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## BODY COMPOSITION AND FLIGHT RANGES OF BAR-TAILED GODWITS (*LIMOSA LAPPONICA BAUERI*) FROM NEW ZEALAND

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**ABSTRACT.**—Body composition analysis was performed on 37 Bar-tailed Godwits (*Limosa lapponica baueri*) that had been illegally shot during migratory fueling in northern New Zealand in March 1992. Adults ( $n = 35$ ) were heavy (442–721 g), with fat loads of 30–45% of body mass. Two first-year males had only 5.4% and 8.9% fat, respectively, and had 13% less lean (fat-free dry) tissue than the average adult male. Males and females scaled along the same size axes, with little overlap between the sexes (females were larger). Larger birds carried more fat, but fat loads did not differ systematically with size (and, therefore, sex). Fatter birds (after accounting for body size) had larger flight muscle and lung masses, implying premigratory hypertrophy. Males that were not in body molt were fatter, but less colorful, than molting birds. They were also longer-winged and had larger testes but smaller intestines and salt glands, which suggests that they may belong to a subpopulation with a different fueling and molt strategy. Comparison between *L. l. baueri* and a smaller subspecies (*L. l. taymyrensis*) indicated that although the two subspecies scaled along the same lean mass–size axes, *L. l. baueri* deposited much more fat for their body size (1.7× more than the equivalent-sized *L. l. taymyrensis*). On the basis of estimated travel costs for *L. l. taymyrensis*, predicted flight ranges for *L. l. baueri* ranged from 6,000 to 8,600 km, depending on whether wind assistance is assumed. That suggests that direct flights from New Zealand to southeastern or eastern Asia are possible (e.g. Philippines, 7,200 km; Japan, 8,700; South Korea, 9,100 km). Received 18 August 2003, accepted 16 February 2005.

**Key words:** annual cycle energetics, Bar-tailed Godwit, *Limosa lapponica*, migration, phenotypic flexibility, sexual size dimorphism, shorebird.

### Composition Corporelle et Distance de Vol chez *Limosa lapponica baueri* de Nouvelle-Zélande

**RÉSUMÉ.**—Des analyses de composition corporelle ont été réalisées sur 37 *Limosa lapponica baueri* qui ont été tirés illégalement au cours d'une halte migratoire dans le nord de la Nouvelle-Zélande en mars 1992. Les adultes ( $n = 35$ ) étaient lourds (442–712 g), avec une masse de graisse représentant 30–45% de la masse corporelle. Les mâles de un an et deux ans avaient seulement 5,4% et 8,9% de graisse, respectivement, et des tissus 13% plus maigres (masse sèche sans gras) que la moyenne des adultes. Mâles et femelles s'échelonnaient selon des axes de même taille, avec un peu de chevauchement entre les deux sexes (les femelles étaient plus grandes). Les oiseaux plus grands possédaient plus de gras, mais la quantité de gras

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ne différait pas systématiquement avec la taille (et, par conséquent, le sexe). Les oiseaux plus gras (en contrôlant pour la taille) avaient des masses musculaires de vol et pulmonaires plus grandes, suggérant une hypertrophie pré-migratoire. Les mâles, qui ne mueaient pas, étaient plus gras, mais moins colorés, que les mâles en mue. Ils avaient également des ailes plus longues et des testicules plus grosses mais des intestins et des glandes à sel plus petits. Ceci suggère qu'ils pourraient appartenir à une sous-population avec des stratégies différentes d'approvisionnement et de mue. Les comparaisons réalisées entre *L. l. baueri* et une sous-espèce plus petite (*L. l. taymyrensis*) indiquaient que *L. l. baueri* accumulait bien plus de graisse pour leur taille corporelle (1,7 fois plus que *L. l. taymyrensis* de taille équivalente), malgré que les deux sous-espèces s'échelonnaient selon les mêmes axes masse-taille. En se basant sur une estimation des coûts de déplacement de *L. l. taymyrensis*, la distance prédite de vol devrait se situer entre 6 000 et 8 600 km, selon que l'assistance par le vent soit considérée ou non. Cela suggère que les vols directs entre la Nouvelle-Zélande et le sud-est ou l'est de l'Asie sont possibles (e.g. Philippines, 7 200 km; Japon, 8 700 km; Corée du Sud, 9 100 km).

IN SPITE OF its remote location in the southwest Pacific, far away from the Arctic tundra, New Zealand is visited by large numbers of Arctic-breeding shorebirds, particularly the Bar-tailed Godwit (*Limosa lapponica*; hereafter "godwits"). Godwits in New Zealand belong to the easternmost and largest subspecies, *L. l. baueri* (Higgins and Davies 1996), which breeds predominantly in Alaska (McCaffery and Gill 2001). Although there is strong circumstantial evidence that godwits from Alaska undertake a single flight of >10,000 km across the Pacific on the southward migration to New Zealand (McCaffery and Gill 2001), it is likely that birds heading north travel via Asia, where band or leg-flag sightings are known from South Korea and Japan (Riegen 1999, 2000). Immediate destinations (and flight lengths) for New Zealand godwits are unknown, but possibilities range from the Gulf of Carpentaria, Australia (17°38'S, 140°06'E; 3,800 km) to the Yellow Sea, China, and Korea (39°45'N, 124°30'E; 9,600 km).

Migratory waders use mostly fat to fuel these flights, though they also catabolize lean tissue from body organs (Battley et al. 2001). Fueling birds can deposit lean tissue as well as fat before migration, which may be discernible in total body content analyses (Lindström and Piersma 1993) and in detailed organ analyses (Piersma et al. 1999, Landys-Ciannelli et al. 2003). Here, we analyze body size, fat loads, organ masses, and molt of 37 godwits from New Zealand (35 of which were about to migrate north) that were recovered from a poacher. Godwits are one of the most sexually

size-dimorphic waders, so we were interested in determining whether relative tissue deposition differs between males and females. We also compare structural characteristics and fuel deposition with a smaller subspecies of godwit, *taymyrensis* (Engelmoer and Roselaar 1998), that migrates from Africa to coastal areas and nearby meadows in The Netherlands en route to central Siberia (see Drent and Piersma 1990, Piersma and Jukema 1990). Because flight lengths may differ between these subspecies, we aim to determine how differences in body size and energy demand affect the relative fuel deposition strategies in the two groups.

This subspecific comparison is not strictly of equivalent stages in the migration, because the *baueri* sample was fueling for the first flight of a migration whereas the *taymyrensis* sample was fueling for their last flight. If tissue deposition was substantially different between migratory stages, then the comparison would be invalid. In general terms, we believe the comparison is appropriate: both populations are fueling for true long-distance flights (>4,500 km), both populations undergo some contour feather molt, and we selected only birds of equivalent fueling level to the *baueri* from the larger *taymyrensis* data set. The main problem would be if *taymyrensis* heading for the breeding grounds deposited large nutrient reserves for use on the breeding grounds, but the limited information available suggests this is not a major problem. Reproduction of a variety of Arctic waders has been shown to involve only local nutrients rather than stored nutrients (Klaassen et

al. 2001), and long-distance migrating waders generally retain some fat even after a flight of many thousands of kilometers (e.g. Battley et al. 2000).

