

Seasonal mass changes of Lesser Knots (*Calidris canutus*) in New Zealand

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ABSTRACT

Lesser Knots (*Calidris canutus*) are high-Arctic breeding waders that migrate to temperate and tropical regions for the non-breeding season. Seasonal mass changes were examined in Lesser Knots in New Zealand at the southern end of their migration. Adults showed a large increase in mass in February before their northward migration in March. They were estimated to depart with a 'fat' load of around 45%. Subadult birds, most of which winter in New Zealand over the northern breeding season, also showed a mass increase. Mass increases in winter are well documented for European waders but contrary to the European situation, this increase in subadult birds in New Zealand is unlikely to be an adaptive strategy to insure against periods of negative energy balance. Instead, it may be an endogenously orchestrated byproduct that has not been selected against in the pre-migratory period. Such increases may be more widespread in Arctic waders in the Southern Hemisphere than is realised.

KEYWORDS: shorebirds, Lesser Knot, *Calidris canutus*, mass

INTRODUCTION

Waders (Charadriiformes) are renowned for long-distance migrations, which in some populations of Arctic-breeding species may span over 100° latitude. To fuel long flights, individuals must undergo several cycles of fat and protein deposition and use for each journey. For some species this involves large flights that may last for 36-48 hours in which stored nutrients are the only source of energy. Failure to deposit enough nutrients can cause death, and it is expected that natural selection has given rise to mass cycles, which are closely linked with migratory flight requirements.

Lesser Knots *Calidris canutus* breed in the extreme high Arctic and migrate as far south as South Africa, Australia, New Zealand, and southern South America (Piersma & Davidson 1992). Five subspecies are recognised, with the subspecies *rogersi* migrating to Australasia (Barter 1992). Given the geographical range of wintering areas, individuals of different subspecies encounter very different environmental demands during the non-breeding season, and birds migrating to the Southern Hemisphere or the tropics experience much lower thermostatic costs than birds remaining in north-temperate zones, but face considerably larger flight costs (Piersma *et al.* 1991; Wiersma & Piersma 1994). Body mass levels may be expected to reflect both migratory demands, the risk of food shortage (e.g. Davidson 1981b) and even stage of moult (Rogers *et al.* 1996). The primary destination for

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Lesser Knots leaving New Zealand on migration is unknown, but is probably northern Australia or Irian Jaya, Indonesia (Riegen 1999), and so departing birds face a flight of up to 4,000-4,800 km (and a minimum of 2,300 km to eastern Australia). Large fuel reserves are expected to be deposited before migration.

In cold-temperate areas, a mid-winter mass peak in many wader species is used as a buffer against poor feeding conditions (Davidson 1981b). In contrast, mild conditions in New Zealand in winter make such a mass increase unlikely, but seasonal mass changes have not yet been studied in an Arctic-breeding wader in New Zealand.

In this paper, body mass changes of three age-classes of Lesser Knots are shown through the year, based on birds captured around the Auckland region, North Island, New Zealand. The base mass (the mass of a bird when carrying minimal nutrient stores: Rogers *et al.* 1996) is estimated from catches during the winter and non-breeding season. Departure mass for adults is estimated from catches made just before migration, and possible explanations for body mass changes in subadult birds in the pre-migratory period are compared. Total body mass provides only a crude indicator of seasonal body composition changes, and the detailed body composition of pre-migratory Lesser Knots from Northland has been examined elsewhere (Battley & Piersma 1997).

METHODS

Lesser Knots were cannon-netted at Jordan's Farm, Kaipara Harbour (36°30'S, 174°20'E), Manukau Harbour (37°05'S, 174°50'E) and the Firth of Thames (37°10'S, 175°10'E) by members of the Miranda Banders and New Zealand Wader Study Group (NZWSG) under the direction of Stephen Davies and Adrian Riegen, from 1987-1996. Of 3295 Lesser Knots caught, 2007 were both weighed and aged (some catches were too large to enable full processing of all birds). Most birds were weighed within two hours of capture but, where the catch was very large, some birds were weighed up to four hours after capture. Masses have not been corrected for mass loss after capture, and this should be kept in mind when interpreting results. Birds were weighed to the nearest gram using Pesola spring balances.

