Body composition of Lesser Knots (*Calidris canutus rogersi*) preparing to take off on migration from northern New Zealand

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ABSTRACT

The body composition of ten adult and five juvenile Knots (*Calidris canutus rogersi*) in the migratory period from Northland, New Zealand, was studied. Basic physical measurements of all individuals are provided. Adults were heavier than juveniles, but showed a large variation in mass - some were at estimated departure mass while others apparently were only in the early stages of mass increase, allowing an investigation of changes during the "fattening" procedure. Changes in fat-free dry tissue (protein) of organs were complicated, with pectoralis and heart muscles increasing with total fat mass, while intestine and stomach mass decreased. This resulted in total fat-free dry tissue firstly increasing with fat mass, then levelling off or decreasing. This reallocation of protein is interpreted as being a method of freeing up muscle protein for redeposition in other organs during premigratory fuelling. Most fat was deposited subcutaneously, apparently in a linear fashion. In contrast, abdominal fat showed proportionately higher masses as total fat increased, while fat around other organs showed the reverse pattern. Adults were significantly larger than juveniles in ten organ comparisons, but only four of these were clearly related to migration. Organ sizes in *C. c. rogersi* were much smaller than in the European-wintering *C. c. islandica*, and slightly smaller than African-wintering *C. c. canutus*. Salt gland mass of *C. c. rogersi* in this sample from New Zealand was much larger than that known from European birds, which may reflect migratory preparation. Lean mass was estimated at around 109 g.

KEYWORDS: shorebirds; migration; physiology; *Calidris canutus*

INTRODUCTION

Long-distance migration, such as that undertaken by Lesser Knots (*Calidris canutus*) is a stressful process. Birds firstly must increase their net energy intake rate before departure to deposit enough nutrients for the flight ahead. Once aloft, they may face a flight of possibly 36 to 48 hours without feeding. They must maintain protein turnover during this 'starvation period' as well as use (and preferably not exceed) stored nutrient deposits for fuel.

Shorebirds have long been known to increase mass before migration (Pienkowski *et al.* 1979; Summers & Waltner 1978). However, not all of this increase is necessarily fat - birds often show substantial protein deposition (Lindström & Piersma 1993; Piersma 1990). There are other possible changes prior to migration, such as in stomach mass (Piersma *et al.* 1993), other organs (Piersma *et al.* 1996) and flight muscles (Davidson & Evans 1988; Evans *et al.* 1992).

Samples of birds taken at intervals before migration from a population will show the average changes in body composition over time. A sample from a single day can, however, be used to gain insight into the changes occurring before migration. Birds do not all fatten synchronously (Fig. 1), so a single sample will encounter birds at different stages of preparation for migration. Two scenarios are presented: Fig. 1A depicts the situation where birds' weight increases run parallel (see Piersma & Jukema 1990; Fig.6) for an example with Bar-tailed Godwits *Limosa lapponica*; similar data exist for European knots (Piersma & Prokosch, unpubl. data); Fig. 1b shows birds with considerable variation in rates of increase. Individuals are analysed according to fat mass rather than a sample analysed by date.

This is complicated by the fact that there can be structural variation among individuals (Piersma & Davidson 1991) which should be accounted for in analyses. If this is done, then the approach outlined above can roughly approximate a 'fattening' trajectory (the changes in mass and body composition over time) for an individual. In our analyses we treat fat mass as our indicator of migratory preparation.

Many migrant wader species moult into breeding plumage before migration (Piersma & Jukema 1993; Zwarts *et al.* 1990), so degree of breeding plumage will also be expected to reflect position along this trajectory (Fig. 1).

Besides assessing changes within a population, carcasses also give the opportunity to explore subspecific differences in body composition, which may reflect both wintering conditions and migratory demands. Lesser Knots are classic long-distance migrants, with five recognised subspecies wintering in discrete geographic regions (Piersma & Davidson 1992). They have been the focus of much in-depth study along the East Atlantic Flyway (e.g. Piersma 1994; Piersma *et al.* 1991).