#### METHODS

On 7 March 1992, 37 godwits were recovered near Great Exhibition Bay, Northland, New Zealand (34°45'S, 173°08'E), having been shot illegally (probably that same day; R. J. Pierce pers. comm.). That is within a day or two of when godwits in New Zealand start their northward migration (Battley 1997; P. F. Battley unpubl. data). Carcasses were stored at -20°C and transported frozen to The Netherlands where they were analyzed in August 1994 (4 godwits) and January 1996 (33 godwits). Birds were thawed and weighed to the nearest gram. The following external dimensions were measured in most birds: wing length (flattened and straightened, accuracy  $\pm 1$  mm), bill length (exposed culmen,  $\pm 0.1$  mm), total head length ( $\pm 0.1$  mm), tarsus length ( $\pm 0.1$  mm), and tarsus plus mid-toe length ( $\pm 1$  mm). Breeding plumage development was scored on a scale from 1 to 7, and intensity of breast molt from 0 to 3 (Piersma and Jukema 1993). No adults were molting flight feathers; one first-year had a primary molt score of 34. Birds were aged on the basis of plumage characteristics.

In body composition analyses, we followed the methods of Landys-Ciannelli et al. (2003); we determined lean tissue, water content, and fat mass for most major organs in the body. Note that the "remaining carcass" after other organs had been removed is included in the "exercise organs," because its lean tissue included skeletal muscle. Organ values were summed to give total body contents. All organ values presented are fat-free dry mass. The lean dry "remaining carcass" was also incinerated at 520–550°C for an hour and weighed to the nearest tenth of a gram to estimate skeletal ash mass. Note that because the lower halves of tibia and feet remained attached to the skin, those pieces of bone are not included in the incinerated portion. Because the New Zealand samples appeared to have dehydrated during storage (average water content of lean tissues was 64%, well below the normal range of 68–70%; Piersma and Van Brederode 1990), total body mass at death was estimated by adjusting lean tissue data to 70%

water content (the average water content of fat-free tissue of perfectly fresh carcasses from The Netherlands; T. Piersma unpubl. data). The "corrected" body masses are used in analyses.

Sex was determined from the gonads. In males, the length and width of the left testis was measured ( $\pm 0.1$  mm), and testis volume was calculated as width-squared  $\times$  length  $\times 0.785$  ( $\pi/4$ , to account for a cylindrical rather than a rectangular shape).

To supplement the external size measurements, several internal measurements of skeletal size were made ( $\pm 0.1$  mm) during dissection. Four sternum measurements that have traditionally been used to estimate standard muscle volume were taken (Piersma et al. 1984; measures *a–d* in Table 1). We also made two additional measurements of the sternum: its ventral edge (*e*) and the "diagonal sternum," from the distal notch of the coracoid to the posterior midpoint of the keel (*f*). To investigate sexual size differences with cubic rather than linear variables (Piersma 1984, Summers 1988, van der Meer and Piersma 1994), we calculated two volume indices from the external and internal measurements. The external volume index (cubic centimeter) represents the product of bill, wing, and tarsus-plus-toe length; the internal volume index (cubic centimeter) represents the square root of the product of the six internal linear dimensions (*a–f*).

Comparative data for the subspecies *taymyrensis* in The Netherlands (53°N, 05°E) were obtained using the same dissection methods as for the New Zealand birds. Landys-Ciannelli et al. (2003) provide sample descriptions. Because fueling birds deposit lean tissue as well as fat (Lindström and Piersma 1993), it was important to select *taymyrensis* of equivalent fueling level to that of the small *baueri* sample. We arbitrarily selected the fattest third of the sample, which resulted in samples with comparable levels of variation within the subspecies (e.g. fat load coefficient of variation of 9.2% for *taymyrensis* and 7.6% for *baueri*).

We used the body composition data for the *taymyrensis* subspecies to estimate the cost of travel (per kilometer) during migration, and then used that cost estimate to calculate potential flight ranges for similar-sized *baueri*. We assumed that *taymyrensis* from The Netherlands would fly 4,600 km from western Europe to Taimyr Peninsula, Russia, and that birds did not exhaust their fat deposits, but

TABLE 1. Age and sex differences in external and internal linear dimensions, body mass, and overall composition of Bar-tailed Godwits from New Zealand. External volume index is based on the product of bill, wing, and tarsus plus toe lengths; internal volume index is the square-root of the product of six internal linear dimensions (*a-f*). For tarsus length, *n* = 22 for adult males and *n* = 7 for adult females. Sex differences are from two-tailed *t*-tests comparing adults; significant values are given in bold.

Variable (unit)	First-year males ( <i>n</i> = 2)			Adult males ( <i>n</i> = 26)			Adult females ( <i>n</i> = 9)			Sex difference?	
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	<i>P</i>
Body mass (g wet measured)	265-284	445.8	32.2	377-503	553.6	53.7	487-624	553.6	53.7	487-624	<0.001
Body mass (g wet estimated)	291-296	502.8	37.0	442-565	617.6	58.9	549-721	617.6	58.9	549-721	<0.001
Total fat mass (g dry)	15.8-26.6	190.5	21.3	147.6-236.5	231.6	28.3	197.0-279.5	231.6	28.3	197.0-279.5	<0.01
Total fat-free dry mass (g dry)	81.1-82.6	93.7	8.4	76.0-108.4	115.8	9.6	105.7-132.4	115.8	9.6	105.7-132.4	<0.001
Skeletal ash mass (g dry)	7.8-7.9	7.9	0.5	6.9-8.8	9.6	2.2	6.2-12.2	9.6	2.2	6.2-12.2	0.158
Fat load (% of total mass)	5.4-8.9	37.9	3.2	30.3-44.9	37.4	1.4	35.9-39.3	37.4	1.4	35.9-39.3	0.551
Total head length (mm)	129.7-131.6	121.3	6.7	108.8-132.9	149.2	9.1	139.8-165.0	149.2	9.1	139.8-165.0	<0.001
Tarsus length (mm)	54.4-54.7	55.0	2.6	49.8-56.7	60.9	2.9	56.7-65.9	60.9	2.9	56.7-65.9	<0.01
External volume index (cm <sup>3</sup> )	1,866-1,990	1,737.7	213.3	1333-2105	2,694.0	281.0	2,360-3,153	2,694.0	281.0	2,360-3,153	<0.001
Bill length (mm)	91.6-93.3	83.5	6.2	71.1-97.4	109.4	7.3	101.7-122.2	109.4	7.3	101.7-122.2	<0.001
Wing length (mm)	219-227	229.4	6.2	217-240	245.7	5.0	240-253	245.7	5.0	240-253	<0.001
Tarsus + toe length (mm)	93-94	90.5	4.9	76-98	100.0	2.8	95-103	100.0	2.8	95-103	<0.001
Internal volume index (cm <sup>3</sup> )	53.2-53.8	52.1	4.0	43.3-61.7	64.6	6.8	56.1-74.9	64.6	6.8	56.1-74.9	<0.001
<i>a</i> (mm)	51.4-52.4	52.1	1.7	48.1-55.2	56.3	2.5	52.4-59.5	56.3	2.5	52.4-59.5	<0.001
<i>b</i> (mm)	23.8-24.0	24.1	0.8	23.0-25.7	26.1	0.9	24.7-27.6	26.1	0.9	24.7-27.6	<0.001
<i>c</i> (mm)	33.8-34.2	33.0	1.3	31.3-36.9	34.8	1.1	33.9-37.5	34.8	1.1	33.9-37.5	<0.001
<i>d</i> (mm)	13.8-14.1	13.5	0.6	12.7-14.8	14.5	0.9	13.1-15.5	14.5	0.9	13.1-15.5	<0.045
<i>e</i> (mm)	60.9-61.2	61.4	1.8	56.2-64.4	66.0	2.3	62.6-69.1	66.0	2.3	62.6-69.1	<0.001
<i>f</i> (mm)	78.8-80.7	79.0	2.6	72.1-85.3	85.1	2.8	80.8-89.0	85.1	2.8	80.8-89.0	<0.001
Testis volume (mm <sup>3</sup> )	1.4-4.7	47.2	23.9	12.6-100.5	-	-	-	-	-	-	-

