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Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent

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Summary

1. Millions of shorebirds migrate each year through a small number of highly productive staging areas where they often conflict with fisheries interests. Delaware Bay, USA, is a major shorebird stopover site where, in spring, many thousands of shorebirds undergo rapid mass gain by feeding on the eggs of commercially harvested horseshoe crabs *Limulus polyphemus*.

2. Environmental factors may cause deviations from the best migration schedule. We used within-year mass gain data from red knot *Calidris canutus* caught in Delaware Bay between 1998 and 2005 to determine the degree of flexibility individuals have to vary migration speed.

3. Mass gain by birds below 133 g was shown to comprise 15·3% fat (39 kJ g^{-1}), the remainder being lean mass (6 kJ g^{-1}). Above this critical level, fat comprised 83·9% of mass deposition. The rates of energy deposition (kJ d^{-1}) were therefore fundamentally different between the two states but were among the highest ever recorded among vertebrates (5–7 × basic metabolic rate).

4. A total of 36–62% of the variation in observed rates of energy deposition between 1998 and 2002 was explained by a year factor, date and mass at initial capture and interaction terms, such that light-weight birds at the end of May had rates of mass gain or energy deposition two to three times higher than birds of similar mass in mid-May, indicating that birds were attempting to achieve a certain mass by a certain date. In 2003 and 2005, this relationship broke down as a result of lower densities of eggs.

5. *Synthesis and application.* The maintenance of high densities of crab eggs required for high rates of mass gain in red knot requires severe cuts in, or the complete cessation of, the crab harvest, reduced human and raptor-related disturbance as well as management of beaches to provide sufficient crab-spawning habitat. These findings are widely

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applicable to other systems where harvesting activities come into conflict with migrating animals and show that certain sections of the population, in this case the long-distance migrants from South America, will be impacted more than short-distance migrants whose physiology may give them access to alternative food resources.

Key-words: migration strategy, phenotypic flexibility, spare capacity, time-minimization

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Introduction

Some shorebirds, such as red knot *Calidris canutus* (L.), regularly undertake exceptional migrations to exploit global seasonality by travelling many thousands of kilometres between Arctic breeding areas and wintering areas in the northern and southern hemispheres. For these extreme long-distance migrants, the migration process comprises a series of movement phases and staging phases, in which the necessary resources to complete the next leg of the migration are attained. Therefore, they have to time their migration to take advantage of food resources that vary in space and time, and make decisions about when to leave the wintering grounds, how long to stop over and gain mass on intermediate sites, and when to arrive in the breeding grounds (Hedenström & Alerstam 1997). Various models of shorebird migration strategy have been put forward. Building on earlier work, Farmer & Wiens (1999) identified three strategies, which included time-minimizers that aim to arrive at the breeding grounds as fast as possible, energy maximizers that arrive at breeding grounds with excess fuel stores, or birds that followed no strategy, termed random. Alerstam & Lindström (1990) predicted that time-minimizers should show a positive relationship between fuel deposition rate and departure mass. Across northward migrating red knot populations world-wide, there is indeed a positive relationship (Piersma *et al.* 2005) and a comparison of five subspecies of red knot showed that they time-minimized by selecting stopover sites with high-quality prey (van Gils *et al.* 2005a).

In spring, Arctic-breeding shorebirds are on a strict timetable to arrive in their breeding areas in time to breed successfully during the short summer (Drent *et al.* 2003). En route, factors such as adverse weather conditions, predation risk and the predictability, availability and quality of food resources could cause deviations from the optimal arrival times, rates of mass gain and departure times from stopover sites. Therefore individuals must possess a degree of flexibility to speed up or slow down their migration (Farmer & Wiens 1999; Ydenberg *et al.* 2002, 2004; Lank *et al.* 2003).

If birds are behind the optimal schedule, they can leave a stopover site at a suboptimum mass, depart at the optimum mass but past the optimum time, spend more time per day feeding or alter the rate at which they put on stores at stopover sites, so that stopover duration is reduced (Piersma 1987). The latter can be achieved in one of two ways. First, migrants can exhibit phenotypic flexibility in terms of altering digestive organ sizes and/or enzyme activities in relation to digestive/energetic bottlenecks (Piersma 1998, 2002; Guglielmo & Williams 2003). This is widespread across migrant shorebirds (Piersma *et al.* 1999; van Gils *et al.* 2005b; Selman & Evans 2005; Stein *et al.* 2005) but may incur a time cost, as it typically takes several days to a week to fully implement these changes, which may need to be reversed before the bird continues its migration (Piersma *et al.* 1999; Dekinga *et al.* 2001; McWilliams & Karasov 2005). Alternatively, birds can exhibit varying degrees of immediate spare volumetric or biochemical capacity (Diamond & Hammond 1992) to ingest and process extra food. For example, in an experiment where fuelling white-throated sparrows *Zonotrichia albicollis* (Gmelin) were switched rapidly from an environment of +21 °C to −20 °C, birds were able to increase their intake rate by 45% in response to the sudden increase in thermoregulatory costs (McWilliams & Karasov 2005). If migrants are behind schedule, then this 'spare capacity' may be the only option to increase fattening rates and leave the stopover site on time.

