

## Do body condition and plumage during fuelling predict northwards departure dates of Great Knots *Calidris tenuirostris* from north-west Australia?

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It is often assumed that strong selection pressures give rise to trade-offs between body condition and time in long-distance migrating birds. Birds that are 'behind schedule' in fuel deposition or moult should delay departure, and this should result in a negative correlation between initial condition and departure date. We tested this hypothesis in the Great Knot *Calidris tenuirostris* migrating from north-west Australia to eastern Asia en route to Siberia. Great Knot gain mass and moult into breeding plumage before leaving northern Australia in late March and early April, and fly 5400–6000 km to eastern China and Korea. We radiotracked 27 individuals (17 males and ten females) to determine departure dates; 23 migrated and four remained in Australia. We characterized body condition at capture using body mass, predicted pectoral muscle mass (based on ultrasound estimates of the size of the pectoral muscles) and breeding plumage scores. Residual condition indices were uncorrelated, indicating that at the individual level, variation in one fuelling component was not strongly associated with variation in the other components. Birds that did not depart had lower residual body mass and breeding plumage indices than those that did migrate; these four birds may have been subadults. Neither sex, size nor the condition indices explained variation in departure date of migrants. Reasons for this are explored. Departure dates for northward migrating waders indicate that the migration window (span over which birds depart) decreases with proximity to the northern breeding grounds. We suggest that migration schedules become tighter as birds get nearer to the breeding grounds. Thus the lack of a relationship between condition and departure date in Great Knots may reflect the fact that the departure episode under study is the first one in sequence and is still 4–8 weeks before breeding.

Body condition should be critical to the fitness of migratory birds. High-quality individuals arrive on breeding grounds (Møller 1994) and mate (Owens

*et al.* 1994) first, and early breeding birds can have higher reproductive success (e.g. Møller 1994, Hasselquist 1998, Currie *et al.* 2000, Drent *et al.* 2003). Early hatched young may also start breeding earlier than late hatched young (e.g. after 1 year instead of 2 years in Black-tailed Godwits *Limosa limosa*; Beintema & Drost 1986). Only high-quality individuals may be able to cope with the higher costs of early arrival (Møller 1994, Kokko 1999). Benefits

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of early arrival should place strong selection on the timing of migration to the breeding grounds, but benefits of early arrival may also occur at stopovers along the migration route. Such benefits would arise if prey became depleted over time (through increased predation pressure or predictable seasonal declines in prey availability; Schneider & Harrington 1981, Zwartz *et al.* 1992, Nolet & Drent 1998), if aerial predators that make heavily loaded individuals more vulnerable to predation increased in number with time (Nebel *et al.* 2000), if intake rates decreased with population size (Stillman *et al.* 2000), or simply if early arrival enabled a bird to reach the final staging site in time to make an early flight to the breeding grounds. Delays in any one fuelling episode could delay all subsequent fuelling periods (Piersma 1987).

There is evidence that the timing of individual migration stages or preparation for migration can be condition-dependent. The arrival time of male Barn Swallows *Hirundo rustica* in Denmark is phenotype-dependent, longer-tailed birds arriving earlier than shorter-tailed birds (Møller 1994). Individual quality is reflected in the extent of migratory preparation in Bar-tailed Godwits *Limosa lapponica* migrating from Africa to The Netherlands (en route to Siberia) (Piersma & Jukema 1990, Piersma *et al.* 2001). Here, heavy, well-moulted birds continue to moult while staging in Europe, whereas light, less well-moulted birds do not continue moult. Fuelling ability and moult status before departure from Africa are apparently correlated, and the appearance of the alternate plumage or supplemental plumage (Jukema & Piersma 2000) can be a reliable indicator of migratory quality. Plumage variation may reveal the relative scheduling of fuelling processes in individuals.

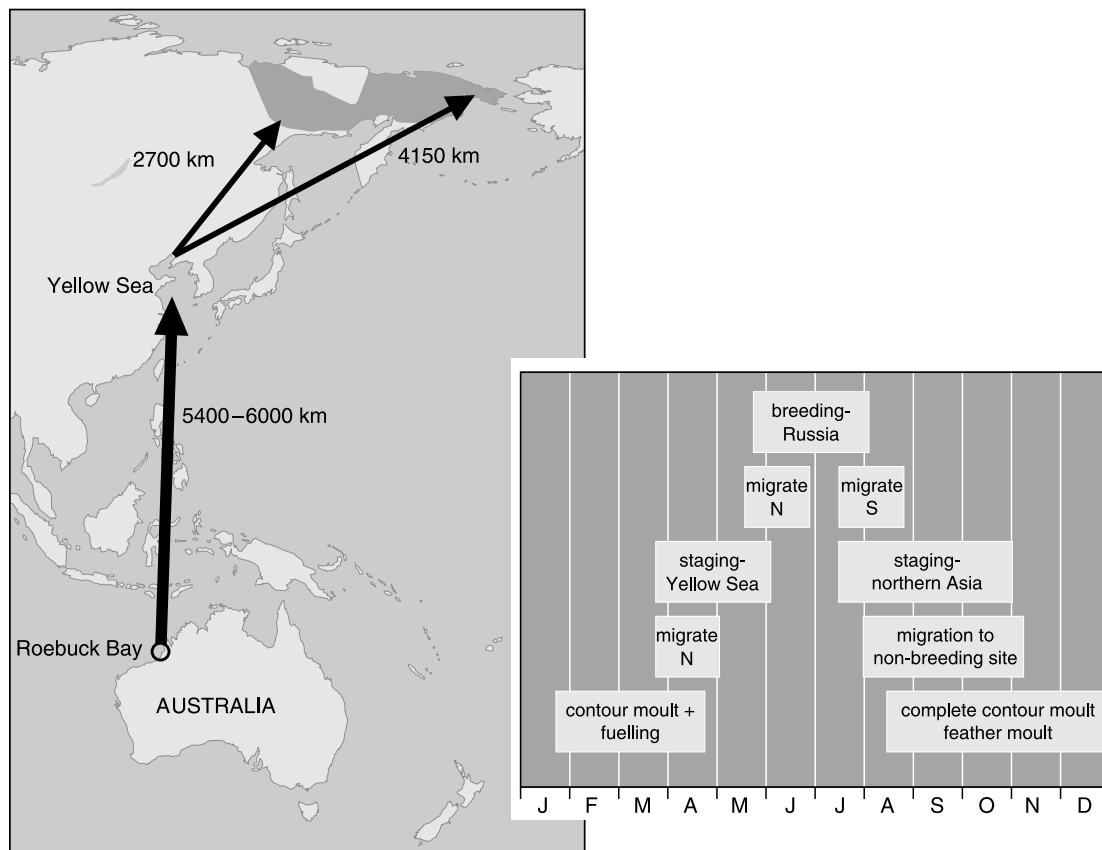
To test how the timing of migratory departure is affected by body condition, feeder experiments with marked individuals can be used to determine the fuelling rate and departure mass. These are key variables in optimality models of migration, but have only been measured in a few passerine species (e.g. Lindström & Alerstam 1992, Weber *et al.* 1999). Such an approach is not possible with waders foraging on tidal flats. Instead, comparing departure date to relative body condition during fuelling may reveal whether early variation in condition translates directly into variation in departure date. This assumes that the relative fuelling 'trajectories' of individuals are similar (e.g. Piersma *et al.* 1990), or at least constant within individuals.

Body condition (incorporating body mass, moult or even internal organ size) can be readily characterized

at the time a bird is caught and marked. Accurately determining departure date is more difficult if banded or colour-banded birds cannot be reliably caught or relocated (cf. Morton & Pereyra 1994, Pfister *et al.* 1998). Instead, radiotracking can be used to establish the presence or absence of individuals on a daily basis (Iverson *et al.* 1996, Farmer & Parent 1997, Warnock & Bishop 1998, Nebel *et al.* 2000) or even, in small samples, to determine departure times (Åkesson *et al.* 1996, Moore & Aborn 1996). In this study we use radiotracking to determine the departure dates of individual Great Knots *Calidris tenuirostris* embarking on a 5500-km flight from tropical Australia to Asia (see Fig. 1; Battley *et al.* 2000 summarize evidence for this flight). We test whether a bird's departure date is related to body condition at capture (roughly 1 month before migration). To characterize body condition, we used a combination of body mass, body size, estimated pectoral muscle mass and breeding plumage score. All three measures are separate, important, components of migratory preparation (albeit not necessarily mutually exclusive): body mass increases primarily with fat deposition for fuel (Piersma *et al.* 1999, Battley *et al.* 2001); flight muscle mass increases with body mass, possibly to maximize flight efficiency (Kvist *et al.* 2001); and birds moult into a distinctive breeding plumage that may have selective importance on the breeding grounds (Owens *et al.* 1994).