retained ~7% at the end of the flight. Total energy was calculated as being derived from fat (95% of the total, at 39.8 kJ g<sup>-1</sup>) and protein (5% of the total, at 17.5 kJ g<sup>-1</sup>; Battley et al. 2001). The cost of travel (kJ km<sup>-1</sup>) was the total energy used divided by flight length (4,600 km), which could then be used to predict flight range for similar-sized *baueri*, with the same assumptions about body composition changes. This requires flight costs to be similar between the two groups, despite *baueri* being heavier (e.g. Kvist et al. 2001 demonstrated that muscle mechanical efficiency in Red Knots [*Calidris canutus*] increased with body mass, so flight ranges did not decrease greatly with fuel load). Calculations were made for birds of three sizes: small (bill length = 80 mm), medium (bill length = 90 mm), and large (bill length = 100 mm). Although these sizes do not encompass female *baueri*, they cover the range of overlap between *baueri* and *taymyrensis*. These calculations are complicated by waders' selective use of favorable winds: radiotagged godwits flying from Europe to Taimyr departed on days with good winds, which resulted in predicted total flight time being 27% lower than on days when no wind assistance was available (Green and Piersma 2003). If godwits depart with fuel loads adjusted to the expectation of such wind assistance, then the travel cost calculated for *taymyrensis* will not represent the real flight cost that birds would experience in a neutral wind environment. We therefore also calculated the flight costs for *taymyrensis* by assuming that the "air distance" flown was only 3,358 km (4,600 km × 0.73). For comparison, flight ranges were calculated from Davidson (1984), with ground speeds of 96 km h<sup>-1</sup> with wind assistance (as recorded by Green 2003 for godwits migrating over Sweden) and 66 km h<sup>-1</sup> without wind assistance (Green 2003).

## RESULTS

*Sexual and age-related differences.*—Most of the New Zealand godwits were males (26 adult and 2 first-year); only 9 were adult females. Adult females were, on average, significantly larger and heavier than adult males in all measures (Table 1), though of all the individual external and internal size measurements, only bill length and total head length did not overlap between the sexes (bill lengths: male, <98 mm;

female, >101 mm; total head lengths: male, <133 mm; female, >139 mm). Females were larger in both internal and external volume indices, though only the external volume index showed no overlap between the sexes (Table 1). There was a close fit between internal and external volume indices (Fig. 1), and the homogeneous distribution of data points around the linear regression line suggests that size differences between males and females reflect opposite ends of a single axis of size variation.

Adults were all very heavy, with 148–248 g of fat, representing fat loads of 30–45% of total body mass (Table 1). Females had larger internal organs than adult males (Table 2), with significant differences in all exercise organs, the liver, and kidneys. The two first-year birds were similar in size to the adult males but were considerably lighter because they were not preparing to migrate (fat loads of 5.4% and 8.9%; Table 1).

Breeding plumage scores were low for females (seven birds had no discernable breeding plumage; two birds had traces only) and moderate for adult males (mean plumage

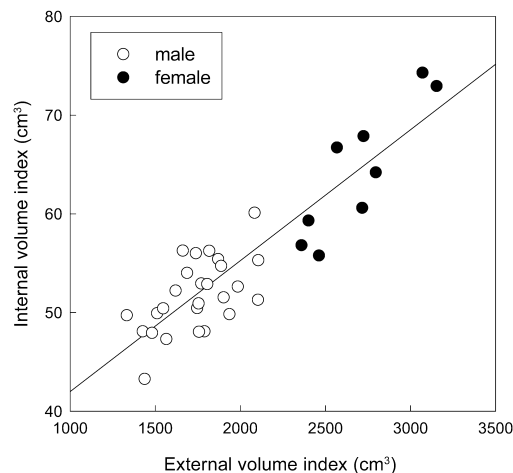


FIG. 1. Relationship between external and internal volume indices of adult male and female Bar-tailed Godwits from New Zealand. Overall regression line is indicated (internal volume = 28.7 + 0.013 × external volume,  $r^2 = 0.806$ ). External volume index is the product of bill, wing, and tarsus-plus-toe length; whereas the internal volume index (cm<sup>3</sup>) is the square-root of the product of six internal linear dimensions.

TABLE 2. Age and sex differences in feather and dry organ masses and the size or mass of other parts of Bar-tailed Godwits from New Zealand. Values are fat-free dry masses (g), except for the salt glands and feathers (dry mass, g). Sex-differences are from two-tailed Student's *t*-tests comparing adults; significant values are given in bold.