To determine the degree to which individual birds have the spare capacity to 'catch up' due to late arrival in a stopover site, we use data from an ongoing monitoring programme of red knot passing through Delaware Bay on the north-east coast of the United States on spring migration. For these birds, Delaware Bay is the last stopover site on the West Atlantic flyway from wintering areas in Patagonia/Tierra del Fuego (TDF), north-western Brazil and the south-eastern United States (Florida and Georgia) before birds reach their Arctic breeding areas. Individuals make stopovers in the bay of 12–14 days (S. Gillings *et al.* unpublished data) and fatten rapidly on an abundance of the eggs of horseshoe crabs *Limulus polyphemus* (L.), deposited in the beaches by spawning females between May and August (Castro & Myers 1993; Gillings *et al.* 2007; G.M. Haramis *et al.* 2007). It is predicted that the knots need to depart at between 180 and 220 g at the end of May or beginning of June, if they are to reach the Arctic with sufficient nutrient stores to breed successfully (Baker *et al.* 2004; Morrison *et al.* 2005). There are likely to be fitness consequences associated with leaving

Delaware Bay with insufficient mass. Indeed, individuals captured at low mass at the end of May were less likely to be seen subsequently in the flyway, thus implying lower survival (Baker *et al.* 2004).

The rate of mass gain in birds is currently used in Delaware Bay as a management tool to assess the 'health' of the shorebird/crab system, but this may not be the ideal way of assessing energy deposition. The breakpoint model of van der Meer & Piersma (1994) hypothesized that body mass should be divided into the 'structural' part and 'stores'. The structural part consisted mainly of water and fat-free lean mass (bone, muscle, etc.), whereas the stores consisted mainly of fat, the fuel needed for migration. As a bird migrates it first uses up the fat stores and, if further energy is required, it then enters a phase of protein catabolism. This switch is known as the breakpoint. When the bird refuels at a staging site, this model is reversed and birds first replace the lean mass before depositing fat. As the energy content of protein (6 kJ g^{-1}) is much lower than fat (39 kJ g^{-1}), these different periods of mass gain may have very different energy requirements; consequently, it is more appropriate to deal with the common currency of energy deposition (Klaassen *et al.* 1990; Jenni & Jenni-Eiermann 1998). Mass gain is, however, measured easily, as it is used as a tool in the management of the shorebird population that passes through Delaware Bay. We therefore combine the two approaches.

We used red knots caught between 1998 and 2005, and retrapped within the same season to determine the degree of flexibility in the rate of energy deposition and mass gain in relation to the time within the migration period, and the mass at which it was initially caught. From the hypothesis that red knots have spare capacity and/or can exhibit phenotypic flexibility, we predict that rates of energy deposition and mass gain should not be constant throughout the migration season. We expect a significant relationship between the rate of energy deposition and mass gain, and the date and mass when the bird was originally caught, such that the rate of energy deposition or mass gain should be higher for individuals that have a low mass at the end of May.

Methods

CAPTURE OF BIRDS AND MEASUREMENT OF MASS

As part of an ongoing monitoring programme, red knots were trapped in Delaware Bay, USA, using cannon nets throughout the spring staging period spanning from the first week in May to the end of the first week in June each year between 1998 and 2005. On capture, birds were banded with an individually numbered metal band and mass was measured using an electronic balance accurate to 0·1 g. Although no special efforts were taken to recapture birds again during the same season, 178 birds in their second year or older were recaptured and their mass recorded for a second time.

DETERMINING THE COMPOSITION OF BODY STORES

A total of 61 red knot were collected from catches over 3 years (1998: 24 birds; 1999; 24 birds; 2000: 13 birds). These birds were taken at random from cannon net catches on dates spread out through the spring migration season. Birds were killed humanely using cervical dislocation and, after weighing to the nearest gram, placed in airtight plastic bags and frozen at –20 °C.

As the red knot that pass through Delaware Bay come from a mix of wintering populations, we identified their wintering location based on the stable isotope ratios of carbon and nitrogen in their flight feathers. $\delta^{13}C$ and $\delta^{15}N$ values were obtained from the sixth primary covert, measured ascendantly, using continuous flow isotope ratio mass spectrometry (CF-IRMS). Atkinson *et al.* (2005) showed that there was a clear division in the values of $\delta^{15}N$ between birds wintering in Patagonia and Tierra del Fuego ($\delta^{15}N > 13{\cdot}5‰$, termed 'southern' birds) and elsewhere ($\delta^{15}N < 13{\cdot}5‰$, termed 'northern' birds). Northern birds comprise two geographically distinct populations from the south-eastern United States and Brazil, but the isotope signatures of birds from each overlap. $\delta^{13}C$ values were checked to ensure that no subadult birds were included. These birds, hatched the previous year, would have a carbon isotope signature typical of the freshwater systems ($\delta^{13}C < -19{\cdot}5‰$) where their feathers were grown. None were found among the specimens.