Ageing was by primary moult, wear, and presence of breeding plumage (Barter & Davidson 1990). Only birds where age was determined are analysed. Individuals were classified as juvenile (in their first year of life), immature (in their second year of life) or adult (in their third or later year of life). Juveniles and immatures are collectively referred to as subadults. These terms are more for convenience than technical correctness. The age of first breeding in Lesser Knots is not known, so adult really refers to birds in definitive moult cycles, rather than reproductively mature individuals. Likewise, most of the juvenal plumage is lost soon after arrival in New Zealand, so first year birds are not technically juveniles for very long. However, these terms will serve to distinguish between the year-classes for this analysis. The 'birthdate' was considered 1 August. 161 juveniles, 346 immatures and 1500 adults were weighed. Dates of the catches are given in the caption to Fig. 1.

In this paper, the non-breeding season refers to the austral summer. 'Winter' as a term will be restricted to the austral winter. Statistical analyses were carried out in Statview.

RESULTS

Boxplots of recorded masses of birds for the three age-classes captured at different times during the year are presented in Fig. 1.

Base mass

Mass of juveniles did not differ significantly over the winter and non-breeding period, with mean masses of 112.4 g (n=38) in July, 115.0 g (n=5) in October and 112.8 g (n=24) on 23 February. For immatures, catches in July, November and December did not differ (114.1 g, n=145; 112.0 g, n=24; and 108.3 g, n=3 respectively), but catches in October (121.8 g, n=34) were significantly heavier than the July and November catches ($t_{177} = 4.059$, $P < 0.0001$ and $t_{56} = 3.616$, $P = 0.0006$ respectively).

For adults, mean mass in November (109.1 g, n=41) was significantly lower than the July (117.7 g, n=41) and October catches (119.4 g, n=210) ($t_{80} = -4.906$, $P < 0.0001$ for July and $t_{249} = -6.161$, $P < 0.0001$ for October).

The mean mass of adults in July was significantly higher than that of juveniles and immatures (which were not different themselves) ($t_{77} = -2.869$, $P = 0.0053$ for adults vs juveniles; $t_{184} = -2.252$, $P = 0.0255$ for adults vs immatures) but there was no difference between ages in October or November.

Together, and allowing for some mass loss between capture and weighing, these indicate a mean base mass of about 112-115 g, with adults in July and October weighing slightly more. Large samples of un-aged birds in winter or during the non-breeding season had similar masses to the known-age birds (4 July, 115.9 g, n=217; 3 November, 112.7 g, n=53; 22 December, 108.0 g, n=102). A mass of 115 g is hereafter used as the base mass level.

Some very low masses were recorded; as low as 98 g for a 3rd-year bird (November), 92 and even 80 g for 2nd-year birds (July and April respectively) and 92 g for a 1st-year bird (February) (Fig. 1).

Pre-migratory mass increase

Accurately estimating departure mass of waders is difficult (see discussion), and I simply used mean catch masses to derive a linear regression to estimate mass at the mid-point of the migration period. This is then compared with the heaviest ten percent of birds from catches in the pre-migratory period.

A regression equation was derived for the pre-migratory mass increase period based on the mean mass of adults in February and March, using 30 January (day 30) as the beginning of this increase (mass = $77.314 + 1.2447 \cdot \text{day}$, $R^2 = 0.986$) and