Knots of the subspecies *C. c. rogersi* breed in the Far East of Siberia, probably in the Chukotka region, and winter in Australasia (Tomkovitch 1992; Piersma & Davidson 1992b). Birds migrating to New Zealand cover up to 14,000-15,000 km between the breeding and non-breeding areas, which is probably achieved in series of 3-4 large flights (A.C. Riegen, pers comm.). This makes them one of the longest-migrating knot subspecies. In addition, they are also smaller than the other well-
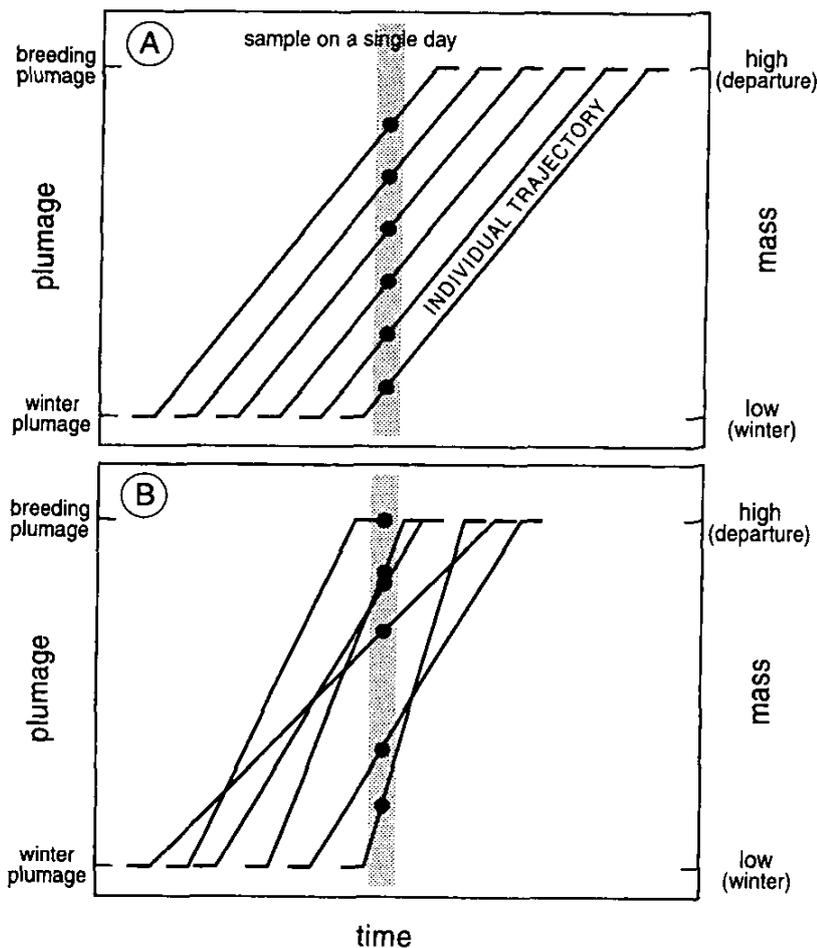
FIGURE 1 – Schematic representation of how a sample of birds on a single day can approximate the 'fattening' trajectory of a hypothetical individual. Time increases along the x-axis, mass and concomitant degree of breeding plumage along the y-axis. Each individual increases mass and breeding plumage over time. However, they do not initiate this synchronously. As a result, a sample on a single day (shaded box) will encounter birds at different stages along their respective trajectories. The upper panel shows a population with parallel trajectories. The lower panel illustrates a population with individual variation in trajectories. A larger fat mass will represent a "later" stage along the time axis for both situations, so fat mass and degree of breeding plumage can be used to infer changes over time.

studied subspecies (*C. c. islandica* and *C. c. canutus*). These factors make New Zealand-wintering knots ideal candidates for comparative studies with other populations.

Although information on pre-departure body composition of knots is available, the subspecies *C. c. rogersi*, which occurs in New Zealand, is smaller than other subspecies and so the published data may not be applicable. In New Zealand, Lesser Knots are the second most abundant species of Arctic waders. Annually, a nationwide total of 40,000 to 65,000 birds were counted in Ornithological Society of New Zealand wader surveys since 1983 (P.M. Sagar, pers. comm.). Arriving from September onwards, they depart mainly in March (P.F. Battley, unpubl. data).

In this study we obtained carcasses of Lesser Knots from northern New Zealand to investigate their body composition in the premigratory period. Our sample size, beyond our control, was small, so our ability to make strong conclusions will be limited. Nevertheless, opportunistic studies such as this will help to fill in the gaps in our knowledge about the physiology of migrant birds.

METHODS

Fifteen dead knots were recovered by Department of Conservation staff at Great Exhibition Bay, Northland (173°08'E, 35°45'S), on 7 March 1992. The birds were illegally shot by poachers, probably on the same day. They had probably been feeding on Houhora Harbour earlier that day (R.J. Pierce, pers. comm.). The birds were frozen and flown to the Netherlands Institute for Sea Research.

Subsequently, the birds were weighed and the following characteristics measured: bill length; total head length; tarsus + middle toe; wing (maximum chord, Evans 1986); wingspan (in some cases this was not possible due to primary moult). Body moult was scored on a scale of 0-3 (0 = no growing feathers on breast and belly tracts, 1 = a few growing feathers, 2 = many growing feathers (c. one quarter), 3 = very many growing feathers (one third to one half), see Piersma & Jukema 1993, Zwarts et al. 1990). The score of wing moult was calculated as the sum of moult scores for the ten primaries on one wing. Individual feather moult scores were assessed on a scale of 0 (old) to 5 (completely developed, new). Breeding plumage was scored on a scale of 1-7 (1=full winter plumage, 2=traces of breeding plumage, 3=1/4 breeding plumage, 4=1/2 breeding plumage, 5=3/4 breeding plumage, 6=fullly developed breeding plumage with traces of winter plumage left, 7=full breeding plumage; see Piersma & Jukema 1993). Birds were aged (based on wing moult: adult or juvenile) and then plucked. Flight feathers (primaries, secondaries, tertials and retrices), back + wing, and underpart + head feathers were separated. The birds were then dissected and sexed. Four measurements on the sternum were made, following Piersma et al. 1984), to determine standard muscle volume (SMV).