After thawing, the total fat mass of each specimen was determined by drying the tissues, weighing them and then extracting the fat in a Soxhlet apparatus using petroleum-ether (boiling-point range 40–60 °C) as the solvent. The body parts were then dried to constant mass and reweighed, the total fat mass being the difference.

To determine the point at which birds deposit fat stores, the total fat mass of each specimen was plotted against the total mass and a two-phase (broken stick) regression model applied using the inbuilt function of SIGMAPLOT version 10. The slopes of the two regression lines reflect the proportion of fat being stored as total mass increases and the breakpoint indicates the point at which that relationship changes.

The energy deposition of fat and protein was calculated as follows. The mass change between captures above and below the breakpoint was multiplied by the appropriate fraction of fat or protein (based on the slopes of the two regression lines) and its calorific value (6 kJ g^{-1} for protein and 39 kJ g^{-1} for fat, following Klaassen *et al.* 1990). Total energy deposition was the sum of these two values.

DOES INITIAL MASS OR DATE INFLUENCE RATES OF ENERGY DEPOSITION?

Generalized linear models (GLM) with normal errors and an identity link function were used to determine the factors associated with the rates of mass gain or energy deposition per day. The factors considered were their mass at initial capture (M), the number of days after 1 May of the first capture (D), the year (Y) and their interaction terms. Permutations of these variables were entered sequentially into GLMs and the Akaike information criterion (AIC) corrected for small sample size (cAIC) was calculated in each case $\{[-2 \times \log$ likelihood $+ 2k + [2k^*(k + 1)] / (n - k - 1)\}$, where n is the sample size and k the number of estimable parameters. cAIC operates on the basis of parsimony by selecting the best-fitting model while minimizing the number of parameters in the final model (Burnham & Anderson 1998). The models were ranked by cAIC and the model with the lowest value was chosen as the final model. It was accepted as more parsimonious than other lower-ranking models if the difference in cAIC was greater than 2 (Burnham & Anderson 1998). To determine the amount of variation in the mass gain data between years explained by the best model, we took the model with the lowest cAIC and tested its performance (using R^2 values) on each year's data in isolation by performing a series of linear regressions for each year between the predicted and observed values, using the PROC REG procedure in SAS.

The rate of mass gain is a function of final mass, initial mass and duration between recaptures. As initial mass was also included as a dependent variable, any significantly large measurement error would result in an automatic negative relationship between rate of mass gain and initial mass. However, as the final result was a significant positive relationship, and as measurement error was thought to be low because most birds were weighed using a digital balance 1 h or more after capture (when most changes in mass take place), we do not consider this to be a major issue.

Using only retrapped birds to measure mass gain is open to bias for two reasons, owing to capture effect (e.g. Warnock *et al.* 2004): first, mass gain after release may show a short-term decline; additionally, departure date may be correlated negatively with rate of mass gain, so that birds with rapid mass gain may not be available for subsequent recapture (Winker *et al.* 1992). Our estimates of mass gain would therefore be an underestimate. We dealt with this in two ways. With the exception of the day after initial capture (–1·42 g day^{-1}), mean mass gain per day was positive and approximately constant thereafter, averaging 4·3 g day^{-1} up to 14 days after first capture (Fig. 1). This lower initial rate was likely to be a capture effect and we have therefore excluded birds with retrap intervals of 1 day *as well as 2 birds with missing data* from the analysis, thus leaving 166 same-year retraps remaining for analysis. Overcoming the second issue of birds leaving the bay requires a more subjective judgement. We selected the best models without further data exclusion but performed an additional analysis, in which we calculated whether a bird caught on a particular date would have reached a target mass exceeding 190 g by the time of the second capture and was therefore likely to have left the Bay. The expected mass was calculated assuming a rate of gain of 4·05 g day^{-1}, the mean mass gain from the 166 retraps. If a bird's predicted mass exceeded 190 g it was excluded from this analysis. This removed a further 25 birds, leaving 141. Where means are given these are quoted ± 1 SE.

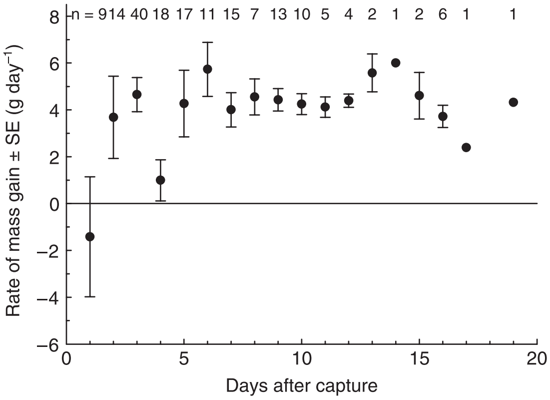

Fig. 1. Rate of mass gain ± 1 SE of red knot retrapped during the same season in Delaware Bay in relation to the number of days after capture. Sample size appears at the top of the graph.

