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Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay

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Most populations of migrant shorebirds around the world are in serious decline, suggesting that vital condition-dependent rates such as fecundity and annual survival are being affected globally. A striking example is the red knot (*Calidris canutus rufa*) population wintering in Tierra del Fuego, which undertakes marathon 30 000 km hemispheric migrations annually. In spring, migrant birds forage voraciously on horseshoe crab eggs in Delaware Bay in the eastern USA before departing to breed in Arctic polar deserts. From 1997 to 2002 an increasing proportion of knots failed to reach threshold departure masses of 180–200 g, possibly because of later arrival in the Bay and food shortage from concurrent over-harvesting of crabs. Reduced nutrient storage, especially in late-arriving birds, possibly combined with reduced sizes of intestine and liver during refuelling, had severe fitness consequences for adult survival and recruitment of young in 2000–2002. From 1997 to 2002 known survivors in Delaware Bay were heavier at initial capture than birds never seen again, annual survival of adults decreased by 37% between May 2000 and May 2001, and the number of second-year birds in wintering flocks declined by 47%. Population size in Tierra del Fuego declined alarmingly from 51 000 to 27 000 in 2000–2002, seriously threatening the viability of this subspecies. Demographic modelling predicts imminent endangerment and an increased risk of extinction of the subspecies without urgent risk-averse management.

Keywords: conservation; demographic collapse; horseshoe crab; migration; shorebird; stopover ecology

1. INTRODUCTION

Key questions in the study of the evolution of migratory strategies in birds are (i) what are the fitness consequences of variation in the timing of arrival at highly seasonal breeding sites, and (ii) to what extent are survival and reproduction dependent on the amount of nutrient stores accumulated at the last stopover site in the annual spring migration (Alerstam & Hedenström 1998; Madsen 2001; Drent *et al.* 2003)? Answers to these questions are critical in forecasting the possible impacts of global climate change, over-harvesting of food supplies, habitat destruction and disturbance at stopover sites. Recent studies strongly suggest that survival and successful reproduction are condition dependent (Sandberg & Moore 1996; Marra *et al.* 1998; Bêty *et al.* 2003) and that long-distance migrants may not be able to adjust their migration schedules to maximize individual fitness in changing environments (Both & Visser 2001; Gill *et al.* 2001).

Species such as Arctic-breeding shorebirds that winter in the Southern Hemisphere and migrate in spring in a series of long flights between a few highly productive stopover sites have been predicted to be highly susceptible to the above factors (Piersma & Baker 2000). Consistent with this prediction, populations of many species of shorebird around the world have recently been reported to be in serious decline. In a broadly based survey of 35 species of shorebird in Canada, negative trends or statistically significant declines were recorded in 28 (80%), while only

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one showed a positive trend (Donaldson *et al.* 2000). The US Shorebird Conservation Plan identified aspects of the biology of these birds that make them particularly vulnerable demographically (Brown *et al.* 2001), including risks associated with long-distance migration, dependency on dispersed and sometimes ephemeral habitats where they concentrate in large flocks, losses of critical refuelling habitats and low reproductive potential (Piersma & Baker 2000; Donaldson *et al.* 2000).

One of the flagship species among long-distance shorebirds is the red knot (*Calidris canutus*), especially the nearctic subspecies *C. c. rufa*. Although a smaller population overwinters in northern Brazil, most birds migrate a prodigious 30 000 km annually between overwintering sites in Tierra del Fuego (TDF) and breeding sites in the Canadian Arctic (Harrington 2001). To achieve this feat they must stop over at a few productive refuelling sites at strategic locations along the flyway, particularly along the northern migration to the breeding grounds. As the red knots move northwards, the timing of departures becomes increasingly synchronized, and at the final stopover site in Delaware Bay in the USA, all birds depart for the breeding grounds within a period of a few days (Myers 1986; Clark *et al.* 1993). Delaware Bay is a crucial site at which to accumulate nutrients for the final flight to the breeding sites and for survival on the initially food-free tundra and through unpredictable bouts of freezing weather, which can cause high levels of mortality (Boyd 1992). Red knots feed almost exclusively on a superabundant supply of eggs of spawning horseshoe crabs (*Limulus polyphemus*) (Castro & Myers 1993; Tsipoura & Burger 1999). There are no major refuelling sites en route to the arctic from Delaware Bay where low-mass birds can belatedly gain substantial reserves and thus compensate for late arrival.