Variable	First-year males ( <i>n</i> = 2)			Adult males ( <i>n</i> = 26)			Adult females ( <i>n</i> = 9)			Difference?	
	Range	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	<i>P</i>
Flight feathers	2.40-3.10	3.72	0.44	2.60-4.60	4.70	0.33	4.20-5.30	4.70	0.33	4.20-5.30	<0.001
Contour feathers	11.00-11.20	20.00	2.10	16.30-24.00	23.75	2.06	21.60-27.20	23.75	2.06	21.60-27.20	<0.001
Skin	11.20-12.00	15.91	5.39	8.10-26.90	18.01	5.97	12.10-30.00	18.01	5.97	12.10-30.00	0.368
<b>Exercise organs</b>											
Supracoracoideus	1.28-1.46	1.61	0.13	1.38-1.85	2.09	0.25	1.72-2.50	2.09	0.25	1.72-2.50	<0.001
Pectoralis	10.50-11.80	14.66	1.48	12.45-18.88	17.85	1.89	15.44-21.60	17.85	1.89	15.44-21.60	<0.001
Leg muscles	2.95-3.15	2.94	0.29	2.43-3.41	4.26	0.48	3.47-5.07	4.26	0.48	3.47-5.07	<0.001
Heart	0.84-0.87	1.00	0.14	0.72-1.38	1.24	0.19	1.00-1.51	1.24	0.19	1.00-1.51	0.004
Lungs	0.71-0.92	1.10	0.25	0.50-1.64	1.38	0.27	0.96-1.92	1.38	0.27	0.96-1.92	0.016
Remaining carcass	25.82-28.47	29.27	2.83	23.48-34.66	38.03	2.81	33.91-42.42	38.03	2.81	33.91-42.42	<0.001
<b>Nutritional organs</b>											
Stomach	1.96-2.84	2.11	0.45	1.22-3.62	2.49	0.53	1.50-3.20	2.49	0.53	1.50-3.20	0.079
Intestine	5.06-6.12	3.46	1.07	1.66-5.17	4.04	1.73	2.06-7.74	4.04	1.73	2.06-7.74	0.366
Liver	2.59-3.17	3.08	0.34	2.40-3.55	3.87	0.84	2.22-5.26	3.87	0.84	2.22-5.26	0.023
Kidneys	0.93-1.13	0.95	0.12	0.70-1.18	1.25	0.18	1.04-1.57	1.25	0.18	1.04-1.57	0.001
Salt glands	0.11-0.12	0.12	0.03	0.06-0.19	0.13	0.03	0.09-0.17	0.13	0.03	0.09-0.17	0.197
Intestine length (cm)	98-107	82.80	7.90	59-95	86.10	5.60	75-92	86.10	5.60	75-92	0.181

score = 3.5, range = 2–6). The first-years had no breeding plumage. None of the females showed visible body molt, whereas 16 of the 26 adult males and both the first-years were in light to moderate molt.

*Body composition and body size.*—Larger birds were heavier, fatter, and had more lean tissue (Fig. 2A–C). As with the structural size variables, females and males represented two ends of the same axis, with females occupying the larger and fatter end. Fat load did not systematically change with size (Fig. 2D), though males were more variable than females (admittedly with a larger sample size).

To assess how organs varied in relation to body size and migratory preparation, we

regressed organ fat-free dry mass against bill length (as a structural size measure) and fat mass (a measure of the relative migratory preparation). Mass of the flight muscles, leg muscles, remaining carcass, stomach, and kidneys at least partly reflected body size, whereas the flight muscles and lungs were also correlated with fat mass, implying premigratory hypertrophy (Table 3).

The plumage scores of males did not reflect their body condition. If anything, fatter birds had lower plumage scores than less fat birds (regression of plumage against fat mass and bill length: fat mass  $t = -2.357$ ,  $P = 0.027$ ). Within the males, however, two subgroups could be distinguished according to whether birds were

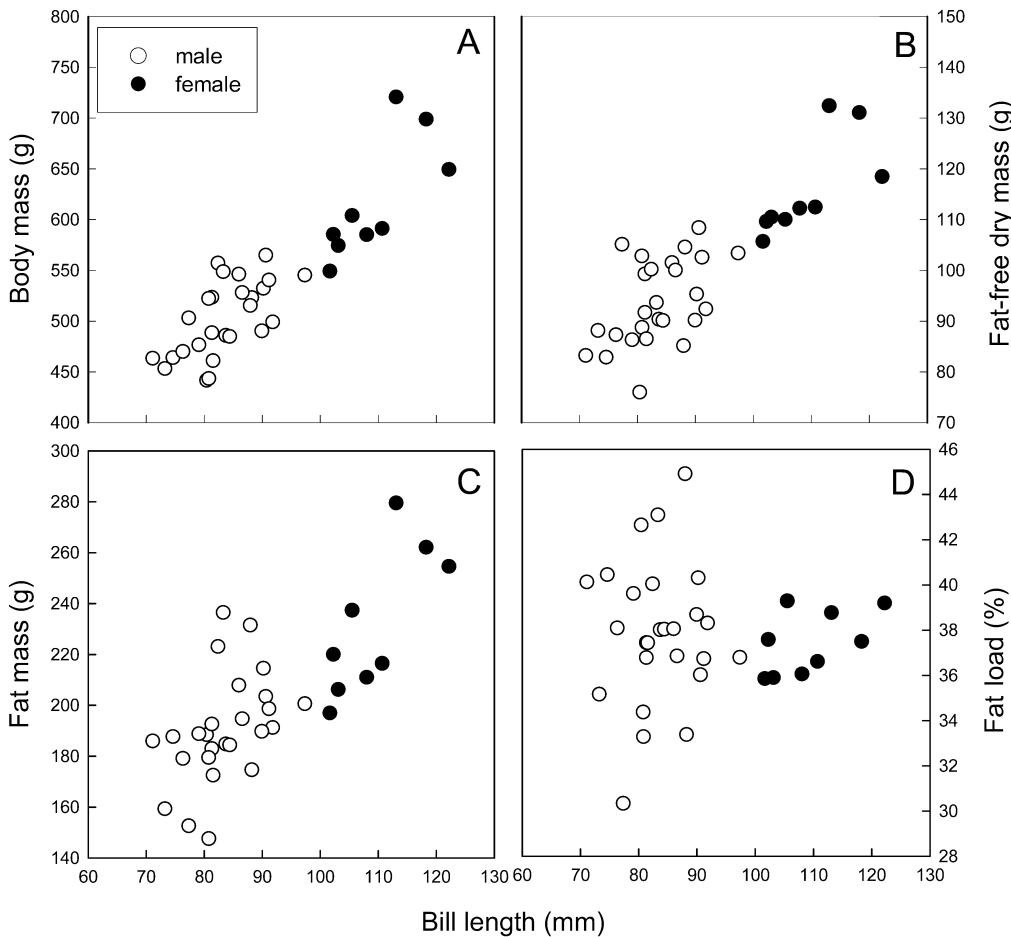


FIG. 2. Overall body composition (body mass, fat-free dry mass, fat mass, and fat load) in relation to bill length for adult Bar-tailed Godwits collected before their northward departure from New Zealand.

TABLE 3. Size- and fueling-related variation of organ lean mass in Bar-tailed Godwits. Results are from least-squares regressions of organ mass on bill length (size) and total fat mass. Slopes are positive if the standardized coefficient was >0.1, and negative if it was less than -0.1. Significant values are given in bold.