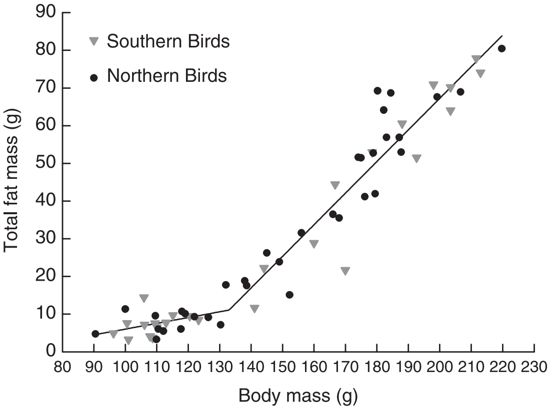

Fig. 2. The relationship between the total mass of individual birds and the amount that is fat. A two-phase regression line is shown. Northern birds are those that winter in northern Brazil and the south-eastern United States; southern refers to those wintering in Patagonia and Tierra del Fuego.

Results

COMPOSITION OF BODY STORES IN RELATION TO TOTAL BODY MASS

The proportion of fat in the body mass laid down changed from 0·153 ± 0·119 to 0·839 ± 0·046 at a breakpoint of 133·01 ± 5·19 g (Fig. 2). The overall fit of the broken-stick model was good ($F_{3,57} = 320{\cdot}2$, $P < 0{\cdot}0001$, adjusted $R^2 = 0{\cdot}94$). Below the breakpoint, the slope of the regression line was not significantly different from zero ($t = 1{\cdot}29$, $P = 0{\cdot}2$) indicating that very little, if any, of the mass gain at this point was deposited as fat.

Table 1. Predicting the rate of mass gain and energy deposition of red knot *Calidris canutus* in Delaware Bay. The model selection table is based on a data set using all birds. Model structure: Y = year (1998–2005, eight-level factor), M = mass (linear variable), D = number of days after 1 May (linear variable). k = number of estimable parameters, × = interaction term

		Energy deposition			Mass gain			
Model no.	Model structure	k	cAIC	ΔcAIC	R^2	AIC	ΔcAIC	R^2
1	Y M D D × M Y × M Y × D	25	1995·74	0	0·54	856·06	3·87	0·59
2	M D M × M	4	2001·36	5·63	0·35	865·95	13·76	0·4
3	M D D × D M × M	5	2001·38	5·65	0·35	866·06	13·87	0·41
4	Y M D D × M Y × D	18	2006·73	10·99	0·54	852·19	0	0·59
5	Y M D D × M Y × M	18	2007·52	11·78	0·44	864·31	12·12	0·51
6	Y M D D × Y	17	2016·78	21·05	0·2	861·75	9·56	0·51
7	Y M D Y × D	17	2016·78	21·05	0·4	861·75	9·56	0·51
8	M D D × M	4	2025·82	30·08	0·35	865·37	13·17	0·41
9	Y M Y × M D	17	2025·86	30·13	0·37	879·73	27·54	0·46
10	Y M M × Y	16	2031·41	35·68	0·34	894·99	42·79	0·35
11	Y D Y × D	16	2033·13	37·39	0·4	914·09	61·89	0·32
12	Y M D D × M	11	2034·51	38·78	0·44	874·13	21·93	0·51
13	M D	3	2037·39	41·66	0·18	875·78	23·59	0·35
14	M D D × D	4	2039·5	43·77	0·18	877·45	25·25	0·36
15	M	2	2041·68	45·95	0·14	890·62	38·43	0·28
16	Y M D	10	2043·92	48·19	0·22	883·82	31·62	0·38
17	Y M	9	2044·76	49·02	0·2	892·89	40·7	0·34
18	Y	8	2061·05	65·32	0·11	935·19	82·99	0·14
19	Y D	9	2062·32	66·58	0·12	936·11	83·92	0·14
20	Intercept only	1	2065·25	69·52	0·00	944·56	92·37	0·00
21	D	2	2067·2	71·46	< 0·001	946·29	94·09	< 0·001

RATE OF ENERGY DEPOSITION AND MASS GAIN IN RELATION TO DATE, INITIAL MASS AND YEAR

The average rate of energy deposition of all 166 retrapped birds was 119·1 kJ day^{-1} (95% CI: −193·7–322·9 kJ day^{-1}). In terms of mass gain, this represented an average rate of 4·05 ± 0·32 g day^{-1} and ranged between −14·4 and 18·8 g day^{-1}. The most rapid mass gain of 18·8 g day^{-1} (514 kJ day^{-1}) was exhibited by a bird caught in 2003 at 117 g on 25 May and retrapped 3 days later on 28 May at a mass of 173·6 g.

Both the rates of energy deposition and mass gain were mass- and time-dependent, and varied between years (Table 1, Fig. 3). Although the form of the model with the lowest cAIC was slightly different in each case, the pattern of the rates of energy deposition and mass gain were similar in that they were both related inversely to the mass at which a bird was caught at (i.e. lighter individuals deposited energy or gained mass at a faster rate). With the exception of year 2000, light-weight birds caught later in May were estimated to have a higher rate of energy deposition than light-weight birds caught early in May, thus enabling late-arriving birds to ‘catch up’ with early arriving birds. The amount of variation explained by the best fitted models (model 1 for energy deposition and model 4 for mass gain) was generally good and overall explained over half the variation in the dependent variable (R^2 values of 0·54 and 0·59, Table 1). When the birds which were predicted to be > 190 g at 31 May were removed the order of models altered slightly, but the two models selected previously still had the lowest cAIC, indicating that departure of birds from the bay was not a confounding factor.