The following organs or body parts were separated: pectoralis, supracoracoideus, heart and leg muscles; stomach, intestines, kidneys, liver; lungs, salt glands, brain; skin (including half the tibia, the tarsus and the feet) and the 'rest'. Two distinct deposits of fat were separated. One was a layer under the skin (subcutaneous) while the other was a deposit in the abdominal cavity (abdominal; see Summers et al. 1992). Other fat was extracted from individual organs. All these were weighed, oven-dried for three days at 60° C, and reweighed. Subsequently, they were fat-extracted in a Soxhlet apparatus using petroleum ether as solvent. After this, fat-free dry mass (FFDM) was measured. From this we could determine the fresh mass, dry mass, FFDM, fat mass and water content (expressed in relation to FFDM). Only dry mass was determined for the salt glands.

RESULTS

Structural details of the birds are given in Table 1. Birds showed a large variation in body mass, indicating that while some birds were at or near the departure mass of 185 g (Battley 1996), others were still in the early stages of fattening. The plumage score of adults was positively correlated with total fat mass (Pearson correlation coefficient $r = 0.673$, d.f. $= 9$, $P = 0.0328$) and with total body mass ($r = 0.742$, d.f. $= 9$, $P = 0.014$), confirming that fat accumulation runs parallel with body moult. We implicitly treat increases in fat mass of adult birds as approximating changes over time.

Figure 2 shows that the large majority of the increase in total body mass was fat, although FFDM appears to increase at a low rate. However, as most organs of juveniles were smaller than those of the adults (see below), this relationship may be misleading. We now treat only adults in our analyses of organ changes.

To assess whether body part and organ mass in adults were related to the structural size of the birds or reflected migrational changes, total fat mass and total FFDM were correlated against all analysed components and three structural measures (Table 2). Total FFDM presumably largely reflects the birds' size, although bill length (which is often taken as a measure of size in wild birds; e.g. Goede & Niebor 1983, references in van der Meer & Piersma 1994) gave the only structural correlation. As it explained only 39.9% of the variance we have not corrected organ FFDMs for this. In contrast, fat mass was strongly correlated with total body mass, strengthening our contention that fat mass can be used to assess migrational changes. While many parts showed no significant correlations with either fat mass or FFDM, those that did so are unambiguous. Four organs showed significant migrational changes: the mass of pectoralis and heart muscles increased, while stomach and intestine masses decreased. These directional changes were also mirrored in supracoracoideus muscle, liver and kidney masses. FFDM only significantly correlated with kidney mass.

The large majority of fat was deposited under the skin (Fig. 3), the proportion of the total fat mass being constant over all total fat masses. In contrast, abdominal fat (which accounted for a much smaller proportion of total fat) showed proportionately higher masses at larger total fat masses. This suggests abdominal fat is more heavily deposited once other fat storage areas are filled (for example, around other organs, which shows the opposite relationship).

It is now recognised that birds, in preparation for long-distance migration, may deposit protein (reflected in FFDM levels) along with fat. The lack of a significant correlation between FFDM and fat mass in this sample would suggest that this is not occurring, yet in our sample the heart and pectoral muscle masses increased. Why this discrepancy? When total FFDM was plotted against total fat mass for all individuals, FFDM seemed to increase and then decrease in a non-linear fashion in adults (Fig. 4). What component organs cause this pattern?

Figure 5 gives the plots of organ FFDM against total fat mass, grouped into three categories - muscles (pectoralis, supracoracoideus, leg and heart), nutritional
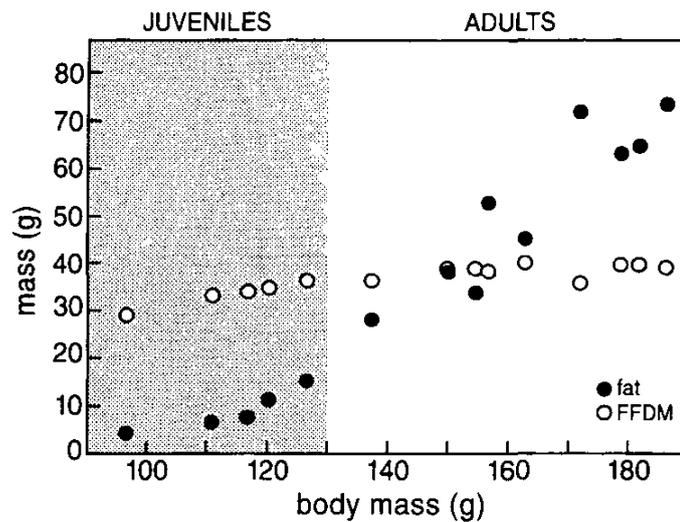
FIGURE 2 – Relationship between total fresh body mass (x-axis) and total fat mass and total fat-free dry mass (FFDM) (y-axis) of knots. Solid circles = fat; open circles = FFDM.