Organ	Size		Fat mass		<i>r</i> <sup>2</sup>
	Slope	<i>P</i>	Slope	<i>P</i>	
Supracoracoideus	+	<b>0.000</b>	+	<b>0.025</b>	0.762
Pectoralis	+	<b>0.000</b>	+	<b>0.011</b>	0.736
Leg muscles	+	<b>0.000</b>	0	0.951	0.706
Heart	+	0.058	+	0.128	0.440
Lungs	+	0.564	+	<b>0.004</b>	0.477
Remaining carcass	+	<b>0.000</b>	0	0.818	0.658
Stomach	+	<b>0.026</b>	-	0.176	0.152
Intestine	+	0.175	0	0.739	0.088
Liver	+	0.113	0	0.886	0.179
Kidneys	+	<b>0.002</b>	0	0.940	0.444
Salt glands	+	0.154	-	0.452	0.047

molting or not. Sixteen of the 26 adult males were not molting when they were killed (Table 4). Those birds had lower breeding plumage scores than the molting birds (Fig. 3), but they were heavier and fatter than molting birds and had larger testes, longer wings, and significantly smaller intestines and salt glands (Table 4). With molt status (as well as size) taken into account, there was no relationship between plumage score and fat mass (ANCOVA, *P* > 0.05).

*Comparisons between New Zealand and European godwits.*—In terms of general body size (fat-free dry mass as a function of bill length), the sexes of the two subspecies scaled similarly with body size (ANCOVA of fat-free dry mass against group [subspecies and sex] with bill length as covariate: group: *F* = 1.59, *df* = 3 and 65, *P* > 0.05; bill length: *F* = 14.40, *df* = 1 and 65, *P* < 0.001; *r*<sup>2</sup> = 0.69; Fig. 4). In terms of fuel deposition, however, *baueri* are much fatter than *taymyrensis* for their size. Between individuals, the two subspecies deposited fat similarly with size (slopes of the relationship between fat mass and bill length did not differ significantly: 1.67 ± 0.26 [mean ± SE] for *baueri* and 1.25 ± 0.26 for *taymyrensis*; Fig. 5A). In terms of the total amount of fat deposited, however, *baueri* were much fatter (intercepts of fat mass vs. bill length: 51.0 ± 23.4 g and 7.16 ± 22.8 g, respectively; note, however, that intercepts overlapped with the 95% confidence intervals). For both subspecies, there was no difference in fat load between small and large birds (or males and females: fat load vs.

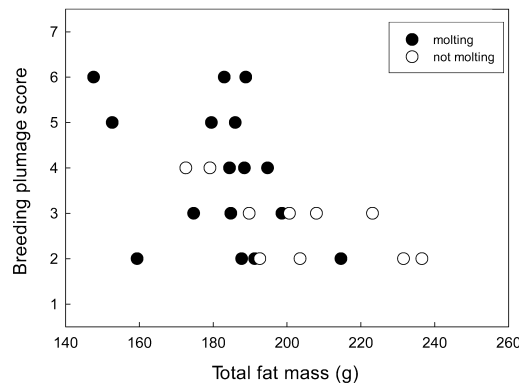


FIG. 3. Breeding plumage score as a function of total fat mass and molt status in adult male Bar-tailed Godwits from New Zealand. Plumage score is on a scale from 1 (complete nonbreeding plumage) to 7 (complete breeding plumage).

size slopes of -0.004 and 0.024, respectively; Fig. 5B), but again *baueri* had significantly higher fat loads (average of 37.8 ± 2.9% [mean ± SD] and 28.4 ± 2.6%, respectively). Across the range of overlap in body size, *baueri* deposited ~1.7× as much fat for their size as *taymyrensis*.

*Flight ranges.*—Travel costs calculated for *taymyrensis* ranged from 0.816 to 1.382 kJ km<sup>-1</sup>, depending on body size and whether wind assistance was assumed (Table 5). Those costs translate to predicted flight ranges for *baueri*

TABLE 4. Differences in condition (mass- or migration-related measures), body size, and organ mass of molting and nonmolting male Bar-tailed Godwits. Organ values are fat-free dry masses, except for the salt glands (dry mass). The larger mean value is given in bold. Differences between the categories for condition and size variables were tested with two-sided Student's *t*-tests. Differences in organ masses were tested in general linear models that related organ mass to fat mass and molt status; *P*-values refer to the molt effect. Significant values are given in bold.

Variable	Molting males ( <i>n</i> = 16)		Nonmolting males ( <i>n</i> = 10)		Difference
	Mean	SD	Mean	SD	<i>P</i>
<b>Condition</b>					
Body mass (g)	490.6	32.3	<b>522.3</b>	37.1	<b>0.040</b>
Total fat-free dry mass (g)	92.52	8.61	<b>95.56</b>	8.08	0.373
Total fat mass (g)	182.25	17.03	<b>203.73</b>	21.47	<b>0.016</b>
Fat load (%)	37.20	3.23	<b>39.00</b>	2.90	0.164
Testis volume (mm <sup>3</sup> )	38.14	17.89	<b>61.62</b>	25.91	<b>0.024</b>
Breeding plumage <sup>a</sup>	3.9	1.5	2.8	0.8	<b>0.025</b>
<b>Size</b>					
Wing length (mm)	227.4	6.8	<b>232.5</b>	3.8	<b>0.023</b>
Bill length (mm)	82.16	6.33	<b>85.66</b>	6.01	0.172
Tarsus (mm)	54.92	3.19	<b>55.07</b>	2.03	0.898
External volume index (cm <sup>3</sup> )	1702.1	239.5	<b>1794.8</b>	157.6	0.246
Internal volume index (cm <sup>3</sup> )	51.20	4.70	<b>53.65</b>	2.11	0.084
<b>Exercise organs</b>					
Supracoracoideus <sup>b</sup>	1.576	0.134	<b>1.652</b>	0.105	0.745
Pectoralis <sup>b</sup>	14.349	1.162	<b>15.147</b>	1.849	0.924
Leg muscles	<b>2.993</b>	0.305	2.862	0.254	0.200
Heart	0.969	0.110	<b>1.038</b>	0.176	0.684
Lungs <sup>b</sup>	1.073	0.271	<b>1.132</b>	0.211	0.271
Remaining carcass	28.615	3.252	<b>30.313</b>	1.630	0.226
<b>Nutritional organs</b>					
Stomach	<b>2.218</b>	0.443	1.940	0.439	0.341
Intestine	<b>3.773</b>	0.906	2.947	1.167	<b>0.022</b>
Liver	<b>3.157</b>	0.354	2.964	0.301	0.218
Kidneys	0.941	0.124	<b>0.972</b>	0.122	0.730
Salt glands	<b>0.129</b>	0.024	0.101	0.024	<b>0.040</b>

<sup>a</sup>Breeding plumage development was scored on a scale from 1–7.