The selection of the interaction terms Y × D and Y × M indicated that energy deposition rates varied between years in relation to the time a bird was caught and its initial mass (Table 2). The average pattern of energy deposition and mass gain (Fig. 4) did not hold in every year and was not always reliable. These interaction terms were most important in 2000 and also 2003, when mass deposition commenced 7 days later compared with other years (Fig. 3). When applied to each year separately, there has been a tendency for the fit of these relatively simple relationships to decline over time (Table 3).

Discussion

MIGRATION STRATEGY AND RATES OF FUELLING BY RED KNOTS

If birds arrive late and conditions are good, red knot passing through Delaware Bay have the flexibility to increase their rate of energy deposition to ensure a departure at the end of May or beginning of June. The tight fit of the broken-stick model when applied to the carcass data indicates that red knot below 133 g first replace their structural stores with protein before laying down fat. They then cease depositing energy at the end of May at a mass of approximately 180 g, thus carrying *c.* 50 g of fat to fuel the final part of their journey to the breeding areas.

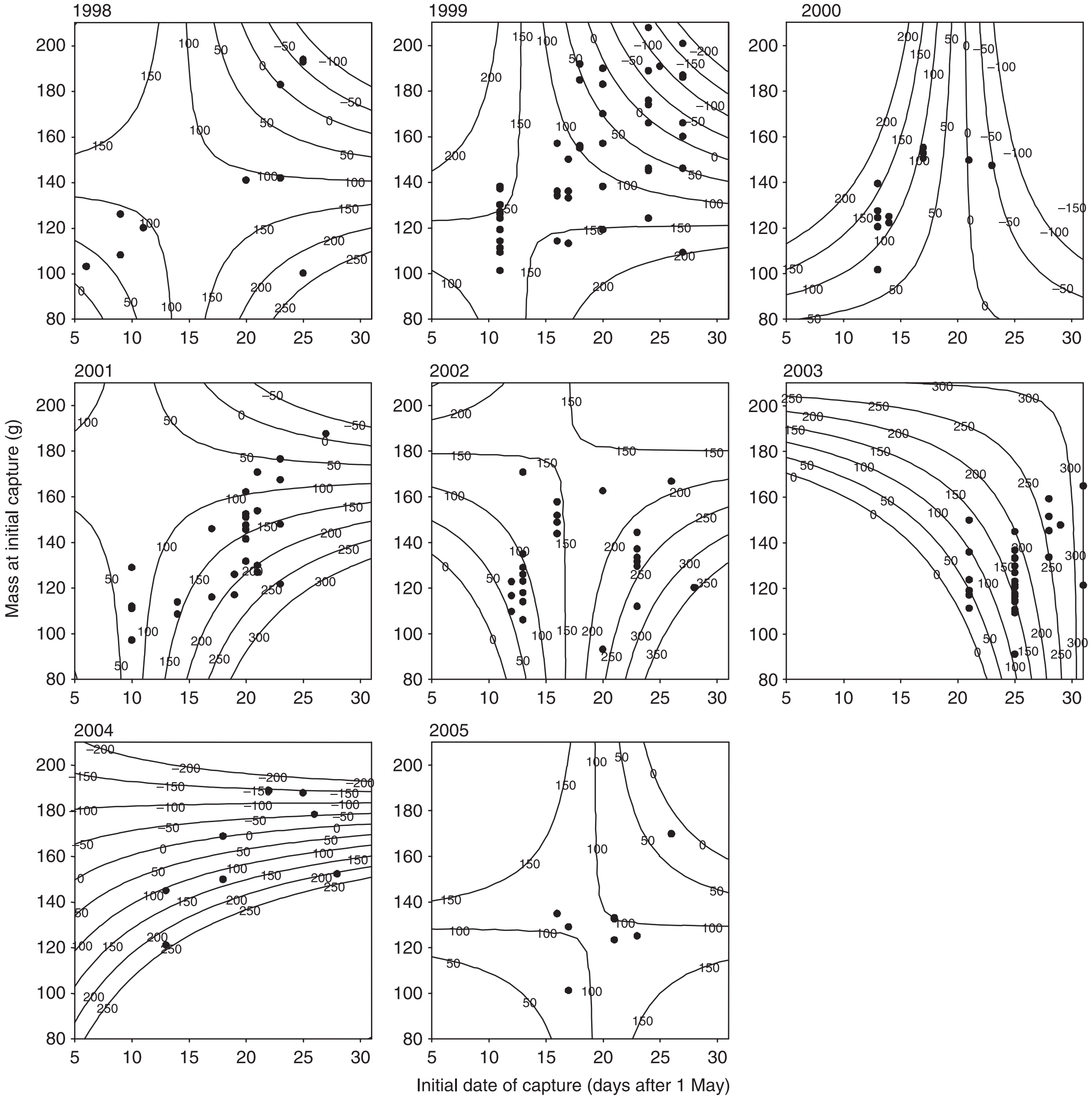

Fig. 3. Contour plots of the rate of energy deposition (kJ day^{-1}) of red knot based on retrapped birds in relation to the date at initial capture and their initial mass. Dots represent individual birds and refer to date and mass at initial capture. To avoid predicting outside the available data, contours are not shown if there were no data points occurring within the space between it and the next contour line.