We predict that if there is limited flexibility in fuelling regimes among Great Knots (i.e. birds cannot change their fuelling rates), a bird that is 'behind schedule' in preparation will delay departure whereas birds in good condition will leave earlier, leading to a negative relationship between relative condition at capture and departure date. Alternatively, if a bird can 'catch up' during fuelling, then departures should be fairly synchronized and show no relationship with initial condition. A similar effect would occur if time was prioritized over energy or plumage, so that birds left early regardless of their condition. In this case, however, condition would vary at departure, and resightings of colour-marked individuals might allow one to discern whether plumage quality is sacrificed in favour of leaving on time.

Great Knots are large socially monogamous sandpipers that breed on mountain tops in eastern Siberia (Fig. 1; Tomkovich 1997). Before northward migration from north-west Australia to Asia they increase in mass from around 141 g (Barter & Minton 1998) to around 240–260 g (Higgins &



**Figure 1.** Generalized annual cycle of the Great Knot. The map shows the major flights (with Great Circle distances) for individuals flying from north-west Australia to Siberia via the northern Yellow Sea. Dark grey area shows the approximate breeding distribution (from Tomkovich 1997). The right hand plot shows the general timing of major events in Great Knot populations spending the non-breeding season in northern Australia.

Davies 1996). Departures for Asia occur in late March to early April (Wilson & Barter 1998, Battley *et al.* 2000).

## MATERIALS AND METHODS

### Study site

This study was performed at Roebuck Bay, Broome, north-west Australia (18°00'S, 122°22'E), a large intertidal bay that is home to tens of thousands of Arctic-breeding shorebirds during their non-breeding season, primarily Great Knots and Bar-tailed Godwits. Roebuck Bay is a departure point for shorebirds on their northward migration to Asia. Physically, the bay is characterized by a huge tidal range (up to 10 m amplitude on spring tides; less than 1 m on neap tides), and large soft mudflats that support one of the most diverse intertidal faunas documented (Tulp & de Goeij 1994, Pepping *et al.* 1999).

### Radiomarked population

Great Knots were caught by cannon-net on the northern shores of Roebuck Bay midway through the fuelling period, on 28 February 2000 (18 birds) and on 4 March 2000 (nine birds). Birds were radio-tagged with small (1.8 g) Holohil two-stage radio-transmitters that were glued to trimmed back feathers and underlying skin (similar to the method of Warnock & Warnock 1993, but using fast-bonding superglue rather than cyanoacrylate epoxy). There was no problem with transmitter loss, and several birds returned from breeding with transmitters still attached. Three age categories of Great Knots could be distinguished during the study period: (1) adults – these undergo extensive pre-alternate moult and premigratory mass gain, and have fresh primary feathers that had been replaced in a complete pre-basic moult during the austral summer; (2) first-year birds that had hatched in the previous boreal

summer (7–9 months earlier) – these do not develop breeding plumage or undergo premigratory mass gain, and retain juvenile primaries that are markedly more worn than in other Great Knots; (3) second-year birds (or older, potentially up to 4 years old) that are not yet old enough to migrate north. Great Knots in north-western Australia show delayed maturity, skipping their first two to four northward migrations and remaining on the non-breeding grounds (Higgins & Davies 1996, D.I.R. unpubl. data). Birds in this category have fresh primaries, similar in wear to those of adults, undergo relatively little premigratory mass gain and moult into a breeding plumage that is considerably duller than that of adults. In the hand, the greatest risk of incorrect ageing was through confusion of second-year birds with adults, especially early in the premigratory period when adults showed little pre-alternate moult or had not yet put on much weight. Only birds aged as in their second year or older were radiomarked, to maximize the chance of including birds about to migrate.

During processing we took biometrics and moult information, made ultrasound estimates of pectoral muscle thickness, took a blood sample for sexing and colour-banded each bird with a unique individual combination (see below). On some catches, birds had to be disturbed from neighbouring beaches, or coaxed to walk or fly into the catching area before firing the net. Such 'twinkling' may affect the composition of the catch, and it has been suggested that heavily twinkled flocks may show bunching of birds and be non-random samples of the local population (Rogers *et al.* 1997).

### The population as a whole

In addition to catches made when radiotagging birds, additional catches were made on 3 March, 19 March and 28 March to track the changes in condition of the Roebuck Bay population as a whole. Some birds from these catches were processed in the same detail as the radiomarked birds.

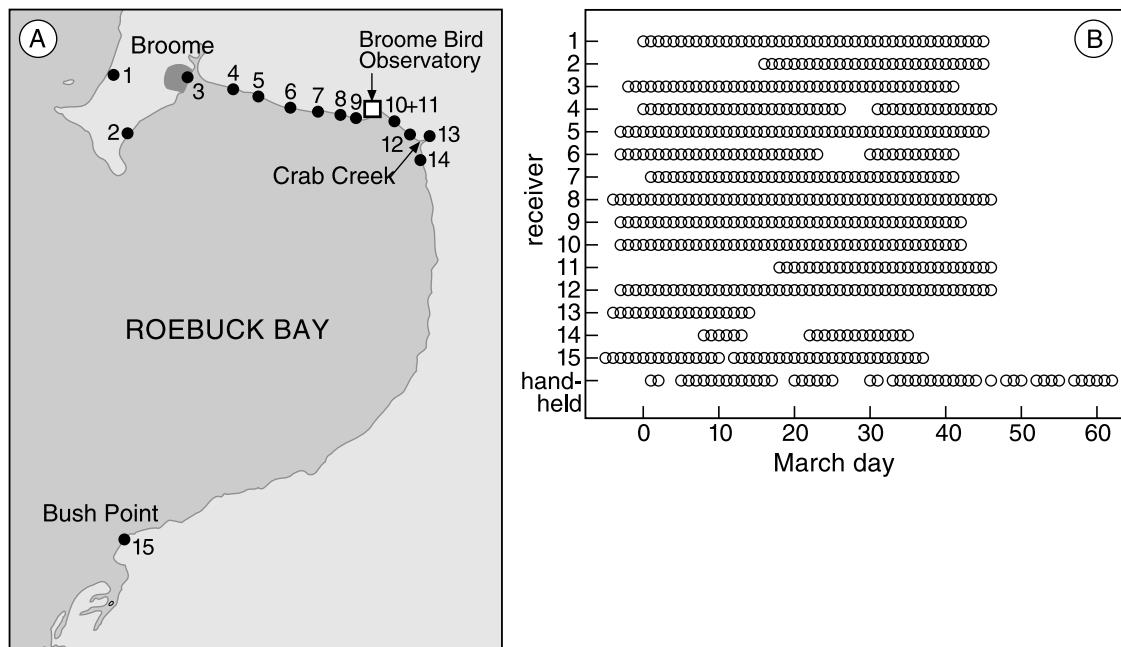
### Banding and biometrics

Each bird received a numbered metal band and a three-ring colour combination on its tarsi. D.I.R. collected all external biometric data using the methods of Higgins and Davies (1996): bill length (to the nearest 0.1 mm), head + bill length (0.1 mm), tarsus length (0.1 mm), tarsus + middle-toe length

(1 mm), wing length (maximum chord, 1 mm) and body mass (1 g). For biometric analyses an overall estimate of structural size was obtained by performing a principal components analysis (PCA) on four external measurements (bill, head + bill, tarsus and tarsus + toe) from all individuals caught. The first principal component (eigenvalue 2.621, explaining 65% of the variation in measurements) was saved and used as the size measure (hereafter 'size'). Loadings ranged from 0.710 to 0.906 for the four measurements. D.I.R. also scored primary wing moult using the methods of Higgins and Davies (1996) and total breeding plumage (as a percentage of the expected appearance of a fully moulted bird, based on both underpart and upperpart assessment). Breeding plumage scores were arcsin transformed for analyses, but original values are presented in figures. A small blood sample (approximately 40 µL) was taken from the brachial vein and stored in alcohol for sex determination, which was performed at the Royal Netherlands Institute for Sea Research (Texel) following the techniques verified for Red Knots (*C. canutus*) by Baker *et al.* (1999). Because birds will have lost an unknown mass between capture and weighing, mass at capture was estimated assuming a loss of 1% of body mass per hour (Wilson *et al.* 1999). This probably overestimated the mass loss for birds held for long periods, as birds were held in an air-conditioned room between capture and processing, and rates of mass loss seem to decline with time (Wilson *et al.* 1999). All biometric analyses were repeated using both original and adjusted body masses. Differences in results were trivial, and analyses presented here refer to the estimated body mass at capture rather than mass at weighing. Biometric relationships given in the results are of the models with the highest explained variance (based on the inclusion or exclusion of factors that were of themselves non-significant). For most analyses, all plausible first-order interactions were non-significant and the simpler models without interactions were used. The only exception (group breeding plumage scores: sex × size) relied on a single data point for significance, a large male with little breeding plumage. The simpler model without interactions was again used.