TABLE 1 – Physical and plumage details of all analysed knots, listed in order of decreasing total body mass. See methods for definitions of measurements.

Indi vidual	Age & sex	Body mass, g	Bill length, mm	Total head length, mm	Tarsus +mid- toe, mm	Wing length, mm	SMV, cm³	Plu- mage	Body moult	Wing moult
1	ad F	185.3	32.9	62.2	58	176	12.19	5	1	0
2	ad F	182.0	31.4	59.3	59	170	13.95	4	2	0
3	ad F	178.9	34.1	62.8	59	172	12.45	3	2	0
4	ad M	172.0	29.8	60.1	57	171	11.98	4	2	0
5	ad F	163.1	32.0	60.5	56	169	12.40	2	1	0
6	ad M	157.1	31.6	58.9	58	165	12.28	5	2	0
7	ad M	154.9	31.2	60.3	56	176	14.69	2	2	0
8	ad M	150.4	33.1	60.8	58	171	11.96	4	2	0
9	ad M	150.2	32.0	60.1	59	164	12.48	2	1	0
10	ad F	137.8	31.8	61.7	57	174	12.81	2	1	0
11	juv M	126.9	32.8	62.1	57	*	11.91	1	0	29
12	juv M	120.4	32.4	62.2	58	*	12.65	1	0	12
13	juv F	117.2	34.8	63.4	60	*	13.16	1	0	49
14	juv M	111.4	32.9	61.4	60	*	11.45	1	0	49
15	juv M	96.9	30.5	58.9	57	*	12.65	1	0	41
Mean		147.0	32.2	61.0	57.9	170.8	12.62			
(s.d.)		(27.6)	(1.29)	(1.4)	(1.3)	(4.1)	(8.73)			

organs (stomach, intestine, liver and kidneys) and "other body parts" (lungs, skin, rest). Three of the four muscle groups were heavier (pectoralis and heart muscles significantly, supracoracoideus muscle not), possibly levelling out at around 50 g fat. In contrast, FFDM of nutritional organs decreased as fat mass increased (significantly for stomach and intestine). The total result was a levelling off or net loss of protein at higher fat masses (Fig. 4).
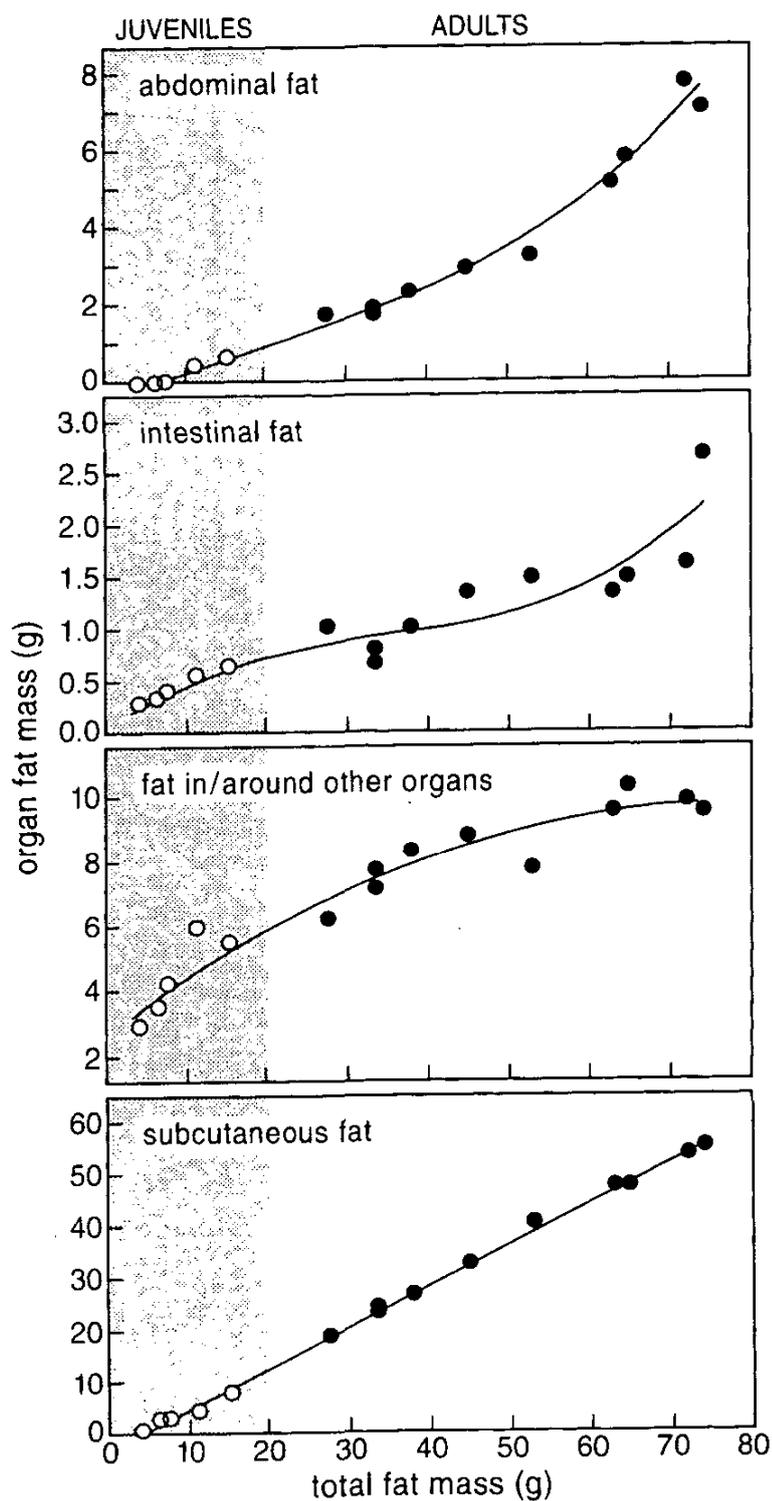
FIGURE 3 – Relationship between the four components of total fat mass, and total fat mass of knots. Juveniles have less than 20 g fat. Fitted lines are distance-weighted least squares smoothing curves. Note the different scales on the 'y' axis.