The rates of energy deposition are among the highest observed in the animal kingdom. With maintenance and activity requirements of a minimum of 200–250 kJ day^{-1} (Piersma 2002), which includes a basal metabolic rate (BMR) component of *c.* 80 kJ day (Wiersma & Piersma 1994), birds were assimilating energy at an average equivalent to 5–5·6 × BMR. At the upper confidence limit this was raised to 6·5–7·2 × BMR and two individuals with energy deposition rates greater than 500 kJ day^{-1} probably exceeded 9 × BMR.

These rates reflect those observed in captive shorebirds, where soft-shelled food (mealworm larvae) was provided *ad libitum* and available 24 h a day (Kvist & Lindström 2003). The authors acknowledged that the high energy assimilation rates (10·4 × BMR for red knot) were unlikely to be replicated in the field, but did suggest situations where high-quality food may be super-abundant (including Delaware Bay) would enable birds to fuel so rapidly. Note that the value of 10·4 × BMR was the average of the highest daily (i.e. 24 h) rate observed within individuals. The rates described in the present study are observed under field conditions and are averaged over the course of a number of days.

Why do birds need these stores? First, they are needed for migration, but red knot also arrive in the Arctic with high lipid and muscle stores (Morrison *et al.* 2005). These stores are generally used up in the 2 weeks after arrival and prior to egg production (Klaassen *et al.* 2001) and are associated with the transformation from a physiological state needed for migration to one needed for successful breeding (Morrison *et al.* 2005). These stores are also important for survival. Birds that were estimated to be of low mass towards the end of May were less likely to be seen in the flyway in subsequent

Table 2. Parameter estimates for the models with the lowest cAIC values. Model number refers to the model numbers in Table 1. Y = year (1998–2005, eight-level factor), M = mass (linear variable), D = number of days after 1 May (linear variable), × = interaction term

Parameter	Factor level	Rate of energy deposition (model 1) Estimate	SE	Rate of mass gain (model 4) Estimate	SE
Intercept		–611·25	319·25	–7·71	9·13
Y	1998	158·62	268·06	2·48	7·24
Y	1999	302·68	252·66	6·31	7·01
Y	2000	205·39	330·47	9·71	8·02
Y	2001	195·66	266·97	1·59	7·30
Y	2002	–108·94	278·95	–2·38	7·21
Y	2003	–960·69	295·92	–18·57	8·44
Y	2004	824·40	360·04	5·03	7·96
Y	2005	0	0	0·00	0·00
M		5·54	2·99	0·05	0·04
D		37·13	18·34	1·12	0·45
M × D		–0·29	0·07	–0·007	0·002
M × Y	1998	–1·45	2·83	–	–
M × Y	1999	–1·80	2·67	–	–
M × Y	2000	0·37	3·47	–	–
M × Y	2001	–2·67	2·85	–	–
M × Y	2002	–0·69	2·77	–	–
M × Y	2003	3·32	2·84	–	–
M × Y	2004	–7·31	3·40	–	–
M × Y	2005	0	0	–	–
D × Y	1998	2·71	16·20	–0·03	0·36
D × Y	1999	–2·06	15·54	–0·26	0·35
D × Y	2000	–16·88	18·82	–0·56	0·43
D × Y	2001	11·98	16·43	0·04	0·37
D × Y	2002	14·69	15·73	0·29	0·36
D × Y	2003	24·15	16·66	0·79	0·39
D × Y	2004	16·15	17·25	–0·18	0·39
D × Y	2005	0	0	0	0

Table 3. The amount of variation explained (expressed as R^2 values) for the energy deposition and mass gain models with the lowest cAIC. Model number refers to the model number in Table 1

Year	Energy deposition (model 1)	Mass gain (model 4)
1998	0·36	0·59
1999	0·58	0·63
2000	0·62	0·63
2001	0·50	0·52
2002	0·63	0·71
2003	0·31	0·19
2004	0·54	0·33
2005	0·00	0·13

years (Baker *et al.* 2004), indicating negative fitness consequences associated with departing late and light from Delaware Bay.

ARE RED KNOTS TIME-MINIMIZERS?