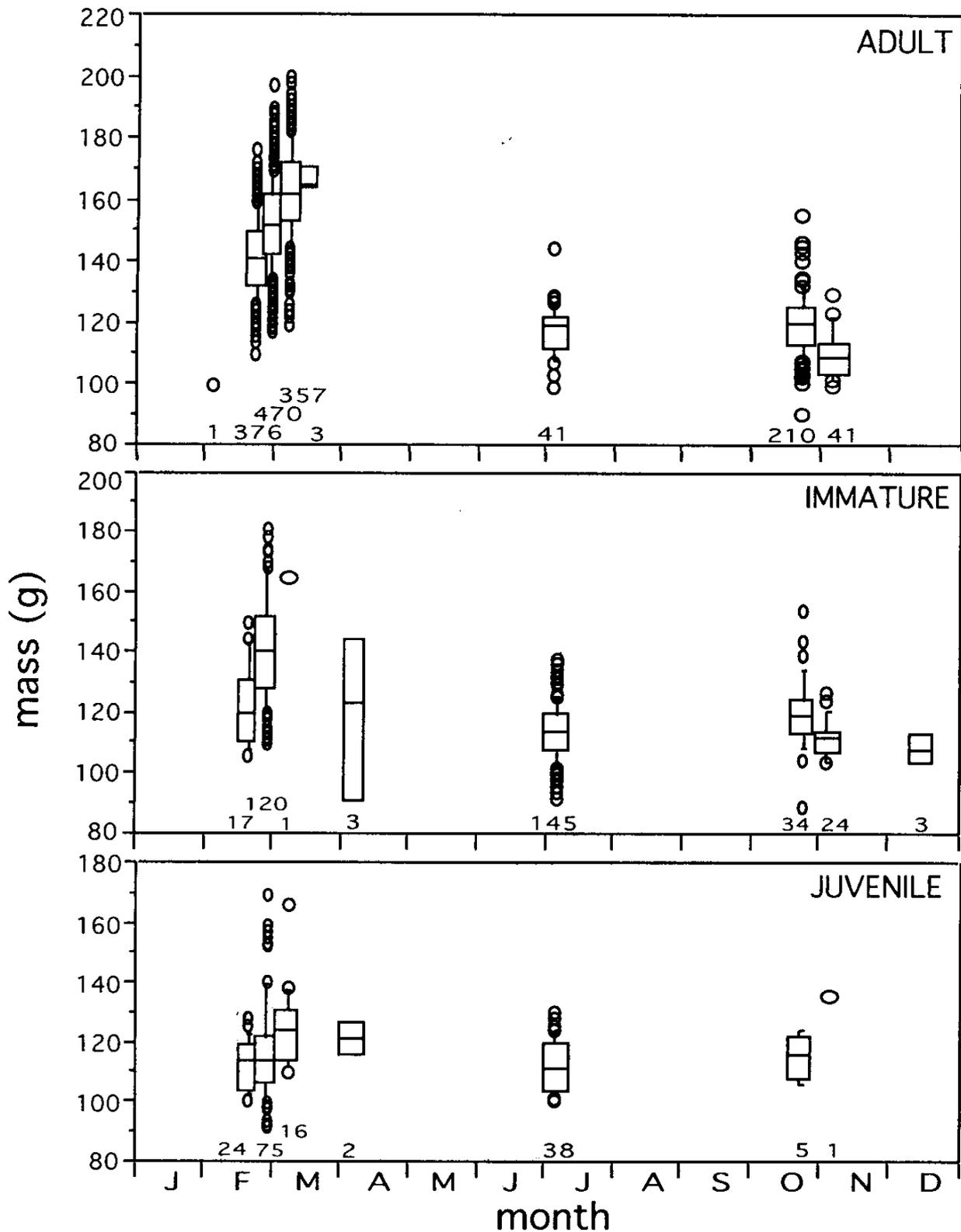


FIGURE 1 - Boxplots of masses of Lesser Knots of three age-classes captured in the Auckland region from 1987-1996. Boxes demarcate the 25th, 50th and 75th percentiles. Vertical lines show the 10th and 90th percentiles. Outliers are shown as circles. Dates of catches were (in date order): 3/2/91, 23/2/89, 28/2/97, 7/3/93, 14/3/93, 5/4/92, 4/7/92, (20/10/96, 23/10/94, 26/10/96, 28/10/96, which were not significantly different from one another for adults and immatures, and so have been summarised as one catch on 24/10), 26/10/96 (juveniles), 3/11/90 and 15/12/88. All birds were caught in the Kaipara Harbour, Manukau Harbour or the Firth of Thames by the Miranda Banders or the New Zealand Wader Study Group.

19 March (day 78) for the departure mass. 30 January was chosen as the starting date for fueling as this gives around 6 weeks to increase mass, similar to periods given in the literature (Zwarts *et al.* 1990). Furthermore, Zwarts *et al.* (1990) show that mass increase is synchronous with moult into breeding plumage. The first Lesser Knots on Farewell Spit, north-western Nelson, show breeding plumage by mid-January, and by the end of January almost 40% show some breeding plumage (unpubl. data). 30 January is apparently not too early to use as a starting date, but this needs confirmation through further captures.