### Ultrasound procedures

Using techniques described elsewhere (Dietz *et al.* 1999), an estimate of the depth of the pectoral muscle adjacent to the keel was made using a Pie 200



**Figure 2.** (A) Location of automatic receivers around Roebuck Bay and the Broome peninsula. (B) Dates when scans were made using hand-held receivers. Hand-held scans did not necessarily cover the entire bay. Place names mentioned in the text are given on the map.

Scanner with a 7.5-MHz linear probe (Pie Medical Benelux BV, Maastricht, The Netherlands). In brief, the bird was placed on its back, the feathers smoothed away with a water-soluble gel and an ultrasound probe pressed against the skin of the bird. On the resulting monitor image, the limits of the organ were marked on screen, and the distance between the limits automatically calculated. A single estimate of the pectoral muscle depth of each bird was made by A.D.

### Ultrasound calibration

Organ size was estimated for ten Great Knot accidental casualties from north-west Australian catches (all from August–October 1998) by ultrasound, and the carcasses subsequently dissected and the fresh lean mass of the pectoral muscles determined (see Battley *et al.* 2000 for dissection protocols). Least-squares regression was used to create a predictive equation relating measured pectoral muscle mass to estimated pectoral muscle size. The ultrasound estimate of muscle thickness gave a good approximation to total pectoral muscle mass (total mass of left and right pectoral muscles): predicted pectoral muscle mass =  $-5.617 (\pm \text{se } 3.774) + 21.697 (\pm \text{se } 2.888) \times$  estimated muscle thickness ( $F_{1,8} = 56.443, P < 0.001,$

$R^2 = 0.876$ ). This equation was used to estimate pectoral muscle mass in Roebuck Bay birds in 2000.

### Automatic radiotracking procedures

Fourteen automatic radiotracking stations were positioned on hill- and dune-tops around northern Roebuck Bay (receivers 2–14) and overlooking Cable Beach (receiver 1), just around the Broome peninsula from Roebuck Bay (Fig. 2A; one unit was repositioned during the study). One receiver (number 15) was mounted above a distant roosting area at Bush Point that may be used by birds from northern Roebuck Bay during spring tides. The systems have been developed for use in the Dutch Wadden Sea (van Gils & Piersma 1999, van Gils *et al.* 2000), and consist of a non-directional antenna mounted on a short mast, attached to an interface, receiver and palm-top computer. Each frequency was scanned four times in 20 s, and the complete cycle of 52 frequencies (the remainder being on Red Knots, which are not analysed in this study) took 17.3 min. The regular spacing of the receivers along the northern shore of Roebuck Bay (Fig. 2A) gave extremely good coverage of the upper tidal flat and high tide shoreline, but birds were often able to walk out of range of the receivers during low tides. The dates on which the receivers were fully

operational in the field are shown in Figure 2(B). Most towers were in the field until mid-April (March day 41–46, where March 1 = March day 1), although two that could be reached only by boat or hovercraft were taken down earlier (Crab Creek, receiver 14, day 35; Bush Point, receiver 15, day 37).

### Hand-held radiotracking procedures

Hand-held radioscans were also made, partly to give immediate indications of the presence of birds (automatic stations were downloaded only every 5–7 days on average). Portable receivers (TRX-2000S, Wildlife Materials Inc., Carbondale, IL, USA) and directional Yagi antennae were used, mainly from cliff edges and dune-tops, but also sometimes from boat or hovercraft at low tide. Days when hand-held scans were made are also shown in Figure 2(B).

### Signal detection

The automatic receivers log the background 'noise' strength and the signal strength during scans. We assumed that a transmitter signal was received when its strength was 1.4 times the background noise. There was, however, a 'background' error rate in the receiving systems, giving rise to apparent signals. From transmitters we knew were not in the field at the time, the frequency of signals appeared to be around 0–3 times per day. If these errors occurred after a bird had departed, the estimated departure date would have been affected. To identify these errors we inspected plots of the number of signals received each day for each bird. In most birds there was an obvious drop in the number of signals each day at some stage during the migration period (e.g. from 25–100 signals down to 1–5). The infrequent signals we treated as errors.

### Determining departure date

Failure to detect a radiotagged bird does not necessarily mean it was absent, so estimates of departure date for individuals must be 'weighted' by the probability of the bird being present but undetected. This can be calculated from the relocation frequency up to the date on which the last record was made (for methods see Nebel *et al.* 2000). Based on the probability of detection over the period up to the last record, we calculated the date at which we were 95% certain that a bird has truly departed. This is referred to as the 95% departure date.

### Resightings

Regular scans of feeding and roosting birds were made using telescopes, looking for colour-banded and radiotagged birds. When a bird was located, its colour-band combination was noted and an estimate of the breeding plumage score was made (at distances of generally 50–100 m). Breeding plumage estimates in the field proved to be highly repeatable. Repeatabilities were calculated after Lessells and Boag (1987) for 15 individuals that were resighted a total of 37 times in the field (range 2–4 sightings per individual). The initial estimate, which was often made long before any field sightings, was not included. Most resightings were made once birds had reached high plumage scores. Consequently, repeatabilities were high, both for all pairs of consecutive estimates ( $r = 0.88$ ) and for all resightings of individual birds (repeatability  $r = 0.89$ ).

## RESULTS

### Variation in initial condition for radiotagged birds

The radiotagged Great Knots varied greatly in the extent of migratory preparation, with estimated capture masses of 155–240 g, flight muscle masses of 19.1–28.4 g and breeding plumage scores of 10–95% (Table 1). Overall variation between individuals in these measures was high (CVs of 11.3–34.7%) compared with equivalent structural measurements (CVs of 2.9–4.4%), reinforcing the view that the variation in our condition measures was due to migratory preparation and not to sexual size differences (females were on average 1.2–3.1% larger in external measurements; see Table 1).

Because captures were close together in time (28 February or 4 March), mean body masses, pectoral muscle masses and breeding plumage scores were not affected by capture date (*t*-tests, all  $P < 0.05$ ). Body mass was affected by sex and size, females being larger and heavier (adjusted least-squares mean 207.8 (se =  $\pm 7.9$ ) g for ten females vs. 184.5 (se =  $\pm 3.5$ ) g for 17 males; size  $F_{1,24} = 9.777$ ,  $P = 0.005$ ; sex  $F_{1,24} = 5.363$ ,  $P = 0.029$ ;  $R^2 = 0.487$ ). Predicted pectoral muscle was related only to body mass (sex  $F_{1,20} = 2.491$ ,  $P = 0.128$ ; size  $F_{1,23} = 0.854$ ,  $P = 0.365$ ; mass  $F_{1,23} = 15.700$ ,  $P = 0.001$ ;  $R^2 = 0.442$ ).

Breeding plumage score was not related to body mass if considered in isolation ( $F_{1,25} = 0.711$ ,  $P = 0.407$ ). This was because females, in particular, and some larger

**Table 1.** Biometric characteristics of radiotagged birds in this study. All birds were aged on plumage characteristics as adult (age 2+ years). Birds are ordered by sex and capture date.