The approximate doubling of mass from arrival at 90–120 g to departure at 180–220 g is achieved annually if conditions are favourable (Baker *et al.* 2001). At an average rate of mass increase of 4.6 g day^{-1}, the highest recorded among the world's subspecies and staging sites (Piersma *et al.* 2004), the birds need to refuel over a period of *ca.* 19–22 days to reach maximum mass. This ideally includes an initial rebuilding of organs such as the gut following a migration leg of 5400 km from northern Brazil to Delaware Bay (Battley *et al.* 2000). Individual red knots can store fat and protein at two to three times the annual average rate (maximum of 15 g day^{-1}; A. J. Baker, P. M. Gonzalez and P. W. Atkinson, unpublished data), probably when horseshoe crab eggs are superabundantly available. Consequently, even migrants arriving late in May should be able to reach large departure masses, thus achieving the nutrient-store levels necessary for migration, survival and maximizing the reproductive potential of the population.

Birds depart Delaware Bay en masse about 28–30 May each year (Baker *et al.* 2001) and need to have stored 1890 kJ of energy or *ca.* 47 g of fat to fly the 2400 km to the Arctic breeding areas (based on empirical relationships between body mass and flight costs in Kvist *et al.* (2001)). An additional 6.5 g of fat per day would be used if birds arrived during inhospitable conditions and were unable to feed. Based on an average fat-free mass of 130 g late in the stopover period (Piersma 2002), red knots need to achieve a departure mass of at least 180–200 g just to cover the costs of the flight to the breeding grounds and to survive an initial few days of snow cover.

We report here studies of the annual survival of red knots relative to refuelling rates and dates of arrival in Delaware Bay. Our objective was to detect any potential impact of the order-of-magnitude increase in the take of horseshoe crabs since the mid-1990s as bait for the fishing and conch fisheries (Walls *et al.* 2002). This huge increase in the harvest of horseshoe crabs has ignited a heated controversy between the fishing industry and conservation agencies concerned with the impact on the long-term demographics of the crabs and the follow-on effect on shorebirds through a diminished supply of eggs for refuelling. This controversy has been fuelled by annual aerial counts of wintering flocks in TDF, which recorded a large decline in the population of red knots from 51 000 to 27 000 between the years 2000 and 2002 (Morrison *et al.* 2004). A January 2003 aerial survey of sites along the Patagonian coast known to support flocks of wintering knots in the 1980s located only 560 birds, and a December 2003 survey in northern Brazil indicated that this population is small (possibly 5000–7000 birds). Thus, there is no evidence that birds are redistributing themselves elsewhere along the flyway.

2. MATERIAL AND METHODS

In 1997–2002 we caught large samples of birds in Delaware Bay ($n = 9851$) with cannon nets, weighed them to assess the fulfilment of energetic requirements of refuelling shorebirds and marked them with numbered metal bands for survival analysis (Niles *et al.* 2004). In addition, we captured and marked birds ($n = 3644$) at the other end of the flyway from 1995 to 2003 in Bahia de San Antonio in northern Patagonia and in TDF (Argentina and Chile). All encounter histories are based solely on physical recaptures in nets. Analysis with the program U-CARE v. 1.3 (Choquet *et al.* 2001) showed that both datasets (table 1) conformed to Cormack–Jolly–Seber (CJS) assumptions. Data were classified into migration years beginning on 1 July each year, so that survival estimates reflect events after the birds leave Delaware Bay each year on their annual migration to return and fatten the following spring. Analyses were run in MARK 3.2 (White & Burnham 1999) using standard CJS models with time intervals set to the corresponding periods between the migration years that we sampled. Both datasets were used to test goodness-of-fit to standard CJS models as well as to the biologically plausible model $\phi\ (t_1, t_2)\ p(t)$, where ϕ is the survival rate, p is the recapture rate and t_1 precedes the 2000/2001 population-reduction event in TDF and t_2 includes it. Model selection was based on the Akaike information criterion (AIC). Because some of the parameter estimates were on the boundary, we used profile likelihood as implemented in MARK to calculate confidence intervals (CIs).