19 March is the mid-departure period for Lesser Knots on Farewell Spit (from observations of departing birds; Battley 1997) and at the Manawatu estuary (from counts, unpubl. data). Extrapolating through to this date indicates a departure mass of around 174.5 g. Masses were not corrected for post-capture mass loss (Castro *et al.* 1991; Davidson 1984a), which would affect primarily any large pre-departure catches (because of the longer processing time required). Actual departure mass is probably higher than that calculated because, if birds lost mass at 1.5%/h (Castro *et al.* 1991; Zwarts *et al.* 1990), the mean masses could be 8-10 g higher for the large catches. This is confirmed by the weights of the heaviest birds in pre-migratory catches, which are presumed to be closest to migrating (first departures observed on Farewell Spit in 1994 were on 8 March; Battley 1997). The heaviest ten percent of adults in pre-migratory catches had mean weights of: 164.0 g on 23 February, n=38; 178.4 g on 28 February, n=47; and 187.5 g on 7 March, n=36. I treat 185 g as the mean departure mass in the rest of this paper.

The rate of mass increase estimated here is 1.24 g per day, equivalent to 1.1% of basic body mass per day. A departure mass of 185 g represents a 'fat' load of 44% if lean mass is 104 g (see discussion) or 41% if lean mass is around 109 g (Battley & Piersma 1997). Birds at 200 g (recorded on 7 March) must have a 'fat' load of 45-48%.

Immature and juvenile Lesser Knots also showed a mass increase during the 'pre-migratory period', despite the fact that these are assumed to remain in New Zealand over the winter (Fig. 1). Mean immature mass increased from 122.6 g on 23 February to 140.9 g on 7 March ($t_{134} = -4.23$, $P < 0.0001$). Mean juvenile mass increased from 112.8 g on 23 February to 125.0 g on 7 March ($t_{38} = -3.458$, $P = 0.0014$).

Age-classes present in winter

Birds remaining over the winter in New Zealand are generally assumed to be juvenile birds, but a large number of these are apparently immatures (Fig. 1). Fig. 1 suggests that all three age-classes are present in New Zealand over the winter, with the July catch showing 38 juveniles, 145 immatures and 41 adults (this was not the entire catch, however; wing-lengths were taken from 66 juvenile, 177 immature and 41 adults). It is surprising that substantial numbers of adults apparently stay over the southern winter. Small numbers of old or sick birds might be expected, but the number recorded suggests that the ageing criteria used may be less accurate in winter than in summer. Stephen Davies (pers. comm.) suggests that these

adults should probably be treated as immature birds. However, while there is no difference in mean wing length between the two age-classes in the July catch ($t_{216} = -0.441$, $P=0.6597$), mean mass of supposed adults is significantly higher (117.7 g cf. 114.1 g; $t_{184} = 2.252$, $P=0.0255$). The ageing criteria apparently do distinguish between different subgroups of birds, but this may be because heavier immatures that have completed a moult cannot be distinguished from adults on the basis of plumage. Ageing of birds in winter obviously requires more investigation.

DISCUSSION

Non-breeding and lean mass

Mean mass of all catches over the winter and non-breeding period ranged from 108-122 g. Some of the variation is probably seasonal, as birds may show a decrease in body mass when moulting (Rogers *et al.* 1996), and all ages of Lesser Knots undergo a complete or partial pre-basic moult in early to mid-summer (Higgins & Davies 1996). Some yearly variation may also occur, as most of the heavy immatures and adults in the October catches were caught in 1996.

A typical non-breeding mass for a Lesser Knot in northern New Zealand is around 115 g. Determining the lean (fat-free) component is problematic – because of differences in the amount of fat carried during the non-breeding season by waders in different climatic conditions, total mass - lean mass relationships in cold-temperate waders (for which the most data exist) cannot be applied to New Zealand birds. Even within Lesser Knots, there is considerable structural variation between the different subspecies (Piersma & Davidson 1992), and lean (i.e. fat-free) mass can vary seasonally within populations (Davidson 1981a).

The most appropriate comparison with New Zealand waders may come from South Africa, where Summers & Waltner (1978) found waders contained 6-7 % fat over the non-breeding season. If New Zealand Lesser Knots had similar levels of fat then a 112 to 115 g bird would have a lean mass of 104 to 107 g respectively. Four juvenile Lesser Knots obtained in March 1992 and analysed by Battley & Piersma (1997) had a mean lean mass of around 109 g (mean total mass was 119 g so fat content = 8.5%). Ten adults from the same sample had lean masses of 111-113 g, although these birds were pre-migratory and were probably depositing protein before migration and so do not represent non-breeding masses.