<sup>b</sup>Also significantly related to fat mass.

from New Zealand of 8,200–8,600 km with wind assistance, and 6,000–6,300 km without wind assistance assumed (Table 5). A conventional prediction method predicted flight ranges for *baueri* of 10,900–11,400 km with tailwinds, and 7,500–7,900 km without wind assistance (Table 5).

#### DISCUSSION

*Fat loads and flight lengths.*—The godwits in the New Zealand sample were probably very close

to migrating. The collection date of 7 March is at the start of the known departure period in New Zealand (8–27 March on Farewell Spit in 1994 [Battley 1997]; second week of March to the start of April at the Manawatu Estuary; from 9 March 2004 and 10 March 2005 at the Firth of Thames [P. F. Battley unpubl. data]), and the sample includes the heaviest godwits on record. Fat loads of most adults were between 35% and 40%, with three birds at 43–45%. Such fat loads are typical of shorebirds about to embark on migratory flights, though they

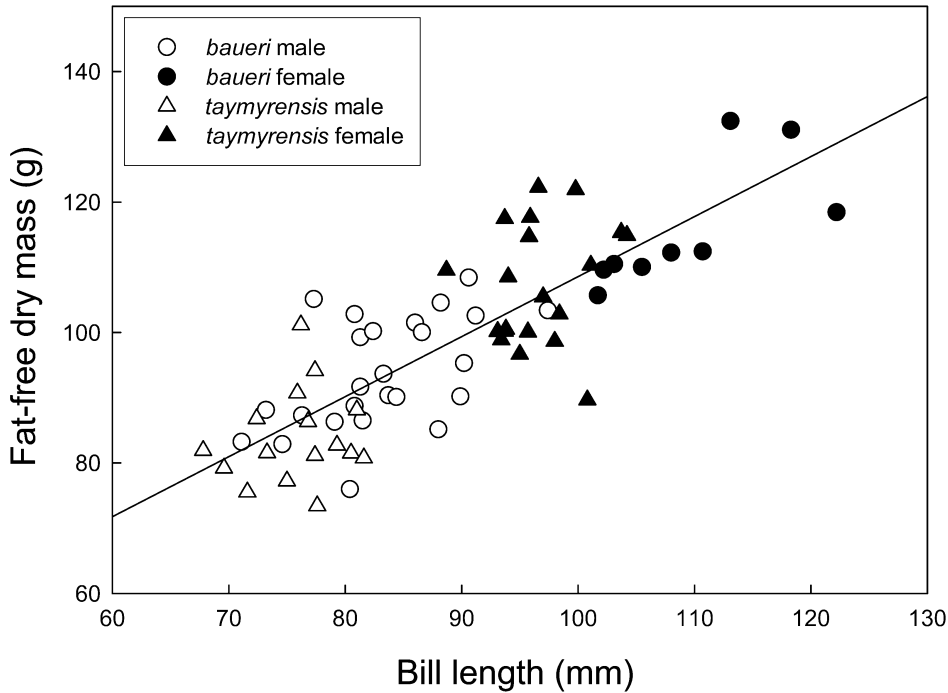


FIG. 4. Fat-free dry mass in relation to bill length for two subspecies of Bar-tailed Godwit. The linear regression is described by fat-free dry mass = 16.590 + 0.920 × bill length ( $t = 11.804$ ,  $P < 0.001$ ,  $r^2 = 0.672$ ).

TABLE 5. Estimated energy use and travel costs for Bar-tailed Godwits (*Limosa lapponica taymyrensis*) flying 4,600 km from the Wadden Sea to Siberia, and predicted flight ranges for subspecies *L. l. baueri* departing from New Zealand based on estimated travel costs or using the method of Davidson (1984). Predictions are made for birds of three body sizes: small (bill length = 80 mm), medium (bill length = 90 mm), and large (bill length = 100 mm). See text for more details.

Body size	<i>L. l. taymyrensis</i>			<i>L. l. baueri</i>				
	Total energy (kJ)	Travel cost <sup>a</sup>		Total energy <sup>b</sup> (kJ)	Predicted range		Davidson <sup>c</sup>	
Wind assisted (kJ km <sup>-1</sup> )		No wind (kJ km <sup>-1</sup> )	Wind assisted (km)		No wind (km)	Wind assisted (km)	No wind (km)	
Small	3,752.8	0.816	1.115	6,994.9	8,574	6,259	10,875	7,477
Medium	4,203.1	0.914	1.249	7,626.8	8,347	6,093	11,157	7,671
Large	4,653.3	1.102	1.382	8,258.8	8,164	5,960	11,424	7,854

<sup>a</sup> For travel cost estimates for *taymyrensis*, wind assistance of 27% was assumed, so that the effective flight length became 3,358 km.

<sup>b</sup> Departure body masses of 487.2, 531.5, and 575.8 g and arrival masses of 249.5, 272.3, and 295.1 g, respectively, with 5% of the energy derived from protein.

<sup>c</sup> Wind assistance was assumed to give a flight (ground) speed of 96 km h<sup>-1</sup>, compared with 66 km h<sup>-1</sup> without any assistance.