To investigate annual patterns of mass gain in Delaware Bay we calculated percentages of red knots in each of four different mass categories (≥160 g, ≥180 g, ≥190 g and ≥200 g) on 28 May (near departure time). Departure masses were predicted in separate binary logistic regressions of each of the four mass categories (1 = yes, 0 = no) on year (categorical independent variable) and date of initial capture (continuous independent variable) with logit link.

In a separate analysis we computed mean masses and 95% CIs of known survivors in the five years 1997–2001. Owing to

Table 1. Samples of adult and second-year red knots captured and banded in TDF, in Bahia de San Antonio in northern Patagonia and in Delaware Bay for mark–recapture analyses of annual survival.
(Only controls are shown in the recapture column.)

	TDF and northern Patagonia		Delaware Bay	
migration year	captures	recaptures	captures	recaptures
1994/1995	204	0	—	—
1995/1996	—	—	—	—
1996/1997	—	—	941	0
1997/1998	1101	1	1200	14
1998/1999	—	—	2525	52
1999/2000	—	—	1404	57
2000/2001	538	9	2135	122
2001/2002	1309[a]	66	1281	120
2002/2003	492	25	—	—

[a] 500 birds were released unbanded.

differences in the slope of mass on date in different years and a significant interaction between year and date, we used a separate-slopes model with log link and normal errors in generalized linear and nonlinear models (GLZ) in STATISTICA v. 6 (Wald $\chi^2_{(5)} = 34.36$, $p < 0.001$, scaled deviance = 1.027, $n = 382$), with day of capture as a continuous predictor and year as a categorical predictor. Observed means were weighted owing to unequal sample sizes in cells. Mean masses near the time of departure of the known survivors were predicted using 28 May as a covariate in the GLZ to standardize among years.

Arrival times in Delaware Bay of knots banded in TDF and northern Patagonia were estimated by scanning flocks regularly for colour-marked birds throughout May and early June each year from 1997 to 2002. Birds from Rio Grande in Argentine TDF were marked with orange flags and site and year combinations of colour bands, and those from Bahia Lomas in Chilean TDF had red flags as well as site and year colour bands. Birds marked during migration with orange flags and colour bands in Bahia San Antonio in northern Patagonia and with blue flags and colour bands in southern Brazil were also included because they also winter in TDF.

To investigate whether the fat stores and organ sizes of refuelling birds in Delaware Bay were affected in the critical years before and during the rapid population decline, small numbers of adult red knots were collected randomly from cannon-net catches made on 28 May 1998 (six females), 29 May 1999 (two males, six females) and 25 May 2000 (one male, six females) close to departure. Sex ratios were biased heavily towards females in these samples, but previous work at a similar spring stopover area in Iceland showed that there are no differences between the sexes in body composition (Piersma *et al.* 1999). Carcasses were stored frozen at −20 °C until they were dissected to organ level, dried to constant mass and the fat extracted following procedures outlined in Piersma *et al.* (1999).

Owing to the annual life cycle of red knots and the recognition of two age classes (because birds first breed in their second year), we used a two-dimensional matrix population model for demographic modelling. The entries or vital rates of this matrix are fecundity, juvenile survival and adult survival. Additionally we have a 2×1 vector of population size containing the estimates of the total numbers of adults and juveniles. To obtain an estimate of the population size after 1 year, we simply multiply the initial population vector by our matrix model

$$\begin{pmatrix} n_1(t+1) \\ n_2(t+1) \end{pmatrix} = \begin{pmatrix} 0 & f \\ \phi_{\text{juv}} & \phi_{\text{ad}} \end{pmatrix} \begin{pmatrix} n_1(t) \\ n_2(t) \end{pmatrix},$$

where $n_1(t)$ and $n_2(t)$ are, respectively, the numbers of juveniles and adults in year t, f is the yearly fecundity and ϕ_{juv} and ϕ_{ad} are juvenile and adult survival, respectively. Assuming that the mean fecundity and annual survivals remain constant, we can calculate the population trend in the near future. However, natural or anthropogenic variability in fecundity and unreliability in our survival estimates can cause the true population trend to deviate from our predicted trend. We used bootstrapping to determine the 95% confidence limits of this predicted trend. Unreliability in the population growth rate is the result of unreliability in the estimation of the vital rates, the model parameters. We assumed a uniform distribution for fecundity with a minimum of 0 and a maximum of 0.30. For each year, a value for fecundity was selected randomly. Survival probabilities were drawn from a binomial distribution varying from 0 to 1. From this distribution, one value for adult and juvenile survival was selected randomly to cover all 10 successive years. These randomly selected values were the input parameters of the matrix population model.