TABLE 2 – Pearson correlation coefficients (r) between body mass, fat mass, total fat-free dry mass (FFDM), fat-free drymass of all body parts and three structural measures, and fat mass and total fat-free dry mass for adult Lesser Knots (n=10). Significance is denoted by asterisks, with * (P < 0.05), ** (P < 0.01), *** (P < 0.001). Asterisks in brackets denote significance marginally less than the given level.

	Body mass	Fat mass	Fat-free dry mass	Pecto-ralis muscle	Supra-cora-coideus	Leg
Fat	0.923***	-	0.482	0.799***	0.509	0.049
FFDM	0.377	0.482	-	0.435	0.321	0.278

	Heart	Stomach	Intes-tines	Liver	Kidneys	Lungs
Fat	0715*	-0704*	-0772**	-0.312	-0153	0.039
FFDM	0.171	0.323	0.373	0.507	0.723(**)	0.564

	Abdomen	Brain	Flight feathers	Contour feathers	Skin	Rest
Fat	0.173	0.005	0.228	0.390	0.276	0.312
FFDM	0.167	-0.025	0.162	0.400	0.118	0.482

	Salt glands	Bill	Total head length	Tarsus+ toe length		
Fat	0.355	-0.054	0.337	0.083		
FFDM	-0.542	0.632*	0.274	0.084		