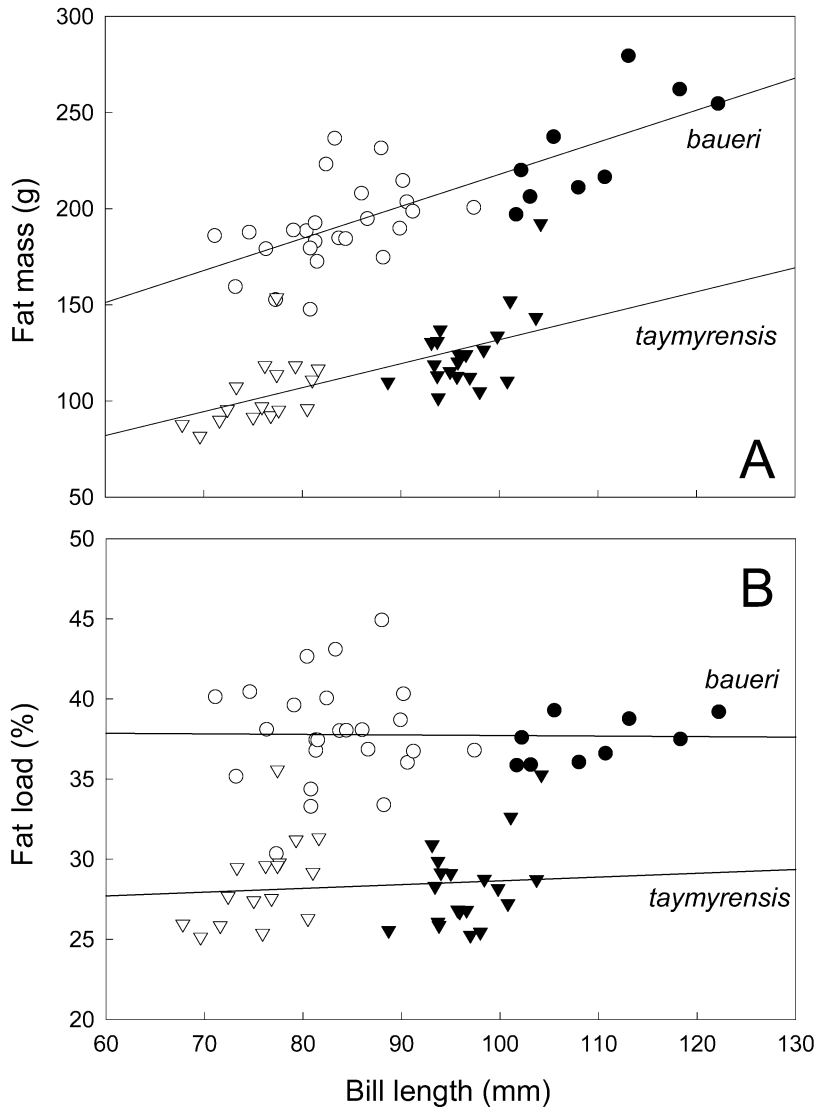


FIG. 5. Differences in total fat mass (A) and fat load (B) in relation to bill length in two subspecies of Bar-tailed Godwit. Fat mass–bill relationships are described by regression lines for *baueri*: fat mass =  $50.986 + 1.668 \times \text{bill length}$  ( $t = 6.501$ ,  $P < 0.001$ ,  $r^2 = 0.569$ ); for *taymyrensis*: fat mass =  $7.160 + 1.247 \times \text{bill length}$  ( $t = 4.819$ ,  $P < 0.001$ ,  $r^2 = 0.406$ ). Fat load–bill relationships are described by regression lines for *baueri*: fat load =  $38.075 - 0.004 \times \text{bill length}$  ( $t = -0.095$ ,  $P = 0.925$ ); for *taymyrensis*: fat load =  $26.276 + 0.024 \times \text{bill length}$  ( $t = 0.595$ ,  $P < 0.556$ ).

are not exceptional (Jehl 1997). The highest fat loads known in birds are from juvenile male godwits migrating south from Alaska (51–58%; Piersma and Gill 1998). Those extreme fat loads, however, may not be representative of all godwits migrating south from Alaska, because the juveniles had not completed growing and

consequently were small (bill, wing, and tarsus lengths were all significantly shorter than in New Zealand adult males;  $P < 0.01$ ) and comparatively light. Body masses and fat-free dry masses were much lower in the Alaska sample (body mass:  $366.9 \pm 26.7$  g vs.  $502.8 \pm 37.0$  g; free-fat dry mass:  $49.9 \pm 3.5$  g vs.  $93.7 \pm 8.4$  g;  $P <$

0.001 for both). As a result, fat loads (calculated as a percentage of total body mass) were higher in Alaska ( $54.8 \pm 2.8\%$  vs.  $37.9 \pm 3.2\%$ ;  $P < 0.001$ ), despite fat masses being similar ( $201.4 \pm 20.4$  g in Alaska,  $190.5 \pm 21.3$  g in New Zealand,  $t$ -test,  $P > 0.05$ ). The female godwits examined here, however, are the heaviest known (McCaffery and Gill 2001). That is partly because of body size—*baueri* is the largest subspecies of godwits, and females are larger than males—but the fat content of the New Zealand females was also very high (197–280 g).

The high fat content of *baueri* is reinforced by comparison with *taymyrensis* in The Netherlands (Fig. 5): birds in New Zealand deposited 75–85 g more fat for their size. This difference is not a result of different scaling functions with size, because lean tissue in the two subspecies appears to be a fairly uniform function with size (Fig. 4). Instead, the fuel load difference must relate to the length or costs of the upcoming migration.

Calculated travel costs for *taymyrensis* ranged from 0.706 to 1.150 kJ km<sup>-1</sup> if birds received the assumed wind assistance, and from 0.967 to 1.575 kJ km<sup>-1</sup> if they did not (Table 5). Those costs are higher than the equivalent value for Great Knots (*Calidris tenuirostris*) migrating from northwest Australia to China (3,644 kJ per 5,420 km = 0.67 kJ km<sup>-1</sup>; data from Battley et al. 2001). The difference in travel cost results from the heavier godwits' higher flight costs. The predicted average cost of flight for the three size-groups of *taymyrensis* ranged from 14.4 to 17.9 W (from equation 6 of Masman and Klaassen 1987); for Great Knots, the cost was 11.4 W. The ratio of travel cost to flight cost, however, was fairly similar for the two species (0.057–0.062 for the godwits; 0.053 for the Great Knots).

Predicted flight ranges for *baueri* from New Zealand ranged from 8,200 to 8,600 km under the assumption of wind assistance, and from 6,000 to 6,300 km with no wind assumed (Table 5). A conventional prediction method (Davidson 1984) predicted flight ranges for *baueri* of 10,900–11,400 km with tailwinds (Table 5). Because Davidson's (1984) method treats mass loss as being only loss of fat, it will overestimate the energy used. The results suggest that predictions based on the travel costs of *taymyrensis* are not unrealistic.

Those flight lengths would be sufficient to allow godwits departing from northern New

Zealand to fly beyond northern Australia and Irian Jaya (3,800–4,500 km) to the Philippines (7,200 km) or potentially to Japan (8,700 km) or South Korea (9,100 km). For the longer flight ranges to be realistic, New Zealand godwits would have to encounter wind assistance equivalent to that of the European birds, or the European birds retain substantial amounts of fat after migration (causing us to have overestimated energy use during migration). For the first part of the migration from New Zealand, godwits are often able to "ride" high-pressure systems situated over the Tasman Sea and probably gain wind assistance as far as Australia (Battley 1997; A. Riegen pers. comm.). Farther north, a predominantly easterly windflow of approximately 20–30 km h<sup>-1</sup> is present at high altitudes between Papua New Guinea and Irian Jaya and the Philippines in March and April, changing to predominantly westerly winds between there and Korea and Japan (Chin and Lai 1974). Substantial wind assistance is likely for much of the northward flight from New Zealand.