One major stumbling block is that two essential vital rates needed in the population model, fecundity and first-year survival, are defined using data from studies conducted elsewhere and are not estimated using field data collected for *C. c. rufa*. However, the number of second-year birds sampled in catches in TDF can be used to derive indirectly an estimate of the population growth rate without knowing the two missing vital rates. We define $\phi_{\text{juv}}(t) = s\phi_{\text{ad}}(t)$, where s is a factor specifying the relationship between first-year and adult survival, $\phi_{\text{juv}}(t)$ and $\phi_{\text{ad}}(t)$, respectively. Assuming that birds first breed in their second year and raise offspring, fecundity is defined as

$$f(t) = \frac{N_{\text{juv}}(t+1)}{N_{\text{ad}}(t) + N_{\text{2nd}}(t)}.$$

N is the total number of individuals in TDF based on count data. In addition, we can define the number of second-year birds $N_{\text{2nd}}(t)$ as $N_{\text{2nd}}(t+1) = N_{\text{juv}}(t)\phi_{\text{juv}}(t) = N_{\text{juv}}(t)s\phi_{\text{ad}}(t)$. Combining these two equations leads to

$$f(t) = \frac{\dfrac{N_{\text{2nd}}(t+2)}{s\phi_{\text{ad}}(t+1)}}{N_{\text{ad}}(t) + N_{\text{2nd}}(t)}.$$

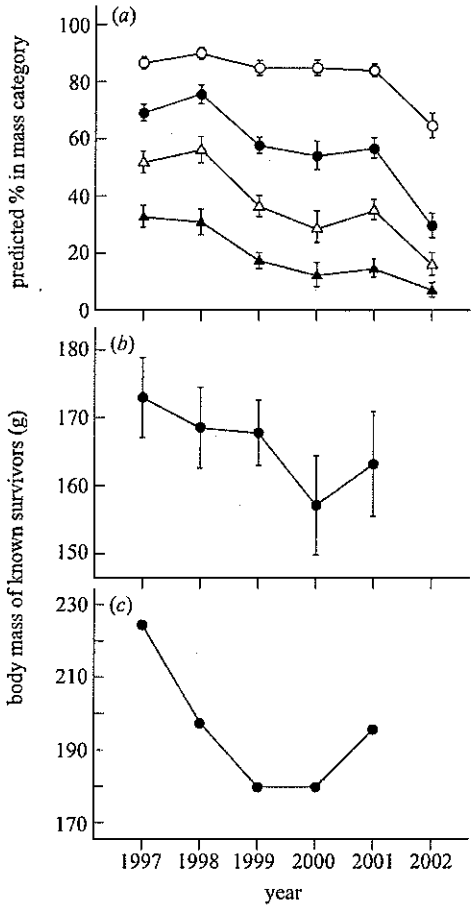

Figure 1. (*a*) Percentages of red knots with 95% CIs in different body-mass categories in Delaware Bay near the departure time each year (28 May) over the period 1997–2002. Mass categories are: open circles, ≥160 g; filled circles, ≥180 g; open triangles, ≥190 g; filled triangles, ≥200 g. (*b*) Observed mean mass at 23 May of birds known to have survived the subsequent year. (*c*) Predicted mean masses near departure on 28 May, computed using day 28 as a covariate.

As fecundity is a known estimate multiplied by $1/s$, as first-year survival is a known estimate multiplied by s and as the elasticities of fecundity and first-year survival are similar (G. Aarts, unpublished data), we conclude that s has no effect on the estimated population trajectory.

3. RESULTS

With thresholds in departure body mass of 180–200 g, red knots have shown increasing signs of energetic stress in refuelling since 1999 (figure 1*a*). From 1997/1998 to 2001/2002 the predicted proportion of well-conditioned knots (200 g or greater) in Delaware Bay near departure time in late May decreased significantly by 70%. The same trend was detected in the most poorly conditioned half of the population on 28 May each year (figure 1*a*). Within 2–3 days of the peak departure for the Arctic, mean body masses declined significantly (t-test: $p < 0.001$) from 182.8 ± 22.6 g in 1997 to 162.3 ± 24.5 g in 2002. There has therefore been a significant increase in the proportion of red knots departing Delaware Bay that are under-conditioned for the joint energetic demands of migration to and breeding success in the Arctic.

