537$ ,  $p = 0.163$ ), despite the females being on average 20 g heavier in total mass. Two of the females (256 g and 259 g) must have been almost ready to depart (the heaviest birds caught here are 261 g; Higgins & Davies 1996). Large catches of great knots in north-west

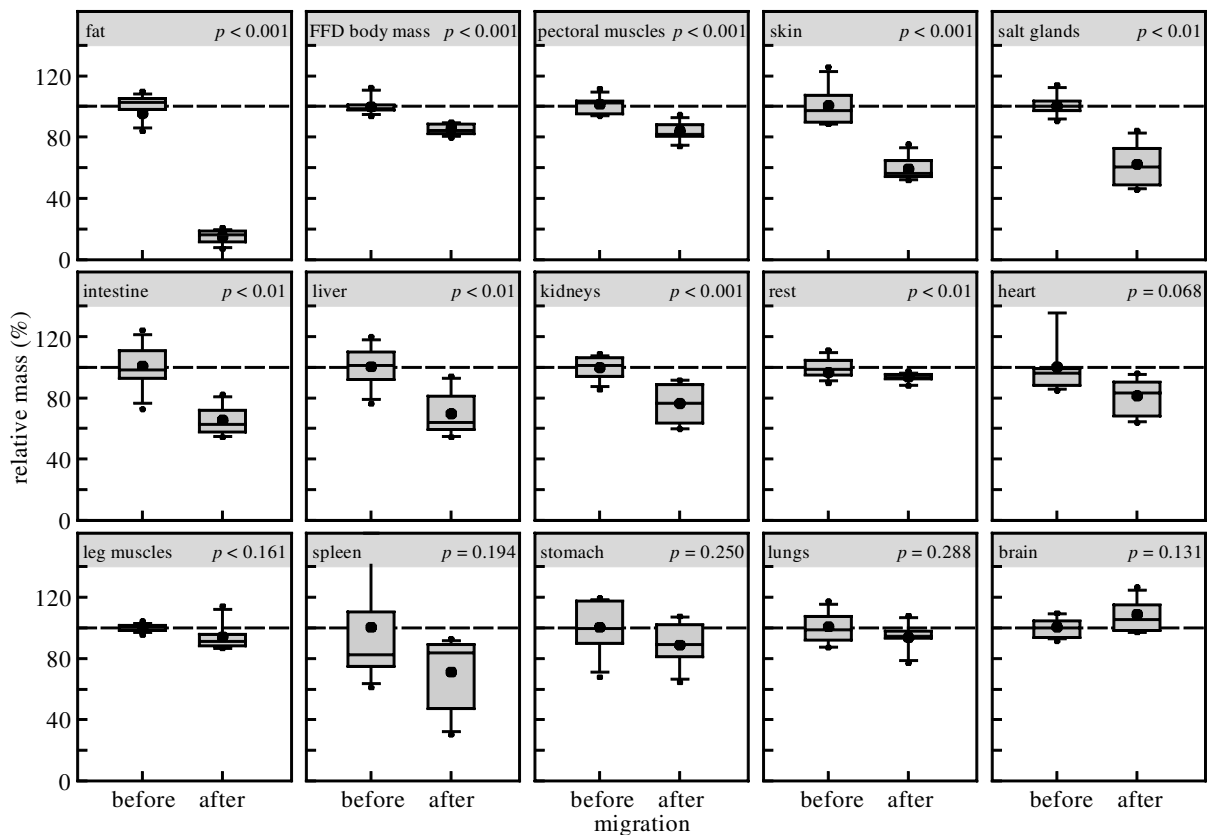


Figure 2. Change in fat content and lean dry mass of different organs in male great knots before and after migration from north-west Australia to China. Plots show the percentage difference between Australia and China, with the Australian mean set at 100%. Boxes show the 25th, 50th and 75th percentiles, whiskers show the 10th and 90th percentiles, and the mean is shown as a closed circle. Outliers of the heart and spleen are out of range. Sample sizes are seven in Australia and six in China. Probability values are results from Student's *t*-tests. 'Rest' refers to the remainder of the carcass after all other organs have been removed.

Australia on consecutive days during the migration period in 1994 indicated that birds weighing 240–260 g departed overnight (Higgins & Davies 1996). We believe that birds of both sexes in our sample are representative of soon-to-depart individuals, and that the reductions in organ masses in this study are largely a consequence of flight rather than changes during fuelling.