Individual (colour band)	Caught	Sex	Bill (mm)	Total head (mm)	Tarsus + toe (mm)	Tarsus (mm)	Wing (mm)	Size <sup>a</sup>	Mass at weighing (g)	Estimated capture mass <sup>b</sup> (g)	Flight muscle mass (g)	Primary moult	BMI <sup>c</sup>	Breeding plumage (%)
BR-YM	28 Feb.	m	42.2	73.1	69	34.4	193	-0.940	172	181	23.2	N <sup>10</sup>	0	90
BY-RM	28 Feb.	m	44.8	76.1	69	35.9	190	1.105	194	199	26.3	N <sup>10</sup>	1	60
BY-YM	28 Feb.	m	42.8	73.4	70	35.5	190	-0.077	172	182	22.2	N <sup>10</sup>	2	60
RB-RM	28 Feb.	m	41.5	71.8	65	32.9	180	-2.921	180	183	26.7	N <sup>10</sup>	0	80
RB-YM	28 Feb.	m	44.1	76.5	68	34.6	189	0.326	169p	176	20.4	N <sup>10</sup>	1	90
RR-YM	28 Feb.	m	42.5	74.8	66	35.1	187	-0.855	179	188	28.5	N <sup>10</sup>	1	60
RW-BM	28 Feb.	m	41.3	72.7	70	36.2	187	-0.440	161	173	21.7	N <sup>10</sup>	2	50
RW-RM	28 Feb.	m	46.5	78.8	69	34.7	190	1.871	213	217	27.2	N <sup>10</sup>	0	80
RW-YM	28 Feb.	m	40.7	71.2	67	33.9	184	-2.495	161	171	21.9	N <sup>10</sup>	1	95
RY-YM	28 Feb.	m	39.9	69.1	63	31.5	181	-5.028	148	155	20.0	N <sup>10</sup>	0	80
YB-RM	28 Feb.	m	44.9	76.1	68	35.5	195	0.764	189	194	25.4	N <sup>10</sup>	0	80
YY-RM	28 Feb.	m	45.5	77.1	70	36.6	194	2.039	186	192	26.7	N <sup>10</sup>	2	50
RR-WM	04 Mar.	m	43.5	75.2	67	36.2	190	0.148	157	166	20.0	N <sup>10</sup>	1	70
RY-WM	04 Mar.	m	42.5	74.9	66	34.4	181	-1.074	181	192	25.0	N <sup>10</sup>	1	90
RY-WM	04 Mar.	m	42.5	74.9	66	34.4	181	-1.074	181	192	25.0	N <sup>10</sup>	1	90
WR-BM	04 Mar.	m	44.7	75.1	70	36.4	194	1.220	181	191	21.7	N <sup>10</sup>	0	50
WY-BM	04 Mar.	m	43.8	75.1	65	34.3	188	-0.918	187	196	25.8	N <sup>10</sup>	1	80
YY-BM	04 Mar.	m	42.6	71.7	66	33.1	188	-2.336	174	183	25.4	N <sup>10</sup>	1	80
BB-RM	28 Feb.	f	44.0	75.5	70	34.1	(182)	0.321	172	176	25.0	N <sup>9</sup> 4 <sup>1</sup> 2 <sup>1</sup>	2	10
BB-YM	28 Feb.	f	45.0	75.2	69	33.0	193	-0.089	202	213	26.1	N <sup>10</sup>	2	80
BR-BM	28 Feb.	f	43.3	74.6	67	34.4	198	-0.696	223	241	28.5	N <sup>10</sup>	1	80
BR-RM	28 Feb.	f	44.1	74.8	68	36.1	196	0.408	208	213	28.0	N <sup>10</sup>	2	90
RY-RM	28 Feb.	f	42.2	73.7	69	35.6	191	-0.364	206	210	25.4	N <sup>10</sup>	0	70
YR-YM	28 Feb.	f	46.4	78.9	72	37.6	195	3.573	215	228	24.5	N <sup>10</sup>	1	70
RO-WM	04 Mar.	f	48.1	74.3	73	36.7	199	4.073	209	223	28.5	N <sup>10</sup>	1	80
RW-WM	04 Mar.	f	42.9	75.0	69	34.7	191	-0.141	191	204	21.7	N <sup>10</sup>	0	90
YR-WM	04 Mar.	f	43.7	73	66	34.2	198	-1.300	147	155	19.1	N <sup>10</sup>	1	10
YW-BM	04 Mar.	f	46.8	78.1	69	35.2	197	1.949	208	218	19.6	N <sup>10</sup>	0	20
Male mean			43.2	74.3	67.5	34.8	188.3		176.7	184.6	24.0			73.2
Male min.			39.9	69.1	63.0	31.5	180		148	156	20.0			50.0
Male max.			46.5	78.8	70.0	36.6	195		213	217	28.4			95.0
Female mean			44.7	75.3	69.2	35.2	194.0		198.1	208.2	24.6			60.0
Female min.			44.2	73.0	66.0	33.0	182		147	155	19.1			10.0
Female max.			48.1	78.9	73.0	37.6	199		223	241	28.4			90.0
Overall mean			43.7	74.7	68.1	34.9	190.4		184.6	193.2	24.2			68.3
CV (%)			4.4	3.0	3.3	3.9	2.9		11.3	11.3	12.3			34.7

<sup>a</sup>First principal component from a principal components analysis of structural measurements from all measured individuals.

<sup>b</sup>Assumes 1% body mass per hour after capture.

<sup>c</sup>BMI, body moult intensity, on a scale of 0 (no moult) to 3 (heavy moult).

birds of both sexes, had low breeding plumage scores. Sex and size had negative effects on breeding plumage (sex  $F_{1,23} = 4.969$ ,  $P = 0.036$ ; size  $F_{1,23} = 6.004$ ,  $P = 0.022$ ), whereas body mass had a positive influence ( $F_{1,23} = 9.309$ ,  $P = 0.006$ ;  $R^2 = 0.348$ ). At capture then, heavier birds had higher breeding plumage scores after size effects were factored out.

To calculate independent relative condition indices for the radiotagged individuals, residuals were saved

from the biometric analyses outlined above. The residuals represent the unexplained variation of body mass as a function of size and sex, predicted pectoral muscle mass and breeding plumage score as functions of body mass, size and sex. These are referred to as residual body mass, residual pectoral muscle mass and residual breeding plumage score, respectively. If all aspects of migratory preparation were tightly linked, then residual variation would be correlated

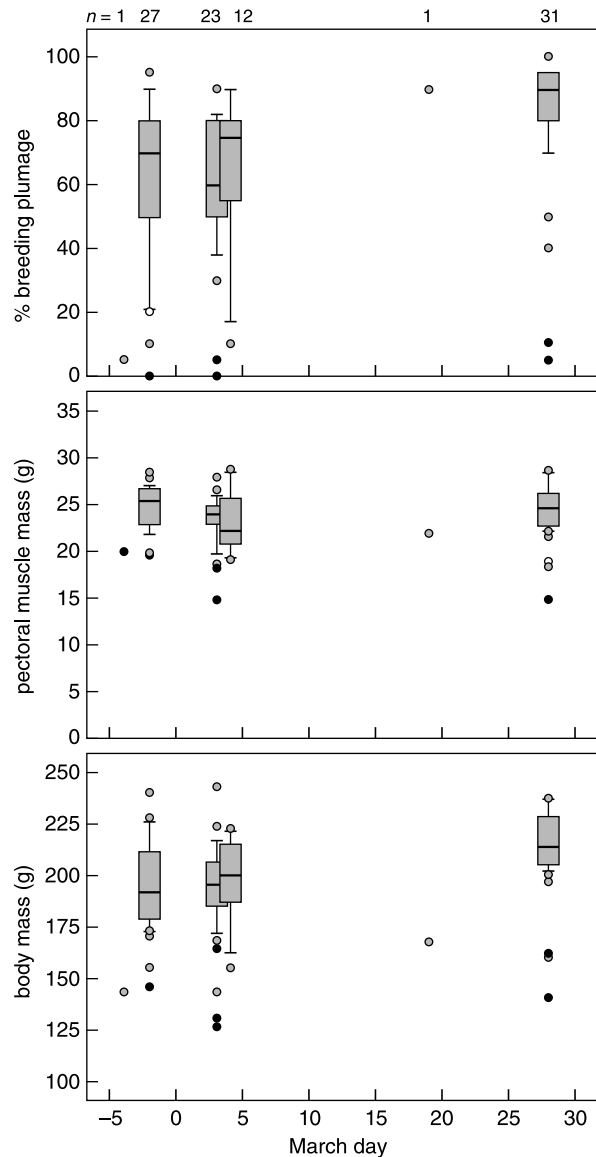
also. A bird 'ahead of schedule' would be heavy, with large pectoral muscles and a high breeding plumage score. However, the residual ranks were not correlated with each other, indicating that at the individual level, there was little association between these three aspects of migratory preparation ( $r < 0.25$ ,  $P > 0.2$ ).

Not all birds had completed wing moult (Table 1). One bird (female, 28 February, colour-band BB-RM) was still growing the outer two primary feathers, and had a very low plumage score (10%). It was obviously 'behind schedule' or, more likely, not going to migrate.