We investigated whether reduced departure masses affected return rates (a product of true survival, site fidelity and recapture rate) of adults caught in Delaware Bay. Red knots known to survive to a later year, through recaptures or resights throughout the flyway, were heavier at initial capture than birds never seen again (one-way ANOVA: $F_{1,7887} = 13.80$, $p < 0.001$). Earlier-arriving birds thus are predicted to have a higher probability of surviving and returning in subsequent years because they have more time to attain higher departure masses. However, even known survivors first captured in the peak stopover period of 15–30 May ($n = 382$) showed strong declines in mean observed mass at 23 May (the covariate mean) and predicted mass at 28 May (near departure) in recent years (figure 1*b*,*c*). This indicates that even among known survivors there is considerable among-year heterogeneity in mean rates of nutrient accumulation in the critical five days before departure, especially in 1999 and 2000: 10.4 g d^{-1} (1997), 5.8 g d^{-1} (1998), 2.6 g d^{-1} (1999), 4.6 g d^{-1} (2000) and 6.4 g d^{-1} (2001).

In 1997 even birds arriving at 130 g on 22 May would have been able to reach 180 g by 28 May, but in later years there has been an increase in the proportion of poorly conditioned birds at the end of the season. This could be attributable to a combination of birds being unable to put on mass at a sufficient rate and an influx of late-arriving birds in poor condition. Arrival time of the southernmost-wintering birds in relation to the more northerly birds has certainly differed over time, although in most years the former appear to arrive later than the latter in Delaware Bay and in 2000 and 2001 the highest proportion of TDF birds occurred at or after the peak aerial count (figure 2). Thus, late arrival and reduced food availability are implicated in the reduced rate of body-mass gain of known survivors, resulting in an increase in the proportion of birds that are poorly conditioned at the departure date.

In addition to the decline in the departure masses of an increasing segment of the population that started in 1999 (figure 1), reductions in the functional size of a few key organs at departure may have contributed to subsequent reproductive failure and/or enhanced mortality. There were no differences between years in body size (bill length, wing length) among the late-May samples, and the variations in body mass (figure 3) were not significant either. Similarly, there were no differences between years in total fat mass, total fat-free mass or the fat-free dry masses (FFDMs) of heart, leg muscles, stomach, kidneys or lungs (ANOVAs). In 1999 the FFDMs of the intestine were significantly reduced compared with both 1998 and 2000 (figure 3). The liver and pectoral muscles were significantly reduced in size in both 1999 and 2000 compared with 1998.

Survival analyses indicated that the best-fitting model for the TDF–northern Patagonia data using the AIC is a time-dependent one (table 2*a*). Annual survival declined significantly from an average of 84.6% in the three migration years from 1994/1995 to 1997/1998 (1994/1995–1995/1996, 1995/1996–1996/1997 and 1996/1997–

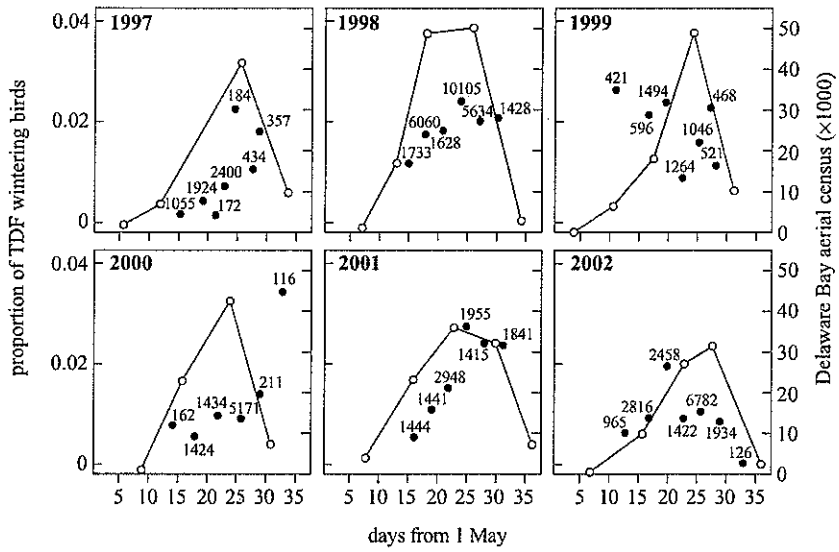

Figure 2. Observed proportions of TDF wintering red knots banded in Lagoa do Peixe (Brazil), Punta Rasa, Bahia de San Antonio and Rio Grande (Argentina), and Bahia Lomas (Chile) that were resighted in Delaware Bay in 1997–2002 (filled circles), relative to the approximately weekly aerial census (open circles). The number of birds scanned is indicated beside each point sample.