For Lesser Knots in Australia, Barter & Wang (1990) assumed a 7% fat component and estimated the lean mass for birds in north-western Australia as 103.2 g, and for birds in south-eastern Australia as 108.8 g. The south-eastern estimate is similar to the New Zealand estimate here, while the north-western birds may belong to a separate sub-species (Higgins & Davies 1996; Danny Rogers, pers. comm.). One Lesser Knot from north-western Australia weighed 117.5 g, but had a lean mass of 102.1 g (15.4 g or 13.1% fat) (Piersma & Barter 1991).

The lean mass of Lesser Knots in New Zealand apparently lies somewhere between 104 and 109 g, though probably nearer the latter. This mass is much higher than the other published estimate of lean mass in Lesser Knots on the Australasian-East Asian Flyway – Barter & Wang (1990) recorded a mean body mass of 87.6 g for 12 Lesser Knots that had recently completed a long-distance flight to near Shanghai, China. These birds had probably depleted their nutrient reserves as well as strategically deposited stores (see King & Murphy 1985; Lindström & Piersma 1993; van der Meer & Piersma 1994 for the difference). This 88 g estimate should not be used to calculate flight ranges, as it will overestimate the level of pre-migratory deposition (cf. Barter 1992; Tulp *et al.* 1994). Even so, birds in New Zealand had masses as low as 80 g, but this was probably due to injury, sickness or parasitism. While birds obviously have the ability to use their protein reserves, it is only in extreme situations that they will do so.

Pre-migratory increase

Problems in estimating departure masses arise from movement of birds into a population, asynchronous departures, capture effects on mass for within-season retraps and, in some species, an apparent lack of synchrony in fueling of individuals between years (Barter & Minton 1998). In addition, Rogers *et al.* (1996) have suggested that birds of similar mass may bunch together. Use of mean catch weights to estimate departure mass is often inappropriate because selective departure of heavy birds will lead to an underestimate of the true departure mass. This should not be a problem with the catches analysed here, as the main pre-migratory catches were all before departures had begun. A greater effect might come from birds that appear to be adults, but which deposit only a little mass and remain in New Zealand (the “adults” in July, for instance). Such birds would lower the mean mass of the autumn catches. Accordingly, I estimated departure mass based on mean catch weights mainly as a guide. The mean mass of the heaviest ten percent of the catch on 7 March (187.5 g) was just above the proposed departure mass based on mean masses. Battley & Piersma (1997) performed body composition analysis on Lesser Knots of up to 185 g killed on 7 March 1992, the heaviest one containing 71.9 g fat. These indicate that 185 g is a realistic departure mass, although a more robust estimate would be desirable.

While Lesser Knots in New Zealand are apparently quite fat when they depart on migration, the rate of mass increase suggested here (1.1% per day) is rather low relative to other studies of waders (Table 4 of Zwarts *et al.* 1990). This rate may be underestimated by the technique used to derive it, however, all eight Southern Hemisphere studies (two in Australia, six in South Africa) of mass increase in waders listed by Zwarts *et al.* (1990), and this one, showed rates of mass increase of 1.5 % per day or less. In contrast, only 12 of 34 Northern Hemisphere examples listed by Zwarts *et al.* (1990) had rates of increase this low (Fisher Exact Test, $P=0.0005$). One reason why waders at the southern end of a migration route have a longer, slower mass increase may be because they have to accomplish a pre-alternate moult at the same time as fueling.

Is the subadult mass increase adaptive?

Immature and juvenile Lesser Knots increased mass in the pre-migratory period. Fig. 1 shows that seven juveniles weighed 153-170 g, well above the rest of the samples. There is a possibility that these birds were aged incorrectly, but even if these juveniles are removed from the analysis, there is still a significant increase from both 23 and 28 February to 7 March (112.8 g vs 122.3 g, $t_{37} = -3.341$, $P=0.0019$ for 23 February, and 113.6 vs 122.3 g, $t_{82} = -2.731$, $P=0.0077$ for 28 February). Barter *et al.* (1988) also record juvenile Lesser Knots with masses of up to 168 g in Victoria, Australia.