### Changes between initial condition and departure condition

#### Group changes over time

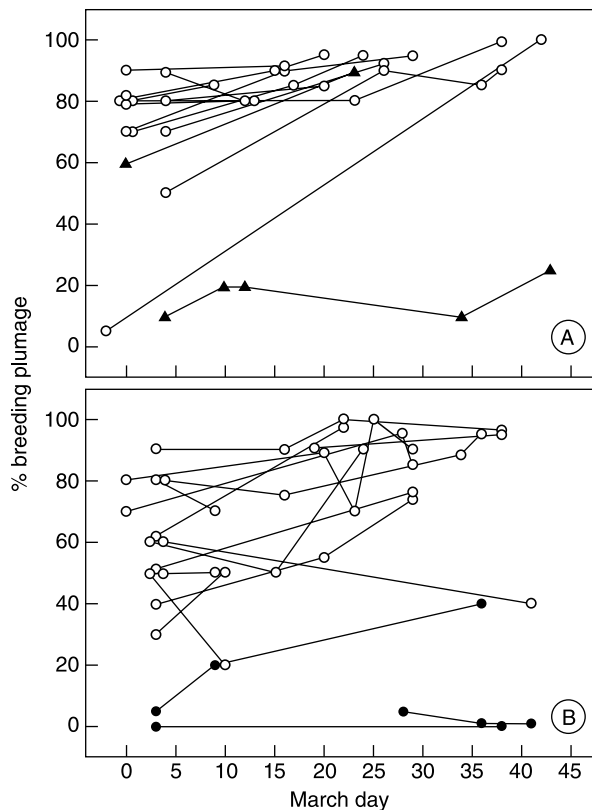
Too few catches were made to describe the changes in the general Great Knot population accurately during migratory fuelling, and even the catches that were made did not appear to describe the changes in body mass and plumage realistically (Fig. 3). Heavy birds were under-represented in the catches. In the late catch, this could have resulted from heavy birds having already left on migration. 'Twinkling' birds into the catching area may also have affected the composition of the catch. Birds had also already undergone considerable body moult before catching started. Whereas individual catches suggested there was no large increase over time in either breeding plumage or body mass, analyses across all adult birds caught during the study showed that both body mass and breeding plumage score increased with date of capture. Just as in the smaller radiotagged sample, larger birds and females were heavier (body mass was positively related to size,  $F_{1,87} = 23.084$ ,  $P < 0.001$ ; sex effect,  $F_{1,87} = 37.846$ ,  $P < 0.001$ ), but body mass also increased with date ( $F_{1,87} = 34.398$ ,  $P < 0.001$ ;  $R^2 = 0.585$ ). Predicted pectoral muscle mass, however, though heavier in males and positively related to body mass (adjusted least-squares means, male =  $25.2 \pm 0.3$  g, female =  $23.4 \pm 0.4$  g,  $n = 49$  and  $42$ , respectively, sex effect,  $F_{1,86} = 11.029$ ,  $P < 0.001$ ; body mass,  $F_{1,86} = 46.525$ ,  $P < 0.001$ ), was not related to body size ( $F_{1,86} = 0.629$ ,  $P = 0.426$ ) and was negatively related to day of capture ( $F_{1,86} = 7.239$ ,  $P = 0.009$ ;  $R^2 = 0.396$ ). The last finding is presumably not a biological reality (as pectoral muscle mass is expected to increase with body mass). Breeding plumage was again lower in females (sex,  $F_{1,86} = 10.196$ ,  $P = 0.002$ ) but increased with body mass and date (mass,  $F_{1,86} = 7.133$ ,  $P = 0.009$ ; date,  $F_{1,86} = 13.399$ ; size was non-significant;  $R^2 = 0.357$ ).



**Figure 3.** Changes in body mass, predicted pectoral muscle mass and breeding plumage over time in Great Knots in Roebuck Bay, north-west Australia, in February–March 2000. Boxes are adults, with sample sizes above the upper plot (note that pectoral muscle mass on day 28 represents only 25 birds). Black circles represent individual subadult birds.

#### Individual changes over time: breeding plumage

Resightings of colour-banded Great Knots showed that breeding plumage scores increased over the fuelling period, with variation in plumage score between birds greatly reduced late in the fuelling period compared with the variation at capture (Fig. 4). The frequency of resightings was too low to determine whether individuals differed in when they reached their final plumage level. Some variation



**Figure 4.** Breeding plumage changes in individual (A) radiotagged and (B) colour-banded Great Knots in February–April 2000. The first point for each bird represents the plumage estimate when caught. Subsequent points represent estimates made in the field. Open circles in (A) are birds that subsequently migrated; black triangles are birds that did not migrate. Open circles in (B) are birds aged as adults (age 2+ years); black circles are birds aged as subadult. Overlapping points have been shifted slightly for clarity.

in plumage score did persist late in the fuelling period (Fig. 4), but breeding plumage score may more reliably have indicated variation in migratory preparation early rather than late in the process. Figure 4 also shows that individuals did not leave Roebuck Bay once they had reached a high breeding plumage score, implying that moult occurred earlier or faster than fuelling, and that early departures did not generally result in departures of partially moulted birds.

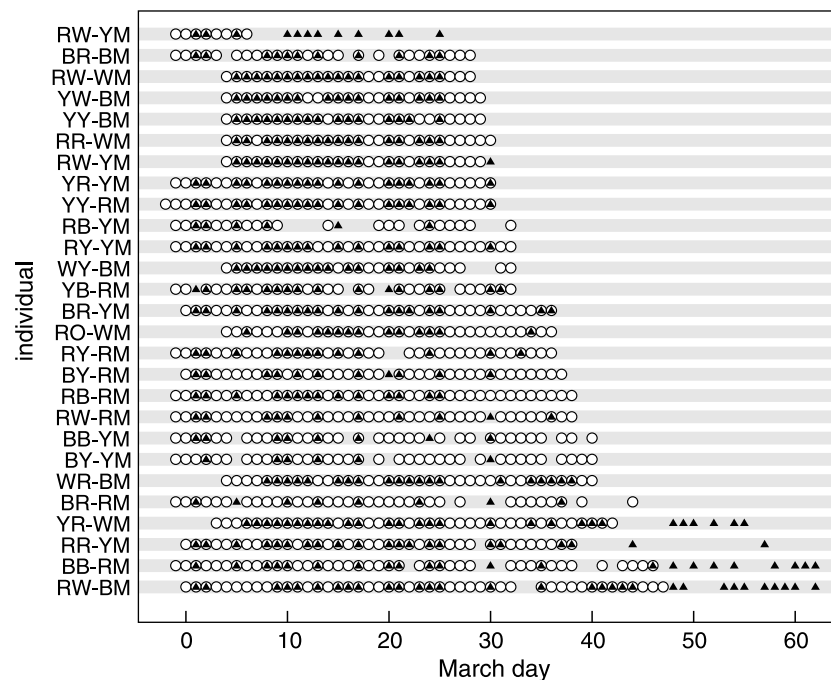
### Departure date in relation to starting condition

Of the 27 radiotagged Great Knots, 23 were assumed to leave Roebuck Bay on migration (Fig. 5). Four birds were still recorded during hand-held receiver scans at the end of April. Because birds were recorded so frequently, there was little statistical uncertainty about the departure dates (median 95% certainty interval = 0 days, mean 0.6 days, range 0–3.0 days). Birds departed from 25 March (day 25) to 13 April (day 44). Male and female Great Knots did not differ in their departure dates (means – male March day 33.4, female March day 33.9; Mann–Whitney  $U$ -test,  $U = 55.0$ ,  $P = 0.75$ ).

To determine whether departure date was affected by body condition, we tested, in turn, whether sex, size or sex + size explained variation in departure date. We then tested each of the three condition variables in combination with sex and size. None of the models tested affected departure date (Table 2). Our conclusions were the same if the 95% departure date was used, and if sexes were analysed separately. Therefore, there was no evidence that variation in

**Table 2.** Results of analyses testing whether departure dates of individual Great Knots were affected by sex, size or three condition indices (body mass, pectoral muscle mass and breeding plumage).

Independent variable(s)	Variable	<i>df</i>	<i>F</i> -ratio	<i>P</i>	<i>R</i> <sup>2</sup>
sex	sex	1,21	0.046	0.832	0.002
size	size	1,21	0.542	0.470	0.025
sex, size	sex	1,20	0.005	0.942	0.025
	size	1,20	0.477	0.498	
sex, size, body mass	sex	1,19	0.056	0.815	0.029
	size	1,19	0.171	0.684	
	body mass	1,19	0.066	0.799	
sex, size, pectoral muscle mass	sex	1,19	0.087	0.771	0.114
	size	1,19	0.210	0.652	
	pectoral mass	1,19	1.896	0.185	
sex, size, breeding plumage	sex	1,19	0.004	0.952	0.026
	size	1,19	0.326	0.575	
	breeding plumage	1,19	0.009	0.926	



**Figure 5.** Daily recording of radiotagged Great Knots by automatic or hand-held receivers. The dark grey panel from March days 41–46 shows when most automatic receivers were taken down. Circles are automatic receiver records; triangles are hand-held receiver records.

condition partway through the migratory fuelling period translated into variation in departure date.