1997/1998) to 56.4% in the ensuing 3-year period to 2000/2001 (table 2*b*). The data are not sufficient to estimate $\phi 3$ (annual survival for 2000/2001–2001/2002) accurately, but the parameter is estimable because fixing it at a value of 0.95 causes the deviance to change. Considering the selection of the time-dependent model and the profile likelihood CIs we can only conclude that $\phi 3 \approx \phi 1$. Using a larger mark–recapture dataset for Delaware Bay for 1997/1998–2001/2002 we detected the same large decline in annual survival, and localized it to after the birds left Delaware Bay in 2000 (table 2).

Although productivity in the 2000 breeding season cannot be measured directly because only a small number of juveniles make a full migration to TDF each year, indirect evidence that the 2000 breeding season was a poor one relative to those of previous years comes from numbers of immature second-year birds in cannon net catches in February 1995, December 2000 and late November 2001. Second-year birds comprised 19% of annual catches of *ca.* 500–600 knots in TDF in 1995, 16% in 2000 and 10% in 2001. The decline in population size by a further 10 000 wintering birds in TDF in January 2002 points to the continuing serious mortality of adults and immatures in the flyway. This increased mortality is contributed to by an increasing proportion of light-weight birds in Delaware Bay at the normal departure date.

To project the possible demographic outcomes of current levels of fecundity, annual survival and recruitment on the population size of red knots that over-winter in TDF we constructed a matrix model under various realistic assumptions (figure 4). Juvenile survival has not been estimated accurately for *C. c. rufa*, but for the closely related subspecies *C. c. islandica*, which also breeds in North America, juvenile survival is one-quarter of adult survival (Boyd & Piersma 2001). If we assume the best-case scenario that juvenile survival is one-half of adult survival, that adult survival in future will average the pre-2000 level of 84.6% and that fecundity is uniformly distributed with a mean of 0.29 (maximum of 0.58, minimum of 0.0), then the TDF population (including first-year birds that winter further north) is predicted to be roughly stable at *ca.* 70 000 birds (figure 4*a*). However, if the 1997/1998–2000/2001 levels of annual survival prevail, the population is predicted to approach extremely low numbers by 2010 when the probability of extinction will be correspondingly higher than it is today (figure 4*b*). The aerial census numbers plotted here suggest strongly that the population was on the latter trajectory through 2002.

4. DISCUSSION

The analysis of the capture–recapture data collected in the wintering populations in TDF–Patagonia and from the critically important last refuelling stop in Delaware Bay reveals the dramatic drop in annual survival that occurred between the 1999/2000 (ending 30 June 2000) and the 2000/2001 (beginning 1 July 2000) migration years. The absence of transience in the two datasets (U-CARE test3.SR: $p > 0.1$) argues against temporary emigration as an explanation for the large reduction in annual survival since July 2000, and corresponds to the expectations of a large mortality event implied by the 14 000 lower bird count in TDF in February 2001. This localizes the large mortality to the period after the knots left Delaware Bay and migrated to the Arctic Canadian breeding grounds and the following southern migration and over-wintering period in TDF. The same pattern seems to have occurred in the next migration year, when the aerial count recorded the loss of another 10 000 birds. Cannon net catches in TDF revealed that part of this decrease was attributable to successively lower recruitment of second-year birds in wintering flocks, indicating that breeding success was reduced by refuelling problems in adults in Delaware Bay.