Juvenile Lesser Knots are unlikely to migrate to Australia. The estimated potential flight range for juveniles using the formula of Davidson (1984) (which gives moderate estimates; using a lean mass of 104 g, peak mass of 125 g and flight speed of 65 km^{hr}) is 1440 km (see Zwarts *et al.* (1990b) and Battley (1997) for discussion of flight range estimations). This is inadequate for a trans-Tasman flight (although extremely heavy birds might be able to do so), so any movements could only be northwards within New Zealand. There is no suggestion from OSNZ national wader censuses that Lesser Knots move to Northland in winter. Over eight summer and subsequent winter complete censuses (Paul Sagar, unpubl.), Northland had proportionately fewer birds than the rest of New Zealand in the winter census compared with the summer count (Northland mean = 5.6%, s.d. = 6.5, n = 8; rest of New Zealand mean = 9.7%, s.d. = 2.1, n = 8). Furthermore, in three of nine winter censuses no birds were recorded, and in another two under 200 were counted in Northland. In only two of the eight seasons was the proportion of birds present in the winter season compared with the previous summer census higher for Northland than for the rest of New Zealand.

The proportion of immature birds that migrate north from New Zealand in autumn is unknown, but many certainly remain in New Zealand and no immature birds banded in New Zealand have been recovered overseas in the same year (Riegen 1999).

Alternatively, birds with high mass could be birds carrying residual fat having just migrated to the Auckland/Northland region from elsewhere in New Zealand. The fact that the mass increase of subadults and juveniles was synchronous with that of adults argues against this. For juveniles to migrate northwards within New Zealand before the migration of adults is unlikely. The occurrence of apparently similar mass increases elsewhere (below) also argues against this.

Mass increase in birds is usually considered to be adaptive (Blem 1990), and mass peaks in early winter followed by a subsequent decrease have been well-documented for European waders (Davidson 1981a; Johnson 1985). This is considered to buffer birds against increased energetic costs and decreased prey availability, when birds are unable to maintain a positive energy balance. Dunlin (*Calidris alpina*) wintering in colder areas in Britain had a mid-winter peak in body mass while birds in milder areas lacked any increased mass in early winter (Davidson *et al.* 1986; Pienkowski *et al.* 1979); there was also a significant negative correlation

between total body mass and mean December temperature (Pienkowski *et al.* 1979), the majority of which was due to changing fat levels (Davidson *et al.* 1986).

In New Zealand, conditions are less severe than in Europe. The temperatures experienced in the study areas in Britain were lower than those around the Auckland region in winter (mean January temperatures being generally 3.5°C to 7°C in Britain, c.f. mean July temperature in the Auckland/Northland area being 10°C to 12°C). Given that depositing nutrient stores actually increases energy demand, their value is probably an insurance against temporary food shortages, such as through tidal flats freezing or remaining covered during storms. The former certainly never happens anywhere in New Zealand. Lesser Knots sometimes feed in fields in winter at the Firth of Thames (pers. obs.), although whether this is forced on them by low prey levels is unknown.

Another possibility is that the mass increase in immature and juvenile birds is an 'involuntary' increase in the pre-migration period, an endogenously orchestrated byproduct that has not been seriously selected against in the young birds. This is suggested by the fact that the mass increase is synchronous with that of adults. Pre-migratory mass deposition is initiated partly endogenously, interacting with daylength (Gwinner 1990; Rankin 1991). Changes in hormone levels in non-migrant first-year birds have not, to my knowledge, been studied, but the expectation would be that these are much reduced, if present at all. Supporting this is the observation that juvenile *islandica* Lesser Knots kept in captivity showed a smaller mass increase in their first spring than in later ones (Piersma *et al.* 1995).

After the period of migration shown by the adults, and the concomitant changes in the internal state of the juvenile and immature birds, body mass could drop to a "seasonally appropriate level". As transport costs increase steeply with mass, any excess mass above requirements will have an energetic cost. In contrast to Lesser Knots, Wrybills (*Anarhynchus frontalis*), which do not migrate at the same time as knots, show no such mass increase (Davies 1997).

Such a mass increase in young birds could be adaptive if it enabled winter dispersal, which may happen in some Australian waders (Rogers *et al.* 1996). There is considerable movement of subadult Lesser Knots from southeastern Australia to New Zealand (Riegen 1999), and so it is feasible that young birds in Australasia are programmed to deposit fuel, which would enable some exploratory movements. These may not be made in New Zealand, and the extra mass not selected against (perhaps through a lack of predation pressure on heavy birds).