The four birds that did not migrate had significantly lower residual body masses and residual breeding plumage scores when caught than the birds that did migrate (Mann–Whitney  $U$ -tests, body mass,  $U_{4,23} = 15$ ,  $P = 0.034$ ; breeding plumage,  $U_{4,23} = 8$ ,  $P = 0.009$ ). Residual pectoral muscle masses did not differ ( $P = 0.133$ ).

## DISCUSSION

The radiotagged birds were caught in the middle of the fuelling period and showed large variation in physical condition, reflecting apparently marked differences in migratory preparation. This variation in condition did not, however, translate directly into variation in departure dates. Condition indices were also not correlated with each other, indicating that whereas a bird may have been heavier than average for its size, this did not necessarily mean that it had equivalently large pectoral muscles or a higher breeding plumage score.

The only significant difference in condition we found was between the 23 birds that migrated and the four that did not, with the non-migrants on average

having lower body masses and breeding plumage scores. This could indicate simply that the birds that remained in Roebuck Bay were immatures that would not have migrated in any circumstances. For the birds that did embark on a long migratory flight, the key finding of this analysis was that none of the fuelling measures explained variation in the dates on which individual birds departed. This result was not because there was no variation in departure date itself; Figure 5 shows that birds left over a span of almost 3 weeks, and the high daily recording rates (themselves usually based on multiple recordings) gave rise to robust departure date estimates.

Our predictions had three outcomes: (1) if birds have inflexible schedules, departures will be spread out and a negative relationship will exist between relative condition and departure date; (2) if birds have flexible schedules and can catch up when fuelling, departures will be synchronized and will not relate to relative condition; and (3) if birds prioritize time over energy or plumage, departures will also be synchronized and unrelated to initial condition. These predictions are all based on the assumption that time of departure is selectively important to individuals. Instead, we had apparently unsynchronized departures that were unrelated to earlier condition.

Does this mean that (a) we have measured the wrong currencies, or at the wrong time, (b) Great Knots are exceptions to general patterns or (c) the observed departure pattern is a more general feature of birds embarking on the first leg of a long migration?

### **Have we measured the wrong currencies, or at the wrong time?**

Optimality models of migratory schedules focus on the rate of fuel deposition as one of the determinants of a (variable) departure fuel load, so there may be no expectation that a one-off measure of body condition would necessarily relate to departure date. We do not think this is valid for our study for two reasons. First, models for birds migrating between discrete, distant sites predict that departure fuel loads will be relatively insensitive to variation in fuelling rate (Weber *et al.* 1998). Secondly, if birds cannot predict winds along the route (Weber & Hedenström 2001), departure fuel loads should be constant and determined by the worst possible wind conditions (Weber *et al.* 1998). Accordingly, we do not expect large differences in departure body condition for waders undertaking such a long flight as that made by Great Knots, where winds on the latter half of the journey are unlikely to be correlated with departure conditions, and the energetic margins of error are slim. We note, however, that body composition data suggest that males may be as fat as females during fuelling, even though lighter in total mass (Battley *et al.* 2001).

Alternatively, we could have caught birds too early for body condition at capture to relate meaningfully to condition during departure. But given that differences in condition at capture represent birds being at different points along their individual fuelling trajectories, for our data to be unreliable birds must either have changed their fuelling rates, or not left immediately upon reaching departure condition. Birds at departure mass are predicted to wait for favourable winds in some conditions (Weber & Hedenström 2000), but in this study departures were spread evenly across the departure window (Fig. 5), suggesting that suitable conditions for departure were present on most days. Although it is undeniable that data on individual fuelling rates and departure masses would be preferable, comparing relative condition during fuelling with departure date should be a valid test of whether early condition influences departure date in birds for which time is of the essence.

### **Are Great Knots exceptions to general patterns?**

In terms of the timing and duration of the departure period, Great Knots are similar to other waders overwintering in Australia (Tulp *et al.* 1994, Hassell 2000) and West Africa (Piersma *et al.* 1990). In terms of consistency of mass gain, the masses of individual Great Knots caught in different years in north-west Australia showed no correlation (a positive relationship between mass and date is expected if birds fuel along similar trajectories in different years; Barter & Minton 1998). Of seven species studied, three did not show the expected relationship. It is possible that Great Knots are unusual in their fuelling patterns; if so, this requires explanation.

### **Is there a more general alternative explanation?**

Birds fuelling for the first flight of a northward migration do so some 2–3 months before the breeding season, and selective pressures may intensify as birds near the breeding grounds. Direct benefits to early arrival are arguably stronger and more immediate in birds arriving on the breeding grounds compared with birds on staging areas. In addition to the breeding benefits described for passerines (see Introduction), early arrival may enable early territory establishment as breeding grounds become snow-free in spring. But the consequences of inadequate preparation may also be higher in breeding than in staging birds. Because internal organs may be reduced in size during flight (Battley *et al.* 2000, 2001), inadequately fuelled birds may suffer a reduction in their functional capacity upon arrival. Such deficits might be redressed during refuelling on the staging grounds, but delays upon arrival on the breeding grounds could counteract any benefits to early arrival. Birds that are inadequately fuelled may also lack the stored nutrients that could be used as a buffer against bad weather (Davidson & Evans 1988), in egg formation (though Klaassen *et al.* 2001 demonstrated that several Arctic waders are not capital breeders) or as energy for displays.

For some species, elaboration of the breeding plumage on the final staging sites could benefit a bird by giving it mating advantages or increasing camouflage when breeding in the open. Hence, the pressure to be adequately prepared before migration to the breeding grounds, combined with the shorter fuelling period compared with earlier staging sites,

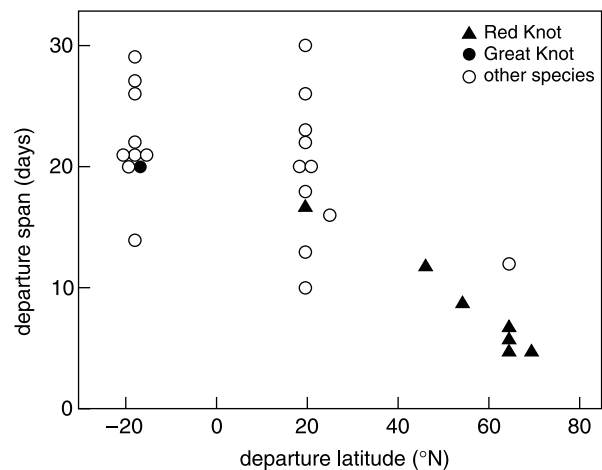
may make waders more time-constrained at the ultimate than at the initial fuelling site.

This could partially explain why most studies that have searched for a relationship between body condition and length of stay on staging grounds (which is an equivalent test to ours when birds are passing through a site; Lyons & Haig 1995, Iverson *et al.* 1996, Figuerola & Bortolero 1998, Warnock & Bishop 1998, Farmer & Wiens 1999) have failed to find a relationship, or found only a weak relationship. A negative relationship between length of stay and body condition has been detected in only two northward-migrating waders – White-rumped Sandpipers *Calidris fuscicollis* heading north in Kansas in one of two years (Skagen & Knopf 1994) and male Western Sandpipers *C. mauri* heading north at one of five sites on the North American Pacific coast (Iverson *et al.* 1996 – note that using an expanded data set, Warnock & Bishop 1998 could not confirm this).

Several studies indicate that the length of stay decreases as the migration season progresses (for both northward and southward migrations; Lank 1983, Skagen & Knopf 1994, Lyons & Haig 1995, Iverson *et al.* 1996, Pfister *et al.* 1998, Farmer & Wiens 1999), suggesting that for some species (at least at some sites), timing of migration becomes more constrained later in the season (or migration strategies differ amongst individuals migrating at different times). In Pectoral Sandpipers *C. melanotos*, the migration window (number of days on which birds were present at a site) became shorter as birds migrated north through North America (Farmer & Wiens 1999). At the individual (length of stay) and population (migration window) levels, migration may become more compressed with time.

Great Knots certainly spend less time fuelling for final flights to the breeding grounds. In north-west Australia, birds begin to moult and increase mass from late January or early February but depart only from late March to mid-April, leaving 8–10 weeks for fuelling. After flying probably directly to eastern Asia, they refuel in the northern Yellow Sea for a final flight to the breeding grounds (Barter *et al.* 1997, Wilson & Barter 1998). Numbers of Great Knots in the northern Yellow Sea increase between mid-April and mid-May (Barter *et al.* 2000), so staging birds probably have a maximum of 4–5 weeks before departures to the breeding grounds from the third week of May.