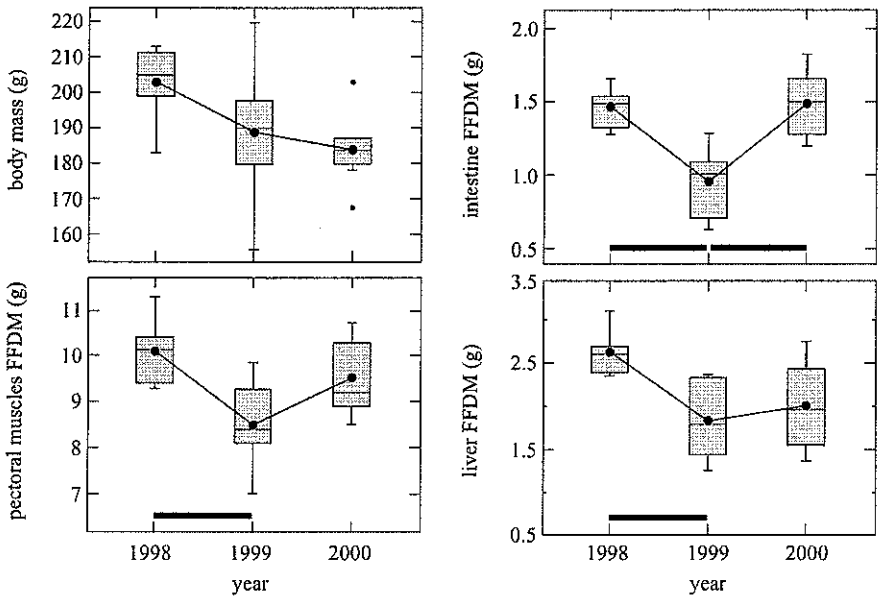

Figure 3. Box plots with averages (filled circles) of body mass and the FFDMs of the pectoral muscles, intestine and liver of knots collected in Delaware Bay in late May 1998, 1999 and 2000. There was significant between-year variation in the masses of pectoral muscles (ANOVA: $F_{2,16} = 5.0$, $p = 0.02$), intestine ($F_{2,16} = 11.8$, $p = 0.001$) and liver ($F_{2,16} = 4.9$, $p = 0.02$). Averages that are statistically significantly different from each other (at the 5% confidence level as indicated by Scheffé tests) are connected by horizontal bars.

Table 2. (*a*) Model selection and (*b*) real function parameters of the best-fitting models for the TDF–northern Patagonia and Delaware Bay datasets with sin link function.
(For the TDF–northern Patagonia dataset $\phi 1$ is for the time period 1994/1995–1997/1998, $\phi 2$ is for 1997/1998–2000/2001 and $\phi 3$ is for 2000/2001–2001/2002. In the Delaware Bay dataset $\phi 1$ is for the period 1996/1997–1999/2000 and $\phi 2$ is for 1999/2000–2000/2001.)

(*a*) model	AICc	delta AICc	AICc weight	model likelihood	number of parameters	deviance
TDF–northern Patagonia						
$\phi(t)p(t)$	926.62	0.00	0.8142	1.0000	7	10.5040
$\phi(.)p(t)$	930.16	3.54	0.1384	0.1700	5	18.0650
$\phi(t)p(.)$	932.31	5.69	0.0473	0.0581	5	20.2100
$\phi(.)p(.)$	995.09	68.47	0.0000	0.0000	2	89.0100
Delaware Bay						
$\phi(t_1,t_2)p(t)$	3703.68	0.00	0.6103	1.0000	7	55.7343
$\phi(.)p(t)$	3705.66	1.99	0.2262	0.3706	6	59.7230
$\phi(t)p(t)$	3706.34	2.66	0.1612	0.2641	9	54.3894
$\phi(t)p(.)$	3715.58	11.90	0.0016	0.0026	6	69.6395
$\phi(.)p(.)$	3716.86	13.18	0.0008	0.0014	2	78.9280

(*b*) parameter	TDF–Patagonia			Delaware Bay		
		95% CI[a]			95% CI[a]	
	estimate	lower	upper	estimate	lower	upper
1:$\phi 1$	0.846	0.529	1.000	0.975	0.862	1.000
2:$\phi 2$	0.564	0.477	0.659	0.617	0.426	0.911
3:$\phi 3$	1.000	0.490	1.000	—	—	—
4:p1	0.0081	0.0008	0.0749	0.0152	0.0085	0.0250
5:p2	0.0409	0.0185	0.0881	0.0252	0.0184	0.0344
6:p3	0.0881	0.0673	0.1145	0.0127	0.0094	0.0175
7:p4	—	—	—	0.0336	0.0226	0.0494

[a] CIs for these ϕ estimates were calculated with profile likelihood (Lebreton *et al.* 1992).