Reports of mass increases in juvenile waders in the pre-migratory period are not unknown in the literature. Barter *et al.* (1988) showed that juvenile Lesser Knots in Victoria increase in mass in March. In South Africa, Summers & Waltner (1978) showed increases for Turnstone (*Arenaria interpres*), Lesser Knot, Sanderling (*Calidris alba*) and Terek Sandpiper (*Tringa terek*) in the southern winter (i.e. non-breeding period), and Elliot *et al.* (1976) showed the same for Curlew Sandpiper (*Calidris ferruginea*). For Lesser Knots and Turnstones this increase was in April and could have been 'incipient pre-migratory fattening' (Summers & Waltner

1978) rather than winter fattening as such. Summers *et al.* (1989) recorded some first-year Turnstones in Scotland undergoing pre-migratory fattening, and assumed that some birds migrated with the adults, but noted that many remained in the wintering area. McNeil *et al.* (1994) suggested that digenian trematode infestations might play a role in causing delayed moult and fat deposition and be important in causing birds to remain on the non-breeding grounds. However, their hypothesis related to delayed or non-existent fattening, and the synchronicity of the mass increase in young birds recorded here with that of adults suggests an endogenous cause.

Juvenile mass increases may be more widespread than is realised, but there will always be the problem of disentangling any environmental effects caused by winter from endogenous effects. Recent developments in the modeling of thermostatic costs of free-living birds (Wiersma & Piersma 1994), combined with detailed ecological studies, mean that accurate assessment of the costs and risks associated with living at different localities is a possibility. This will allow meaningful conclusions about the adaptive value of behaviours to be made in a quantitative manner.

NOTE ADDED IN PROOF. Twenty-three adult Lesser Knots were mist-netted on 27 March 1998 at Karaka, Manukau Harbour. The mean weight of this catch was 192.7 g (s.d.=12.0, range 171 g - 212 g), which suggests that departure mass may be somewhat heavier than that suggested in this paper. However, the catch was probably biased towards the heaviest and least manouverable birds that failed to clear the net (Adrian Riegen, pers. comm.). Also, recent weather conditions had not been very favourable for migration, and so birds may have delayed departure slightly and continued fuelling.

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LITERATURE CITED

- BARTER, M. 1992. Distribution, abundance, migration and moult of the Red Knot *Calidris canutus rogersi*. Wader Study Group Bull. 64, Suppl.: 64-70.
- BARTER, M.; DAVIDSON, S. 1990. Ageing Palearctic waders in the hand in Australia. Stilt 16: 43-51.
- BARTER, M.; JESSOP, A.; MINTON, C. 1988. Red Knot *Calidris canutus rogersi* in Australia, Part 2: biometrics and moult in Victoria and North-Western Australia. Stilt 13: 20-27.
- BARTER, M.; MINTON, C. 1998. Can pre-migratory weight gain rates be used to predict departure weights of individual waders from north-western Australia? Stilt 32: 5-14
- BARTER, M.; WANG TIAN HOU 1990. Can waders fly non-stop from Australia to China? Stilt 17: 36-39.
- BATTLEY, P.F. 1997. The northward migration of Arctic waders in New Zealand: departure behaviour, timing and possible migration routes of Red Knots and Bar-tailed Godwits from Farewell Spit, North-West Nelson. Emu 97: 108-120.
- BATTLEY, P.F.; PIERSMA, T. 1997. Body composition of Lesser Knots (*Calidris canutus rogersi*) preparing to take off on migration from northern New Zealand. Notornis 44: 137-150.
- BLEM, C.R. 1990. Avian energy storage. Pp. 59-113 *in* Power, D.M. (ed.) Current Ornithology 7. Plenum Press, New York.
- CASTRO, G.; WUNDER, B.A.; KNOPE, F.L. 1991. Temperature-dependent loss of mass by shorebirds following capture. J. Field. Ornithol. 62: 314-318.