The results from this study have indicated that the migration strategy is more complex than assumed previously. Fuelling rates among red knot in Delaware Bay are state- and time-dependent and, thus, birds are attempting to achieve a certain mass by a certain date. Mean mass gain rates for birds arriving in the Bay at 110 g on 10 May were 4 g day^{-1} but individuals can increase this by a factor of two to three times later in May. This raises the question of why birds arriving earlier do not deposit fuel at the high rates observed towards the end of May. The question remains to be answered, but several possibilities exist. First, as egg loads in beaches increase in May due to successive spawnings of crabs, there may be insufficient food available early in May to achieve the rates necessary to fuel at high rates, or a digestive bottleneck such that birds were not able to gain mass faster without increasing the size of their digestive organs. This may be so, but in mid-May, when presumably similar food densities are available to all birds, heavier birds fuelled at a lower rate and therefore both the food limitation and digestive bottleneck hypotheses seem unlikely to explain the patterns fully. Alternatively, there may be other costs associated with fuelling at a high rate, such as increased energetic costs and reduced vigilance leading to increased predation risk (Brodin 2001; MacLeod *et al.* 2005a, MacLeod *et al.* 2005b), or reduced manoeuvrability of high mass birds leading to increased predation (Weber *et al.* 1998; Dietz *et al.* 2007). Indeed, predation risk from raptors may have increased due to the local provision of artificial nest sites for peregrine falcons *Falco peregrinus* (Tunstall) within Delaware Bay. There may

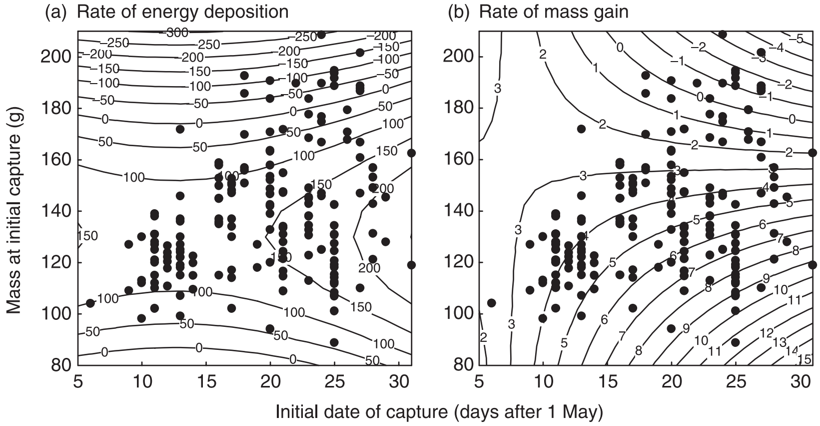

Fig. 4. Contour plots of the average rate of (a) energy deposition (kJ day^{-1}) from model 1 and (b) mass gain (g day^{-1}) from model 4 in relation to the date a bird was initially caught and its mass at initial capture, excluding any year effects. Model number refers to Table 1.

also be costs associated with departing the bay early. For example, early-departing birds may arrive in the Arctic breeding areas before snow melt and experience a poor feeding environment. Thus, birds appear be aiming to leave Delaware Bay within a relatively short time window.

Several other studies have shown that individuals behind schedule can respond by reducing stopover time and migrating faster, which is analogous to the results found here, but without information on rates of energy deposition or mass gain it is not possible to determine which type of strategy birds were following. For example, stopover time of dunlin *Calidris alpina* (L.) and male western sandpipers *C. mauri* (Cabanis) at their last stopover before reaching the Arctic breeding area (the Copper River Delta in Alaska, USA) was related inversely to arrival date (i.e. late in the migration season migration timing became more compressed) (Warnock *et al.* 2004; Warnock & Bishop 1998; Bishop *et al.* 2005); individual dunlin caught at staging sites further south migrated faster to the Delta, the later they left the capture site. These stopover patterns could be explained either by birds leaving at suboptimal masses, or leaving at optimum masses achieved by a greater rate of mass gain. Although these studies do not address specifically whether birds are aiming to leave by a certain date, the flexible stopover durations suggest that birds may be using a similar strategy to the red knots, in that they aim to depart the last staging area by a certain date.

POPULATION-SPECIFIC CONSEQUENCES OF A REDUCTION IN HORSESHOE CRAB EGG DENSITIES

That date of initial capture, initial mass and interaction terms explained such a high proportion of the variance in rate of mass gain between 1998 and 2002 demonstrates that, when sufficient resources are available, the relationship is robust between years. In 2003, the late-spawning of crabs due to cold sea temperatures (L.J. Niles, unpublished) severely reduced the numbers of eggs available to birds early in the season and, even allowing the day parameter to vary between years (and, thus, allowing for mass gain to commence later in the month), the final model was a relatively poor fit compared with other years. In 2004, a warm spring allowed for early spawning of crabs and high densities of eggs in beaches compared with 2003. In 2005, however, the fit was exceptionally poor. Fuelling rates were generally low, averaging 2·7 g day^{-1}, and these did not fit with the simple relationship observed in previous years. Although sample size was lower in the latter years due to an intentional reduction in catching effort, there is no reason to expect these to be non-random samples, and the coefficient of variation in rates of mass gain were not significantly different in the latter years.