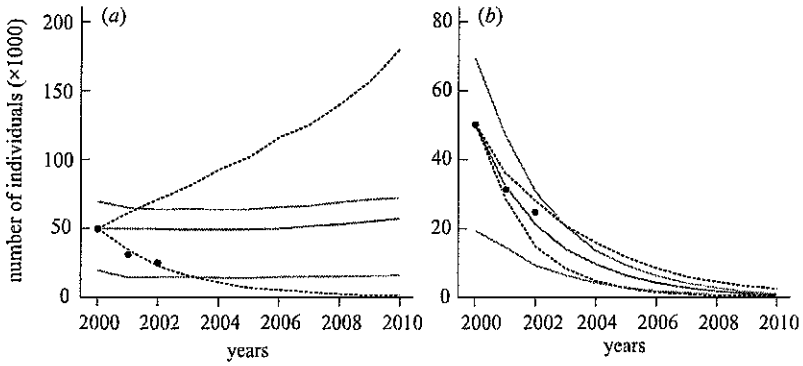

Figure 4. Predicted population trends and associated 95% confidence limits for adults (dashed lines), predicted population trends for juveniles (lower grey line) and the sum of these two (top grey line) for 10 years from 2000, with (*a*) constant adult survival of 85% and juvenile survival of half that of adults (population growth parameter $\lambda = 1$) and (*b*) constant adult survival of 56% and juvenile survival of half that of adults ($\lambda = 0.66$). The closed dots represent the aerial censuses of the overwintering flock of adults in TDF. The 95% upper and lower confidence limits are based on 1000 bootstrap iterations.

Thus, we have demonstrated that there are striking fitness consequences for both adult survival and the numbers of second-year birds in wintering populations of red knots that are correlated with the amount of nutrient stores accumulated in Delaware Bay, the last stopover site before they migrate to breeding grounds in the Canadian Arctic. However, our analysis does not permit separation of reductions in breeding success from declines in juvenile survival as the cause of decreased recruitment, though both might have occurred. Lower survival of juveniles might imply further problems during the southern migration and/or at wintering sites. Adult survival rates are way below those recorded in any other population of red knot (e.g. *C. c. islandica* in the UK: estimates over intervals of *ca.* 10 years varying from 76.4% to 85.8%; Boyd & Piersma 2001). The amount of food available and the timing of arrival at this last site directly affect the departure masses the birds can achieve. Furthermore, during fuel storage in 1999 and 2000 some critical organs were reduced in size compared with 1998 and smaller than expected on the basis of data collected from other stopover sites. The reduced pectoral muscles in late May 1999 relative to the expected size (Piersma *et al.* 1999) could have compromised flight. The lining of the intestine and the mucosa it produces protect the body against pathogens ingested with the food (Schat & Myers 1991). Reductions in intestinal mass (33% lower in 1999) have been experimentally shown to suppress immune function (Sanderson 2001). The liver plays a prominent part in the detoxification process, so that a reduction in size by a third as in 1999 and 2000 could easily compromise long-term health.

The decline in the average departure masses of red knots follows the dramatic increase in commercial fishing that began in 1990 and peaked in 1995/1996 to provide bait for eel and conch fisheries (Walls *et al.* 2002), and also reflected a sixfold decline in the numbers of horseshoe crabs caught in survey trawls in Delaware Bay by the Delaware Division of Fish and Wildlife (S. Michels, unpublished data, cited in Andres (2003)). We contend that the over-harvesting of horseshoe crabs in the past and the erosion of beaches in Delaware Bay have jointly reduced the number of quality foraging areas for shorebirds, and has concentrated the birds into a few key locales where crab eggs are locally abundant. There is strong evidence that the increasing dependence of birds on so few vulnerable areas and the increasing proportion of poor-conditioned birds at departure time have direct and serious implications for the continuing viability of the *rufa* subspecies.

The annual February aerial census in TDF reported that the overwintering population had stabilized at *ca.* 30 000 red knots in 2003 (Morrison *et al.* 2004). However, the peak weekly aerial count in Delaware Bay in May 2003 declined to 16 000 birds from 31 000 the previous year, following a very late spring migration in and very restricted spawning of horseshoe crabs in 2003. The late arrival and reduced supplies of crab eggs are expected to have even more severe fitness-reducing effects on red knots through decreased breeding success, recruitment and annual survival than we have reported here.

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