Count data from eastern Asia do not reveal whether direct flights from New Zealand occur. In the coastal Yangtze region of China, Tang and Wang (1995) recorded godwits caught by hunters as early as 25–31 March, but numbers peaked in the second or third weeks of April. In South Korea, substantial numbers have been recorded at the start of April (e.g. 600 around 1 April 2003 at Suncheon on the south coast; M. Sutherland via N. Moores pers. comm.), but peak numbers generally occur in mid-April (Barter 2003; N. Moores pers. comm.). Color-flagged birds from New Zealand have been seen in Japan as early as 28 March, 1 April, and 6 April (A. Riegen pers. comm.). These dates seem too late for direct flights of birds that leave New Zealand in March, because the predicted flight time from New Zealand to the Yellow Sea would be ~95 h if wind assistance is assumed. However, comprehensive counts have not been made in March to rule out the possibility of earlier arrivals, and it is possible that some birds make direct flights to eastern Asia from New Zealand.

If stopovers are made, the flight ranges predicted from body composition analyses suggest that the destinations are likely to be farther north than Australia or Papua New Guinea and Irian Jaya. The Philippines would be a potential destination, and Dickinson et al. (1991) record that godwits "can be common on passage,"

and note their presence in January, February, March, and up to 5 May. Again, however, we do not know of any extensive shorebird surveys in southeastern Asia in mid- to late March. There is no evidence to back up the claim of Heather and Robertson (1996) that some birds may fly north across the Pacific.

*Organ dynamics during fueling.*—Substantial evidence has accumulated in recent years demonstrating that complex changes occur in the organs of migratory waders before migration (e.g. Piersma 1998, Piersma et al. 1999). In New Zealand godwits, size increases in certain exercise organs were evident from positive relationships between organ mass and fat mass. Unlike the Red Knots analyzed by Battley and Piersma (1997), this sample of godwits showed no evidence of substantial reductions in the digestive organs as fat mass increased. This is at odds with claims that long-distance migrants reduce the size of those organs before flight (Piersma et al. 1993, 1999; Battley and Piersma 1997; Piersma and Gill 1998). Possible explanations include reductions having already taken place or an absence of dramatic digestive organ changes because the species feeds predominantly on soft-bodied prey (e.g. Scheiffarth 2001).

The clearest demonstrations of digestive-organ reductions before migration have been found in the Red Knot, a species that feeds on hard-shelled prey and, consequently, has the heaviest relative stomach mass among the shorebirds (Battley and Piersma 2005). It is possible that digestive-organ reductions are less important in species with comparatively lighter guts. In a large sample of *taymyrensis* in The Netherlands, Landys-Ciannelli et al. (2003) documented a leveling-off of digestive-organ increases in well-fueled birds. Piersma et al. (1993) had earlier shown that gizzards of godwits fueling in The Netherlands were smaller just before departure than in the middle of a stopover, but also that stomach mass varied with diet (soft ragworms [*Nereis diversicolor*] vs. tipulid larvae [Diptera sp.], bivalves, and crabs). We re-analyzed those data, selecting just those males feeding on hard prey (which constituted most of the data;  $n = 30$ ) and dividing the staging period in May into three 10-day periods. Stomachs were heaviest in the middle of the stopover ( $F = 5.076$ ,  $df = 2$  and  $27$ ,  $P = 0.013$ ), reflecting an increase from arrival condition (Tukey's *post-hoc* test,  $P = 0.007$ ) and a subsequent decrease before departure ( $P =$

0.018). There were insufficient data to explore whether the same held for females or birds feeding on soft prey.

The largest organ reductions in migrating shorebirds were claimed by Piersma and Gill (1998), who showed that nine juvenile godwits on southward migration in Alaska had digestive organs only 52–71% of the mass of those of the adult New Zealand males analyzed here. Those ratios were much lower than the differences in body mass or exercise organs (0.82–0.88). Piersma and Gill (1998) concluded that the Alaska godwits had dramatically reduced their digestive organs before departure.

Because the juvenile godwits were not fully grown (bill, wing, and tarsus were 4–14% shorter in Alaska than New Zealand adult males;  $t$ -tests,  $P < 0.05$ ), it is also possible that their organs had not reached adult size. We re-analyzed the Alaskan and New Zealand data using ANCOVA to test whether fresh organ masses differed between the sites, first using external structural size measures (wing or bill lengths), then total fat-free dry mass of the body, as a covariate. Although analyses using size measures indicated significantly smaller digestive organs (gizzard, intestine, kidneys, and liver) in the Alaskan birds, the equivalent analyses with fat-free dry mass as the covariate found that only the liver was smaller. Instead, intestines and kidneys were related significantly to total lean mass. Flight muscles (supracoracoideus and pectoralis combined) varied with size or lean mass in all analyses, and were proportionately larger in Alaska if lean mass was used as the covariate. Together these results indicate that the juvenile birds in Alaska were structurally approaching adult size (hence the significant differences when size measures were used as the covariate) but were much smaller in organs and general body musculature (and had only half the lean mass of the New Zealand adult males). The differences in lean mass between the Alaskan and New Zealand birds (both of which nevertheless represent birds in departure condition) may represent incomplete soft-tissue growth as much as extensive breakdown of existing organs in the Alaska birds. This calls for further work on compositional changes in adult as well as juvenile godwits before departure from Alaska.

*Molt and departure schedules*—Consistent with other godwit subspecies (Piersma and Jukema

1993), New Zealand females had little discernable breeding plumage. Males had substantial breeding plumage, but there was no relationship between plumage and body condition. By contrast, godwits departing from Mauritania seem to have a strong relationship between molt status (plumage) and condition, because better-plumaged birds are heavier on arrival in The Netherlands, and therefore are able to continue molting (Piersma and Jukema 1993). The condition-dependent molt and fueling pattern found in *taymyrensis* may reflect the time-constrained departure and staging strategy of this subspecies (Scheiffarth et al. 2002), which has an unusually short departure span from Mauritania (10 days; Piersma et al. 1990). New Zealand birds migrate farther than Afro-Siberian birds, start migration more than a month earlier (early March rather than mid-April; Piersma et al. 1990, Battley 1997), and depart over a period of 3–4 weeks. Individuals in New Zealand may be less synchronized in their fueling than *taymyrensis* in Africa and Europe.

Ten of the 26 New Zealand adult males had no active body molt when they died. Suspension of body molt is often an indicator that birds are about to depart on migration (Zwarts et al. 1990). Consistent with this idea, the males in this sample that were not molting were heavier and fatter than the molting birds, with larger testes. However, they had lower breeding-plumage scores than those that were still molting. This is counter to expectation and suggests that birds in New Zealand may have different molting strategies, one in which males depart earlier with low breeding plumage scores and either undergo substantial molt on the staging grounds or breed with relatively little breeding plumage, or another in which birds perform most (or perhaps all) of their molt before departing slightly later from New Zealand. The difference in wing length between these groups suggests that the birds may come from different breeding populations, but the biometrics of godwits from eastern Siberia and Alaska are not sufficiently documented to test whether those putative differences in New Zealand correspond with regional differences on the breeding grounds (McCaffery and Gill 2001, P. S. Tomkovich pers. comm.). But if birds have different molting strategies, there is no reason to expect their migration strategies to be identical.

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