The reduction in lean tissue mass during flight was reflected in a more than proportional decrease in both total and mass-specific BMR. The reduction in mass-specific BMR is in contrast with the general rule that the mass-specific BMR increases with lower body mass (which normally applies to both intra- and interspecific comparisons) (Aschoff & Pohl 1970; Heusner 1982; Daan *et al.* 1989, 1990). This suggests that after migration either the organs that contribute much to BMR were highly reduced (kidneys have been implicated in interspecific variation in BMR) (Daan *et al.* 1990), or the overall metabolic rate per gram of lean organ tissue had decreased. BMR was reduced three times more than lean tissue mass in these birds.

While fat provides most of the energy during flight, the main role of protein may be to maintain metabolic processes involved in fuel supply, such as to generate citric acid cycle intermediates, or for gluconeogenesis to supply glucose to the brain (Jenni & Jenni-Eiermann 1998). If

the functional role of an organ declines during flight, then a reduction in organ size could free up protein without any adverse effects. For example, as a bird uses stored fuel and becomes lighter, pectoral muscle mass might reduce and maximize the muscle conversion efficiency, reduce overall body mass, and release protein (Pennycuik 1998). In contrast, the kidneys and the liver showed some of the largest reductions in mass, despite their primary roles (removing nitrogenous wastes, and gluconeogenesis and replacement of citric acid cycle intermediates, respectively) being unlikely to lessen during migration. This suggests that some protein loss may be inescapable. Selective catabolism of functionally inactive tissues (e.g. intestines, salt glands) will buffer other more important organs from increased protein demands during flight, as well as keep total body mass low.

In birds migrating across inhospitable barriers, species as different as shorebirds and warblers (Biebach 1998; Karasov & Pinshow 1998) show dramatic reductions in organ non-fat tissue masses. The 'aircraft refuelling paradigm' is therefore clearly no longer appropriate for long-distance migrating birds. Pennycuik (1998) recently coined the term 'airframe mass' to represent the invariant portion of the body, the total mass minus fat and pectoral muscles. Our work suggests that even the airframe mass is not constant over a long flight. A better understanding of

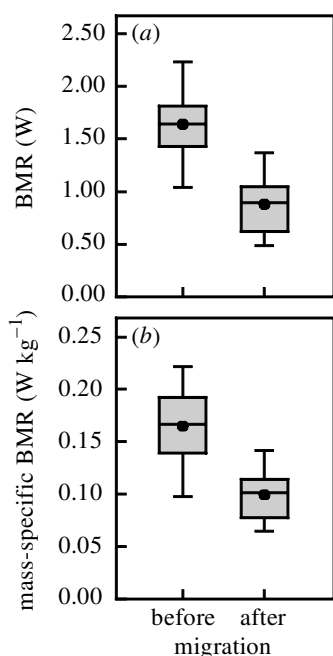


Figure 3. Metabolic rate of five great knots during migratory fuelling in Australia and five great knots caught immediately after migration to China. (a) Total basal metabolic rate; (b) mass-specific basal metabolic rate (calculated from fresh fat-free mass). Samples comprise five males in Australia, and one male and four females in China. Boxes are as in figure 1.

the physiological adaptations enabling birds like great knots to cross the South China seas non-stop, calls for detailed studies at the organ level during long-distance flights. Such long flights have recently proved feasible in the latest generation of wind tunnels (e.g. Pennycuik *et al.* 1996).

Thanks to the Ian Potter Foundation, M. A. Ingram Trust and a PIONIER grant to T.P. from the Netherlands Organization for Scientific Research, for funds. The fieldwork in Australia could not have succeeded without the assistance of Chris Hassell, Janet Sparrow, Danny Rogers, Karen Hedstrom, Grant Pearson and the permission of the Broome Bird Observatory Committee. Mark Barter's ongoing assistance and encouragement was greatly appreciated. We thank Professor Yuan Chonggang and Professor Zhou Zhongliang for assistance and permission to work in Shanghai, and Edzo Paap and Ger Veltman for doing a magnificent job in completing the respirometer in the nick of time. Vincent Paeper and Daniel van Os helped with the dissections, and Clare McKee (Australian Quarantine Inspection Service) gave essential assistance over permits for importing the Chinese birds. Band and departure records were provided by the Australasian Wader Studies Group and the Australian Bird and Bat Banding Scheme. Steritech (Sydney) gamma-irradiated the Chinese specimens free of charge. Dick Visser produced the figures extremely quickly. This research was approved by Griffith University's Ethics sub-Committee for Experimentation on Animals. Åke Lindström commented on a draft. This is NIOZ publication number 3377.