That the relatively simple model of mass gain seemed to have broken down in 2 of the past 3 years is extremely worrying in conservation terms, especially given the link between departure mass and the likelihood of an individual being seen again in the flyway (Baker *et al.* 2004). Conditions in Delaware Bay have changed over the past 10 years. The harvesting of horseshoe crabs for bait and the biomedical industry has undergone an order of magnitude increase since the mid-1990s (Walls *et al.* 2002) and has been restricted recently due to concerns that the reduction in the number of adult spawning crabs has reduced the number of eggs available to shorebirds, impinging on their ability to fatten successfully. A reduction in adult red knot survival has been attributed to late arrival into, and reduction in departure masses from, Delaware Bay (Baker *et al.* 2004). This study has shown that in 2000, 2003 and 2005, at least, fuelling did not proceed as normal and was caused by poor foraging and weather conditions within the bay. However, an increase in the number of lightweight birds late in May in the preceding period (between 1997 and 2002; Baker *et al.* 2004) could well be attributable to an increase in the number of later-arriving birds into Delaware Bay, as our analysis indicated that fuelling proceeded as normal. Although late arrivals may represent individual adjustments to local fuelling difficulties encountered in previous years, we also need to know about conditions at wintering and staging sites elsewhere in the flyway to understand more clearly the increase in later arrivals.

Peak numbers of red knot have declined in Delaware Bay (L.J. Niles *et al.*, unpublished), similar to severe declines that have occurred in the wintering areas in Patagonia and Tierra del Fuego, where numbers declined from 67 000 birds in 1982–85 to 17 650 in February 2005 (Morrison *et al.* 2004; R. I. G. Morrison personal communication). Birds from wintering areas in northern Brazil and also the south-eastern United States (both populations in the order of 7500–10 000 birds) also pass through Delaware Bay (Atkinson *et al.* 2005) and there has been no evidence of similar declines in these groups of birds (L.J. Niles *et al.*, unpublished).

The abundance of crab eggs in Delaware Bay underpins the exceptional rates of mass and energy gain shown here. Using stable isotopes as above, the wintering areas of birds passing through the Bay in 2004 and 2005 were determined (Atkinson *et al.* 2006). In these years, there was a non-random distribution of birds within the Bay. In 2005, at least, those birds feeding on hard-shelled mussels *Mytilus* sp. on the Atlantic side of Delaware Bay were mainly short-distance migrants from wintering areas in the south-eastern United States, although some were from Tierra del Fuego. Mussel feeders were generally heavier than longer-distance migrants from Tierra del Fuego and northern Brazil. Although we were not able to measure gizzard size, fattening on mussels would not be an option for newly arrived long-distance migrants due to the atrophy of their digestive organs prior to and during the long-distance flight (Piersma 1998; Piersma *et al.* 1999). The situation is similar to the Dutch Wadden Sea, where there is evidence that recently arrived birds (i.e. those having small gizzards) feed on soft food (crabs and shrimps), while those that have been there for longer (i.e. those having bigger gizzards) feed on hard-shelled bivalves (van Gils *et al.* 2005c). The mussel feeders in Delaware Bay were therefore assumed to have either arrived earlier or to be short-distance migrants whose short-hop strategy did not require them to reduce the size of their digestive apparatus.

Therefore, for later arrivals to achieve high rates of mass gain and catch up with earlier-arriving birds requires a sufficient density of crab eggs to be available because fuelling rate on soft-shelled prey is independent of gizzard size (van Gils *et al.* 2003, 2005b). The harvest of spawning crabs over the past decade will have reduced egg loads within beaches. It is likely that the bulk of shorter-distance migrants feeding on mussels (which does not enable such high fuelling rates, van Gils *et al.* 2005a) would, through earlier arrival compared with longer-distance migrants, still be able to fatten successfully. Reducing egg densities would have a disproportionately higher impact on longer-distance migrants. Indeed, when staging in the Wadden Sea in spring, knots with the smallest gizzard size, which may be those that have travelled the longest distance, were found to suffer the highest mortality rate. This increased mortality rate was due to the large-scale harvesting of the knots' food resources by the commercial fishing industry (van Gils *et al.* 2006).

Conclusion

The red knot passing through Delaware Bay in spring are on a schedule to depart at a certain mass by a certain time. When sufficient crab eggs are available, late-arriving birds have the flexibility to increase the rates of mass gain to over three times the mean rate to 'catch up' with earlier-arriving birds. Based on the model using data from all years, a bird arriving at 110 g on 21 May could expect to depart by 31 May at a mass of greater than 180 g. Between 1997 and 2004, the proportion of light-weight birds has increased (Baker *et al.* 2004). The simple model of mass gain has showed signs of breaking down in the latter part of the 9-year study period and it is likely that a reduction in the availability of crab eggs in the bay and increased late arrival are responsible for these poorly conditioned birds. Further reductions in the availability of crab eggs are predicted to have a greater impact on the longer-distance migrants that physiologically do not have access to alternative food supplies, such as mussel spat. A reduction in the number of crabs harvested or closure of the fishery, together with management of beaches to provide optimum crab spawning habitat and reduction in disturbance (both human and from raptors), will maximize the numbers of eggs available to the birds.

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