- DAVIDSON, N.C. 1981a. Survival of shorebirds (Charadrii) during severe weather: the role of nutritional reserves. Pp. 231-249 in Jones, N.V.; Wolff, W.J. (eds.) Feeding and Survival Strategies of Estuarine Organisms. Plenum Press, New York and London.
- DAVIDSON, N.C. 1981b. Seasonal changes in nutritional condition of shorebirds (Charadrii) during the non-breeding season. Unpublished PhD thesis, University of Durham, England.
- DAVIDSON, N.C. 1983. Formulae for estimating the lean weight and fat reserves of live shorebirds. Ringing & Migration 4: 159-166.
- DAVIDSON, N.C. 1984a. Changes in the condition of Dunlins and Knots during short-term captivity. Can. J. Zool. 62: 1724-1731.
- DAVIDSON, N.C. 1984b. How valid are flight range estimates for waders? Ringing & Migration 5: 49-64.
- DAVIDSON, N.C.; UTTLEY, J.D.; EVANS, P.R. 1986. Geographic variation in lean mass of Dunlins wintering in Britain. Ardea 74: 191-198.
- DAVIES, S. 1997. Population structure, morphometrics, moult, migration, and wintering of the Wrybill (*Anarhynchus frontalis*). Notornis 44: 1-14.
- ELLIOT, C.C.H.; WALTNER, M.; UNDERHILL, L.G.; PRINGLE, J.S.; DICK, W.J.A. 1976. The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. Ostrich 47: 191-213.
- GWINNER, E. 1990. Circannual Rhythms in Bird Migration: Control of Temporal Patterns and Interactions with Photoperiod. Pp. 257-268 in Gwinner, E. (ed.) Bird Migration. Springer-Verlag, Berlin Heidelberg.
- HIGGINS, P.J.; DAVIES, S.J.J.F. 1996. Handbook of Australian, New Zealand and Antarctic Birds. Vol. 3. Oxford University Press, Melbourne.
- JOHNSON, C. 1985. Patterns of seasonal weight variation in waders on the Wash. Ringing & Migration 6: 19-32.
- KING, J.R.; MURPHY, M.E. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? American Zool. 25: 955-964.
- LINDSTRÖM, Å.; PIERSMA, T. 1993. Mass change in migrating birds: the evidence for fat and protein storage re-examined. Ibis 135: 70-78.
- MCNEIL, R.; DIAZ, M.T.; VILLENEUVE, A. (1994). The mystery of shorebird overwintering. Ardea 82: 143-152.
- PIENKOWSKI, M.W.; LLOYD, C.S.; MINTON, C.D.T. 1979. Seasonal and migrational weight changes in Dunlins. Bird Study 26: 134-148.
- PIERSMA, T.; BARTER, M. 1991. Wader catching casualties for body condition analyses: rationale and first results for Great Knots. Stilt 19: 36-38.
- PIERSMA, T.; DAVIDSON, N.C. 1992. The migration of Knots. Wader Study Group Bull. 64, Suppl. 1-209.
- PIERSMA, T.; DRENT, R. & WIERSMA, P. 1991. Temperate versus tropical wintering in the world's most northerly breeder, the Knot: metabolic scope and resource levels restrict subspecific options. Pp 761-772 in Acta XX Congressus Internationalis Ornithologici. Christchurch, New Zealand.
- PIERSMA, T.; CADEE, N. & DAAN, S. 1995. Seasonality in basal metabolic rate and thermal conductance in a long-distance migrant shorebird, the Knot (*Calidris canutus*). J. Comp. Physiol. B 165: 37-45.
- PIERSMA, T.; BRUINZEEL, L.; DRENT, R.; KERSTEN, M.; VAN DER MEER, J.; WIERSMA, P. 1996. Variability in basal metabolic rate of a long-distance migrant shorebird (Red Knot, *Calidris canutus*) reflects shifts in organ sizes. Physiol. Zool. 69: 191-217.
- RANKIN, M. 1991. Endocrine effects on migration. American Zool. 31: 217-230.
- RIEGEN, A.C. 1999. Movements of banded Arctic waders to and from New Zealand. Notornis 46: 123-142.
- ROGERS, K.G.; ROGERS, D.I.; MINTON, C.D.T. 1996. Weights and pre-migratory mass-gain of the Red-necked Stint *Calidris ruficollis* in Victoria, Australia. Stilt 29: 2-23.
- SUMMERS, R.W.; WALTNER, M. 1978. Seasonal variations in the mass of waders in southern Africa, with special reference to migration. Ostrich 50: 21-37.
- TULP, I.; MCCHESENEY, S.; DE GOEIJ, P. 1994. Migratory departures of waders from north-western Australia: behaviour, timing and possible migration routes. Ardea 82: 201-221.
- VAN DER MEER, J.; PIERSMA, T. 1994. Physiologically inspired regression models for estimating and predicting nutrient stores and their composition in birds. Physiol. Zool. 67: 305-329.
- WIERSMA, P.; PIERSMA, T. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of knots. Condor 96: 257-279.
- ZWARTS, L.; ENS, B.J.; KERSTEN, M.; PIERSMA, T. 1990. Moulting, mass and flight range of waders ready to take off for long-distance migrations. Ardea 78: 339-364.



Chatham Island Oystercatcher (*Haematopus chathamensis*) nesting on Mangere Island.

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