## REFERENCES

Åkesson, S., Karlsson, L., Pettersson, J. & Walinder, G. 1992 Body composition and migration strategies: a comparison between robins (*Erithacus rubecula*) from two stop-over sites in Sweden. *Vogelwarte* **36**, 188–195.

- Aschoff, J. & Pohl, H. 1970 Der Ruheumsatz von Vögeln als Funktion der tageszeit und des Körpergrösse. *J. Ornithol.* **111**, 38–47.
- Barter, M., Tonkinson, D., Tang, S. X., Yuan, X. & Qian, F. W. 1997 Staging of great knot *Calidris tenuirostris*, red knot *C. canutus* and bar-tailed godwit *Limosa lapponica* at Chongming Dao, Shanghai: jumpers to hoppers? *Stilt* **31**, 2–11.
- Biebach, H. 1998 Phenotypic organ flexibility in garden warblers *Sylvia borin* during long-distance migration. *J. Avian Biol.* **29**, 529–535.
- Daan, S., Masman, D., Strijkstra, A. & Verhulst, S. 1989 Intraspecific allometry of basal metabolic rate: relations with body size, temperature, composition, and circadian phase in the kestrel, *Falco tinnunculus*. *J. Biol. Rhythms* **4**, 267–283.
- Daan, S., Masman, D. & Groenewold, A. 1990 Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *Am. J. Physiol.* **259**, R333–R340.
- Fry, C. H., Ferguson, I. J. & Dowsett, R. J. 1972 Flight muscle hypertrophy and ecophysiological variation of yellow wagtail *Motacilla flava* races at Lake Chad. *J. Zool. (Lond.)* **167**, 293–306.
- Heusner, A. A. 1982 Energy metabolism and body size. I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact? *Respir. Physiol.* **48**, 1–12.
- Higgins, P. J. & Davies, S. J. J. F. 1996 *Handbook of Australian, New Zealand and Antarctic birds*, vol. 3. Melbourne, Australia: Oxford University Press.
- Hill, J. 1972 Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. *J. Appl. Physiol.* **33**, 261–263.
- Jenni, L. & Jenni-Eiermann, S. 1998 Fuel supply and metabolic constraints in migrating birds. *J. Avian Biol.* **29**, 521–528.
- Karasov, W. H. & Pinshow, B. 1998 Changes in lean mass and in organs of nutrient assimilation in a long-distance passerine migrant at a spring-time stopover site. *Physiol. Zool.* **71**, 435–448.
- Lindström, Å. & Piersma, T. 1993 Mass changes in migrating birds: the evidence for fat and protein storage re-examined. *Ibis* **135**, 70–78.
- McLandsness, M. R. & Raveling, D. G. 1981 Changes in diet and body composition in Canada geese before spring migration. *Auk* **98**, 65–79.
- Odum, E. P., Rogers, D. T. & Hicks, D. L. 1964 Homeostasis of the non-fat components of migrating birds. *Science* **143**, 1037–1039.
- Pennycuik, C. R. 1998 Computer simulation of fat and muscle burn in long-distance bird migration. *J. Theor. Biol.* **191**, 47–61.
- Pennycuik, C. R., Klaassen, M., Kvist, A. & Lindström, Å. 1996 Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *J. Exp. Biol.* **199**, 2757–2765.
- Piersma, T. 1998 Phenotypic flexibility during migration: optimization of organ size contingent on the risks and rewards of fueling and flight? *J. Avian Biol.* **29**, 511–520.
- Piersma, T., Koolhaas, A. & Dekinga, A. 1993 Interactions between stomach structure and diet choice in shorebirds. *Auk* **110**, 552–564.
- Piersma, T., Gudmundsson, G. A. & Lilliendahl, K. 1999 Rapid changes in size of different functional organ and muscle groups during refuelling in a long-distance migrating shorebird. *Physiol. Biochem. Zool.* **72**, 405–416.
- Starck, J. M. 1999 Structural flexibility of the gastro-intestinal tract of vertebrates: implications for evolutionary morphology. *Zool. Anzeiger* **238**, 87–101.
- Wang, T. H. & Qian, G. Z. 1988 *Shorebirds in the Yangtze Estuary and Hangzhou Bay*. Shanghai: East China Normal University Press.