The proposition that the timing of migration becomes more constrained as the breeding grounds are approached is supported by a comparison of



**Figure 6.** Departure span (days from first to last migratory departure) of northward migrating waders in relation to latitude of the departure site. The sites with multiple departures are Roebuck Bay, north-west Australia at  $-18^{\circ}\text{N}$  and Banc d'Arguin, Mauritania, at  $+20^{\circ}\text{N}$ . Sources of data are: this study; Dick *et al.* (1987), Alerstam *et al.* (1990), Piersma *et al.* (1990), Gudmundsson and Lindström (1992), Morrison and Wilson (1992), Strann (1992), Marks and Redmond (1994) and Hassell (2000). If reported, only studies involving > 10 flocks are used. Red Knot data refer to the subspecies *islandica* leaving Norway and Iceland for Greenland and north-east Canada, and *canutus* leaving France for Germany, and leaving Germany for Siberia. Some points are offset along the x-axis to avoid overlapping. Three species (Redshank *Tringa totanus*, Dunlin *Calidris alpina* and Ringed Plover *Charadrius hiaticula*) with extremely wide ranges in breeding latitudes and very long departure spans in Piersma *et al.* (1990) were not included in the analysis.

departure spans of waders embarking on migration in relation to the latitude of the departure site (Fig. 6). Birds leaving non-breeding or southerly staging grounds departed over periods of 10–30 days (mean 20 days). Although data for northward departures from northern staging sites are fewer, those for Red Knots migrating along Atlantic coasts show that the migration span decreases the further birds are through the migration, from 17 days in Mauritania to 5 days in Norway and Iceland (span =  $22.413 - 0.251 \times \text{latitude}$ ,  $P < 0.001$ ,  $R^2 = 0.968$ ). Not only are departures in the far north compressed in time, but they are also consistent between years. Over 6 years of study in Norway and 3 years in Iceland, the majority of Red Knots departed within the same 5–6-day period at the end of May (Strann 1992 and Alerstam *et al.* 1990, respectively).

Because final departures to the breeding grounds are so tight in their timing, there may actually be little scope for condition-dependent variation in the

timing of departure from the staging sites. The costs of being late may be so high that birds simply must leave on time if they are to have any chance of securing a mate. In the only study of breeding Great Knots, Tomkovich (1996) found that males appeared on the territories in late May, where they were soon joined by females. Of eight recognizable males that arrived between 22 and 26 May, two that arrived on 26 May did not pair up during that season. Females paired with males from the day of arrival up to 5 days later. If birds must arrive early on the breeding grounds then differences in condition during fuelling are likely to result in variation in body condition on arrival rather than variation in arrival time.

Although we found no evidence for condition-dependent departures in Great Knots leaving Australia on the northward migration, we do not believe that this necessarily means that time is not a selective factor in their migration. Instead, strong selective pressures may occur only during the second major staging period, in northern Asia. Testing for individual variation in departure dates of Great Knots at the final staging site may be complicated by the geographical extent of the breeding grounds. Although almost all Great Knots are found in the northern Yellow Sea in May, there is an almost twofold range in the distance to breeding destinations for birds migrating to different parts of eastern Russia. For birds fuelling at Laiodong Wan in the northern Yellow Sea, China (41°00'N, 121°30'E), a flight to the Aldan River basin (62°N, 140°E) would be 2700 km, whereas a flight to Chukotka Peninsula (66°N, 172°E) would be 4150 km (see Fig. 1). Such large differences in flight length could give rise to individual variation in optimal departure time, particularly if snowmelt also varied systematically between areas.

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## REFERENCES

- Åkesson, S., Alerstam, T. & Hedenström, A. 1996. Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at night. *J. Avian Biol.* **27**: 95–102.
- Alerstam, T., Gudmundsson, G.A., Jönsson, P.E., Karlsson, J. & Lindström, Å. 1990. Orientation, migration routes and flight behaviour of Knots, Turnstones and Brant Geese departing from Iceland in spring. *Arctic* **43**: 201–214.
- Baker, A.J., Piersma, T. & Greenslade, A.D. 1999. Molecular vs. phenotypic sexing in Red Knots. *Condor* **101**: 887–893.
- Barter, M.A. & Minton, C. 1998. Can pre-migratory weight gain be used to predict departure weights of individual waders from North-Western Australia? *Stilt* **32**: 5–15.
- Barter, M., Tonkinson, D., Tang, S.X., Yuan, X. & Qian, F.W. 1997. Staging of Great Knot *Calidris tenuirostris*, Red Knot *C. canutus* and Bar-tailed Godwit *Limosa lapponica* at Chongming Dao, Shanghai: Jumpers to Hoppers? *Stilt* **31**: 2–11.
- Barter, M.A., Wilson, J.R., Li, Z.W., Li, Y.X., Yang, Y.C., Li, X.J., Liu, Y.F. & Tian, H.S. 2000. A comparison of shorebird numbers in the Shuangtaizihekou National Nature Reserve, Liaoning Province, China, during the 1998 and 1999 northward migrations. In Chen, *et al.* (eds) *Shorebird Survey in China. 1999*: 72–84. Beijing: Wetlands International-China Program, and Canberra: Wetlands International-Oceania.
- Battley, P.F., Piersma, T., Dietz, M.W., Tang, S., Dekinga, A. & Hulsman, K. 2000. Empirical evidence for differential organ reduction during trans-oceanic bird flight. *Proc. R. Soc. Lond. B* **267**: 191–195.
- Battley, P.F., Dietz, M.W., Piersma, T., Dekinga, A., Tang, S. & Hulsman, K. 2001. Is long-distance bird flight equivalent to a high-energy fast? Body composition changes in freely migrating and captive fasting Great Knots. *Physiol. Biochem. Zool.* **94**: 435–449.
- Beintema, A.J. & Drost, N. 1986. Migration of the Black-tailed Godwit. *Le Gerfaut* **76**: 37–62.
- Currie, D., Thompson, D.B.A. & Burke, T. 2000. Patterns of territory settlement and consequences for breeding success in the Wheatear *Oenanthe oenanthe*. *Ibis* **142**: 389–398.
- Davidson, N.C. & Evans, P.R. 1988. Prebreeding accumulation of fat and muscle protein in Arctic-breeding shorebirds. *Acta Congr. Int. Ornithol.* **19**: 342–352.
- Dick, W.J.A., Piersma, T. & Prokosch, P. 1987. Spring migration of the Siberian Knots *Calidris canutus canutus*: results of a co-operative Wader Study Group project. *Ornis Scand.* **18**: 5–16.
- Dietz, M.W., Dekinga, A., Piersma, T. & Verhulst, S. 1999. Estimating organ size in small migrating shorebirds with