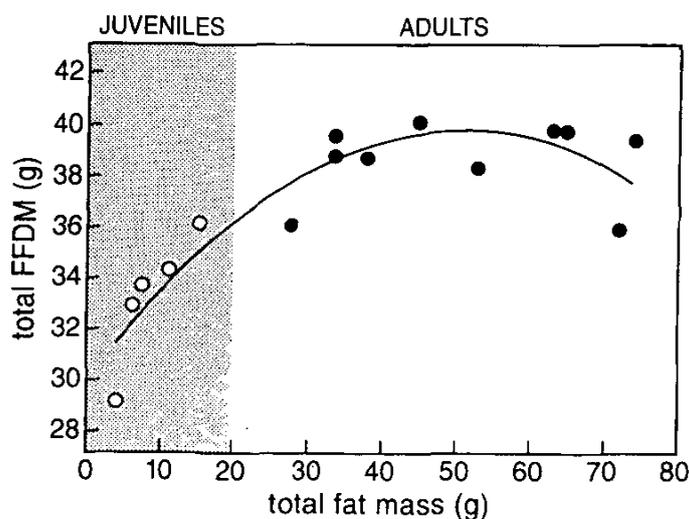FIGURE 4 – Total FFDM of knots plotted against fat mass. A polynomial regression describes the relationship $(Y = 30.022 + 0.38226*X - 0.0037739*X2, r = 0.92, P=0.0001)$. Juveniles (solid circles) have less than 20 g fat.
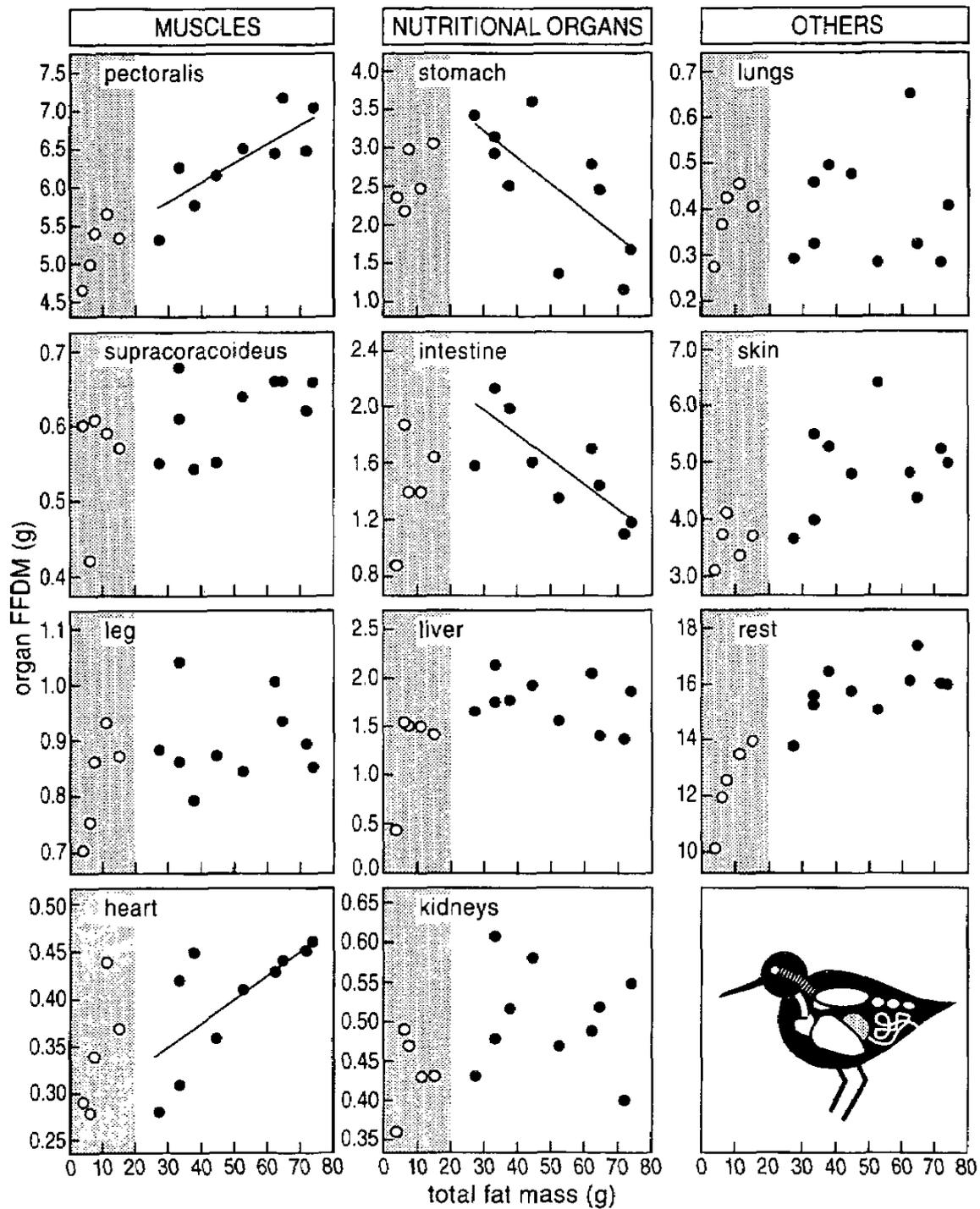
FIGURE 5 – Organ fat - free dry masses (FFDM) of knots plotted against total fat mass. Juveniles have less than 20 g fat. Significant relationships (Pearson correlation coefficients P<0.05) have fitted regressions. Note the different scales on the 'y' axis.

Given the complex inter-relationships between FFDM of organs, and lacking the size and independence of samples to estimate protein deposition accurately (see Lindström and Piersma 1993) we only coarsely estimated lean mass. We distinguished three groups of birds: juveniles showing no breeding plumage and little total fat (4-15 g; individuals nos 11-15), adults in the early to middle stages of migratory preparation (20-60 g fat; individuals nos 5-10), and adults in the late stages of preparation (over 60 g of fat; individuals nos 1-4). The mean lean masses (total mass minus fat mass) were: juvenile 105.8 g (s.d. = 7.6, n = 5), light adult 113.7 g (s.d. = 6.2, n = 6) and heavy adult 111.1 g (s.d. = 7.9, n = 4). One juvenile was extremely light (total mass 96.9 g; lean mass 92.9 g).Without this bird, the mean mass of juveniles becomes 109.2 g (s.d.=2.9, n=4).

Mass of body parts for adult and juvenile knots are given in Table 3. In ten of the eleven comparisons with significant differences, adults had the greater mass. Juveniles had significantly more water than adults did (Table 3).

DISCUSSION

Zwarts et al. (1990) suggested that plumage score of birds might be able to be used to estimate the degree of preparation for migration, but noted that it is likely to give underestimates of departure mass. They treated birds as ready to take off when they completed or suspended their body moult. Our data show a positive correlation between adult plumage score and fat mass. However, Table 1 shows that there is much variation. One bird had reached a plumage score of 5 while having a body mass of only 157.1 g, while another bird had reached 178.9 g with a plumage score of only 3. There was also no clear trend in the body moult scores for adults. Plumage certainly does on average increase with migratory preparation, but its value as a quantitative tool based on small samples seems limited.

The knots shot in Northland were in very different stages in their preparation for migration. The heaviest birds were probably very near to migrating (knots were observed departing from Farewell Spit, NW Nelson, from 8 to 27 March: Battley 1997), while the light adults were presumably only in the early stages of premigratory preparation. We were lucky to have an even spread of masses for comparison.

Most of the mass deposited by these birds was fat, but protein was also being deposited in muscle tissue, with pectoralis (used for flight) and heart muscles increasing with fat mass (supracoracoideus muscles, also used for flight, increased but non-significantly, P=0.133).

Flight is an energetically demanding activity, with costs estimated at 6-10x basal metabolic rate (BMR: the level of energy expenditure for a resting animal in the thermoneutral zone: see evaluation in Piersma & Jukema 1990).

Increased heart mass may allow for a prolonged raised heart rate while an increase in flight muscles may be needed for the actual flight itself. However, Davidson & Evans (1988) calculated that the usage of breast muscles was less than expected in knots migrating from the United Kingdom to Norway, which they interpreted as

TABLE 3 – Comparison of masses of different body parts for adult and juvenile Lesser Knots. Unless stated, n = 10 for adults and n = 5 for juveniles. Results of T-tests for difference between means are given in the right two columns. d.f. = 13 unless stated. Significant values are given in bold. Percentage breakdown of components of total fat-free dry mass are given. Water % is the percentage water of fat-free mass, ie. total lean mass = FFDM/((1-Water %)/100)

	Adults			Juveniles				
	Mean	s.d.	%	Mean	s.d.	%	T-value	P
Body mass	163.7	15.8		114.6	11.4		6.09	**0.0000**
Fat	50.49	17.0		8.74	4.34		5.28	**0.0001**
Fat-free dry mass	38.60	1.48		33.24	2.58		5.18	**0.0002**
Water %	0.657	0.014		0.686	0.006		-4.51	**0.0006**
Pectoralis muscle	6.315	0.538	16.36	5.194	0.387	15.62	4.13	**0.0012**
Supracoracoideus muscle	0.617	0.053	1.60	0.558	0.079	1.68	1.74	0.11
Leg	0.896	0.077	2.32	0.822	0.094	2.47	1.63	0.13
Heart	0.401	0.063	1.04	0.344	0.065	1.04	1.64	0.13
Stomach	2.482	0.861	6.43	2.602	0.396	7.83	-0.29	0.77
Intestine	1.622	0.391	4.20	1.434	0.363	4.31	0.90	0.39
Liver	1.741	0.259	4.51	1.264	0.468	3.80	2.58	**0.023**
Kidneys	0.505	0.065	1.31	0.436	0.050	1.31	2.08	0.058
Abdomen	0.071	0.037	0.18	0.014	0.020	.04	3.22	**0.0068**
Lungs	0.439	0.144	1.14	0.424	0.085	1.28	0.21	0.84
Brain	0.103	0.023	0.27	0.093	0.010	0.28	0.89	0.39 (a)
Skin	4.895	0.782	12.39	3.616	0.372	10.88	3.42	**0.0045**
Rest	10.959	0.410	28.39	10.294	0.551	30.97	2.65	**0.020**
Flight feathers	1.620	0.161	4.20	1.304	0.117	3.92	3.88	**0.0019**
Contour feathers	5.903	0.441	15.29	5.116	0.559	15.39	2.99	**0.010**
Saltglands	0.098	0.015		0.097	0.022		0.03	0.98 (b)

a. d.f. = 11. n = 9 for adults and 4 for juveniles
b. d.f. = 12. n = 10 for adults and 4 for juveniles

indicating that part of the preparation for (spring) migration was to ensure that birds could lay as soon as they arrived on the breeding grounds.