- ultrasonography: an intercalibration exercise. *Physiol. Biochem. Zool.* **72**: 28–37.
- Drent, R., Both, C., Green, M., Madsen, J. & Piersma, T.** 2003. Pay-offs and penalties of competing migratory schedules. *Oikos* **103**: 274–292.
- Farmer, A.H. & Parent, A.H.** 1997. Effects of the landscape on shorebird movements at spring migration stopovers. *Condor* **99**: 698–707.
- Farmer, A.H. & Wiens, J.A.** 1999. Models and reality: time–energy trade-offs in Pectoral Sandpiper (*Calidris melanotos*) migration. *Ecology* **80**: 2566–2580.
- Figuerola, J. & Bortolero, A.** 1998. Sex differences in the stop-over ecology of Curlew Sandpipers *Calidris ferruginea* at a refuelling area during autumn migration. *Bird Study* **45**: 313–319.
- van Gils, J. & Piersma, T.** 1999. Day- and night-time movements of radiomarked Red Knots staging in the western Wadden Sea in July–August 1995. *Wader Study Group Bull.* **89**: 36–44.
- van Gils, J., Piersma, T., Dekinga, A. & Spaans, B.** 2000. Voortdurend in de lucht: zender-onderzoek aan Kanoeten in de westelijke Waddenzee. *Limosa* **73**: 29–34.
- Gudmundsson, G.A. & Lindström, Å.** 1992. Spring migration of Sanderlings *Calidris alba* through SW Iceland: wherefrom and whereto? *Ardea* **80**: 315–326.
- Hassell, C.** 2000. *Migration Report April 2000 for Broome International Airport*. Unpublished report.
- Hasselquist, D.** 1998. Polygyny in Great Reed Warblers: a long-term study of factors contributing to male fitness. *Ecology* **79**: 2376–2390.
- Higgins, P.J. & Davies, S.J.J.F.** 1996. *Handbook of Australian, New Zealand and Antarctic Birds*, Vol. 3. Melbourne: Oxford University Press.
- Iverson, G.C., Warnock, S.E., Butler, R.W., Bishop, M.A. & Warnock, N.** 1996. Spring migration of Western Sandpipers along the Pacific coast of North America: a telemetry study. *Condor* **98**: 10–21.
- Jukema, J. & Piersma, T.** 2000. Contour feather moult of Ruffs *Philomachus pugnax* during northward migration, with notes on homology of nuptial plumages in scolopacid waders. *Ibis* **142**: 289–296.
- Klaassen, M., Lindström, Å., Møltøfte, H. & Piersma, T.** 2001. Arctic waders are not capital breeders. *Nature* **413**: 714.
- Kokko, H.** 1999. Competition for early arrival in migratory birds. *J. Anim. Ecol.* **68**: 940–950.
- Kvist, A., Lindström, Å., Green, M., Piersma, T. & Visser, G.H.** 2001. Carrying large fuel loads during sustained bird flight is cheaper than expected. *Nature* **413**: 730–732.
- Lank, D.B.** 1983. *Migratory Behavior of Semipalmated Sandpipers at Inland and Coastal Staging Areas*. Unpubl. PhD Thesis, Cornell University.
- Lessells, C.M. & Boag, P.T.** 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**: 116–121.
- Lindström, Å. & Alerstam, T.** 1992. Optimal fat loads in migrating birds: a test of the time-minimization hypothesis. *American Naturalist* **140**: 477–491.
- Lyons, J.E. & Haig, S.M.** 1995. Fat content and stopover ecology of spring migrant Semipalmated Sandpipers in South Carolina. *Condor* **97**: 427–437.
- Marks, J.S. & Redmond, R.L.** 1994. Migration of Bristle-thighed Curlews on Laysan Island: timing, behaviour and estimated flight range. *Condor* **96**: 316–330.
- Møller, A.P.** 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. *Behav. Ecol. Sociobiol.* **35**: 115–122.
- Moore, F.R. & Aborn, D.A.** 1996. Time of departure by Summer Tanagers (*Piranga rubra*) from a stopover site following spring trans-gulf migration. *Auk* **113**: 949–952.
- Morrison, R.I.G. & Wilson, J.R.** 1992. Observations of Knot migration in Iceland 1970–1971. *Wader Study Group Bull.* **64** (Suppl.): 91–94.
- Morton, M.L. & Pereyra, M.E.** 1994. Autumnal migration departure schedules in Mountain White-crowned Sparrows. *Condor* **96**: 1020–1029.
- Nebel, S., Piersma, T., van Gils, J., Dekinga, A. & Spaans, B.** 2000. Length of stopover, fuel storage and a sex-bias in the occurrence of Red Knots *Calidris canutus* and *C. c. islandica* in the Wadden Sea during southward migration. *Ardea* **88**: 165–176.
- Nolet, B.A. & Drent, R.H.** 1998. Bewick's Swans refuelling on pondweed tubers in the Dvina Bay (White Sea) during their spring migration: first come, first served. *J. Avian Biol.* **29**: 574–581.
- Owens, I.P.F., Burke, T. & Thompson, D.B.A.** 1994. Extraordinary sex roles in the Eurasian Dotterel: female mating arenas, female–female competition, and female mate choice. *Am. Natur.* **144**: 76–100.
- Pepping, M., Piersma, T., Pearson, G. & Lavaleye, M. (eds)** 1999. *Intertidal Sediments and Benthic Animals of Roebuck Bay, Western Australia*. NIOZ-Report 1999–3. Texel: NIOZ.
- Pfister, C., Kasprzyk, M.J. & Harrington, B.A.** 1998. Body-fat levels and annual return in migrating Semipalmated Sandpipers. *Auk* **115**: 904–915.
- Piersma, T.** 1987. Hop, skip or jump? Constraints on migration of arctic waders by feeding, fattening and flight speed. *Limosa* **60**: 185–194.
- Piersma, T., Gudmundsson, G.A. & Lilliendahl, K.** 1999. Rapid changes in the size of different functional organ and muscle groups during refueling in a long-distance migrating shorebird. *Physiol. Biochem. Zool.* **72**: 405–415.
- Piersma, T. & Jukema, J.** 1990. Budgeting the flight of a long-distance migrant: changes in nutrient reserves levels of Bar-tailed Godwits at successive staging sites. *Ardea* **78**: 315–337.
- Piersma, T. & Jukema, J.** 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. *Condor* **95**: 163–177.
- Piersma, T., Klaassen, M., Bruggeman, J.H., Blomert, A.-M., Gueye, A., Ntiamoa-Baidu, Y. & van Brederode, N.E.** 1990. Seasonal timing of the spring departure of waders from the Banc d'Arguin, Mauritania. *Ardea* **78**: 123–134.
- Piersma, T., Mendes, L., Hennekens, J., Ratiarison, S., Groenewold, S. & Jukema, J.** 2001. Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the Bar-tailed Godwit. *Zoology* **104**: 41–48.
- Rogers, K.G., Rogers, D.I. & Minton, C.D.T.** 1997. Weights and pre-migratory mass-gain of the Red-necked Stint *Calidris ruficollis* in Victoria, Australia. *Stilt* **29**: 2–23.
- Schneider, D.S. & Harrington, B.A.** 1981. Timing of shorebird migration in relation to prey depletion. *Auk* **98**: 801–811.
- Skagen, S.K. & Knopf, F.L.** 1994. Residency patterns of migrating shorebirds at a midcontinental stopover. *Condor* **96**: 949–958.

- Stillman, R.A., Caldow, R.W.G., Goss-Custard, J.D. & Alexander, M.J.** 2000. Individual variation in intake rate: the relative importance of foraging efficiency and dominance. *J. Anim. Ecol.* **69**: 484–493.
- Strann, K.-B.** 1992. Numbers and distribution of Knot *Calidris canutus islandica* during spring migration in north Norway 1983–1989. *Wader Study Group Bull.* **64** (Suppl.): 121–125.
- Tomkovich, P.S.** 1996. A third report on the biology of the Great Knot *Calidris tenuirostris* on the breeding grounds. *Stilt* **28**: 43–45.
- Tomkovich, P.S.** 1997. Breeding distribution, migrations and conservation status of the Great Knot *Calidris tenuirostris* in Russia. *Emu* **97**: 265–282.
- Tulp, I. & de Goeij, P.** 1994. Evaluating wader habitats in Roebuck Bay (Northwestern Australia) as a springboard for northbound migration in waders, with a focus on Great Knots. *Emu* **94**: 78–95.
- Tulp, I., McChesney, S. & de Goeij, P.** 1994. Migratory departures of waders from north-western Australia: behaviour, timing and possible migration routes. *Ardea* **82**: 201–221.
- Warnock, N. & Bishop, M.A.** 1998. Spring stopover ecology of migrant Western Sandpipers. *Condor* **100**: 456–467.
- Warnock, N. & Warnock, S.** 1993. Attachment of radio-transmitters to sandpipers: review and methods. *Wader Study Group Bull.* **70**: 28–30.
- Weber, T.P., Ens, B.J. & Houston, A.I.** 1998. Optimal avian migration: a dynamic model of fuel stores and site use. *Evol. Ecol.* **12**: 377–401.
- Weber, T.P., Fransson, T. & Houston, A.I.** 1999. Should I stay or should I go? Testing optimality models of stopover decisions in migrating birds. *Behav. Ecol. Sociobiol.* **46**: 280–286.
- Weber, T. & Hedenström, A.** 2000. Optimal stopover decisions under wind influence: the effects of correlated winds. *J. Theoret. Biol.* **205**: 95–104.
- Weber, T. & Hedenström, A.** 2001. Long-distance migrants as a model system of structural and physiological plasticity. *Evol. Ecol. Res.* **3**: 255–271.
- Wilson, J.R. & Barter, M.A.** 1998. Identification of potentially important staging areas for 'long jump' migrant waders in the East Asian–Australasian Flyway during northward migration. *Stilt* **32**: 16–26.
- Wilson, J.R., Minton, C.D.T. & Rogers, D.I.** 1999. Weight loss by waders held in captivity following capture by cannon-netting. *Stilt* **35**: 25–33.
- Zwarts, L., Blomert, A.-M. & Wanink, J.H.** 1992. Annual and seasonal variation in the food supply harvestable by Knot *Calidris canutus* staging in the Wadden sea in late summer. *Mar. Ecol. Prog. Series* **83**: 129–139.

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