Pectoralis muscles are predicted to increase in mass by 34% as body mass rises from 115 to 185 g (estimated non-breeding and departure masses from Battley 1996: pectoralis muscle and fat mass data from this study; pectoralis = 5.05 +0.0251 fat mass, over fat masses from 1.9 g to 71.9 g fat; fat mass = -113 + 0.999 body mass). This is similar to the increase (30%) shown by Dunlin (*Calidris alpina*) captured on their wintering grounds in England before departing on the final leg of their migration to the breeding grounds (Davidson & Evans 1988). If birds do retain some breast muscle protein for use on the breeding grounds, then this does not necessarily have to be deposited until late in the migration. The exponent of the power relationship between pectoralis mass and body mass for New Zealand knots (0.59) was similar to that of knots about to depart from Norway (0.64; Davidson & Evans 1988), which suggests that preparation for these flights is similar. Hence, either flight costs are greater for New Zealand birds than British ones, or New Zealand birds are retaining protein even on this first leg of a long migration.

Migrant birds appear to have great flexibility in internal organs, especially nutritional organs (Piersma & Lindström 1997). Our data indicate that knots' nutritional organs may decrease in mass before migrating. As birds will not be feeding during a flight, any protein may best be stored in a usable form, such as in muscle tissue elsewhere in the body.

For a mollusc-eating bird such as the knot (e.g. Piersma *et al.* 1994; Zwarts & Blomert 1992) a big stomach is probably a prerequisite for processing large amounts of hard food. Perhaps stomach mass in knots increases from a low level held by juveniles to a high level by adults preparing for migration, but then, once a certain mass is reached (one within which departure mass is readily achievable), decreases quickly before migrating (see Fig. 4). Fig. 5 shows that stomach and intestine FFDM drops at 30-40 g fat mass, parallelled by increases in pectoralis, supracoracoideus and heart muscles masses. If this proposed stomach atrophying is real, then we have to assume that the benefits of flying with a reduced stomach mass are greater than the costs of arriving at a new location with a small one (when replenishment of nutrient stores is essential). These costs should be measured.

Wiersma & Piersma 1995) showed that abdominal fat mass in *C. c. islandica* and *C. c. canutus* subspecies correlated well with fat mass (r=0.88) and body mass (r=0.81). Their data consisted primarily of birds held in captivity, with only 6 freshly wild birds. Our data show much less scatter, and the plot of abdominal fat mass on total fat mass clearly shows an increase in relative fat content at high masses, which is not apparent from the equivalent plot (Fig. 2B in Wiersma & Piersma 1995). It is possible, therefore, that this "last-minute" filling of the abdominal cavity might be a feature of wild birds that is lost in captive birds.

Of the 11 significant differences found between adults and juveniles, at least three (body mass, fat mass, Pectoralis mass) were probably due to migratory preparation. FFDM was also lower in juveniles. This may be partially related to migration, with adults initially increasing FFDM tissue levels, but juveniles may also have not yet achieved an adult body size: a sample from mid-summer would determine whether there are size differences between ages before migratory preparation.

Salt glands in *C. c. rogersi* were very large compared with other subspecies. The mean fresh salt gland mass in a sample of ten wild-caught knots from Europe (*C. c. islandica*) was around 180 mg (range 110-230: Fig 30, p.131 in Piersma 1994). Estimating fresh salt gland mass of our *rogersi* birds, assuming a 75% water content (so fresh mass = 97.7 mg x 4), suggests a fresh mass of around 390 mg, which is over twice the size of their conspecifics'. This may reflect the need to process large amounts of food during premigration hyperphagia, which would increase the salt intake for intertidal birds. The European birds were sampled before migratory preparation had begun.

These data confirm *C. c. rogersi* knots to be small in comparison with the European-wintering *C. c. islandica*, both in linear measurements and most internal organs (Piersma *et al.* 1996). They are much more similar to the tropical African-

wintering *C. c. canutus* (Piersma *et al.* 1996, but note that the African birds were not migratory individuals). This accords with the explanation that organ size reflects energetic requirements - the milder the conditions experienced, the less a bird requires large organs to allow a high level of energy expenditure for survival. That *C. c. rogersi* tend overall to be even smaller than *C. c. canutus*, however, suggests that other factors in addition have been important in shaping the size of New Zealand-wintering knots.

Waders overwintering in South Africa have been shown to carry around 7% fat (Summers and Waltner 1978), and this figure has been used to estimate lean mass of waders in Australia (Barter & Wang, 1990). Using this approach, Battley (1996) estimated the lean mass of knots around Auckland (based on masses of live birds) to be around 104 g. This is much lower than the lean masses derived in this study, except for the juveniles. That the mass of adults was higher is not unexpected as they were preparing for migration. However, the mean mass of the four larger juveniles was over 5 g more than the estimate based on live mass. This suggests that New Zealand knots may carry less fat than assumed over the non-breeding season. Body composition analysis of knots in the middle of the southern summer (ie. pre-deposition) would clarify this.

ACKNOWLEDGEMENTS

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