Science

A MIGRANT'S PLIGHT

Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range

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Reductions in body size are increasingly being identified as a response to climate warming. Here we present evidence for a case of such body shrinkage, potentially due to malnutrition in early life. We show that an avian long-distance migrant (red knot, *Calidris canutus canutus*), which is experiencing globally unrivaled warming rates at its high-Arctic breeding grounds, produces smaller offspring with shorter bills during summers with early snowmelt. This has consequences half a world away at their tropical wintering grounds, where shorter-billed individuals have reduced survival rates. This is associated with these molluscivores eating fewer deeply buried bivalve prey and more shallowly buried seagrass rhizomes. We suggest that seasonal migrants can experience reduced fitness at one end of their range as a result of a changing climate at the other end.

Phenological changes and geographical range shifts are well-known responses to climate change (*1*). A third broadly observed response to global warming appears to be shrinkage of bodies (*2–5*). It has been hypothesized that body shrinkage is a genetic microevolutionary response to warming, due to smaller individuals being better able to dissipate body heat because of the larger surface/volume ratio of their bodies [e.g., Bergmann's rule (*2*)]. Alternatively, it has been put forward that climate change may disrupt trophic interactions, potentially leading to malnutrition during an organism's juvenile life stage (*6, 7*). Because poor growth may not be compensated for later in life (*8*), this would lead to smaller bodies (i.e., shrinkage as a phenotypically plastic response).

Under climate change, some regions are warming faster than others. Especially in the Arctic, warming has been observed at unprecedented rates (*9, 10*). Hence, body-size reductions would be expected to be most pronounced in the world's most northerly region (*6*). Many Arctic-breeding avian species, however, are long-distance migrants that spend the northern winter at lower latitudes (*11*), where the impacts of climate change are less obvious.

Based on analysis of satellite data, we show here that over the past 33 years, snowmelt has occurred progressively earlier in the high-Arctic breeding grounds of the red knot (*Calidris canutus canutus*) at Taimyr Peninsula (76° to 78°N; Fig. 1), changing at a rate of about half a day per year [coefficient of determination (R^2) = 0.32, $F_{1,31}$ = 14.77, $P < 0.001$; Fig. 2A, table S1, and figs. S1 to S3]. Over these three decades, 1990 juvenile red knots were caught and their body sizes measured in Gdańsk Bay, Poland, during their first southward migration to their West African nonbreeding grounds (Fig. 1). These measurements show that juvenile birds were smaller after Arctic summers with early snowmelts, particularly with respect to body mass [corrected Akaike information criterion (AIC_c) = 14775.24, $P < 0.0005$; Fig. 2B and table S2], bill length (AIC_c = 7610.48, $P < 0.005$; Fig. 2C and table S3), and overall body size [first principal component (PC1) on bill, tarsus, and wing; AIC_c = 5925.22, $P < 0.05$; table S4]. The models that best explained the variation in bill length and overall body size additionally included the Normalized Difference Vegetation Index [NDVI, a proxy for total primary biomass production (*12*)] of the breeding ground; longer-billed, bigger birds were captured after summers with high NDVI values (Fig. 2C). These size variations were still apparent when juveniles arrived at their main wintering ground on the Banc d'Arguin, Mauritania (annual average juvenile bill lengths in Poland and Mauritania correlated strongly: Pearson's r = 0.73), where red knots showed no signs of compensatory growth (measurements of body size dimensions, including bill length, were highly consistent within individuals; fig. S4B).

In this tropical nonbreeding area, red knots use their tapered bills to detect and retrieve mollusk prey buried in intertidal sediments (*13*). Stable isotope analysis of 2340 birds caught at Banc d'Arguin between 2002 and 2013 shows that longer-billed birds relied mostly on the abundant bivalve prey species *Loripes lucinalis* (hereafter, *Loripes*), whereas shorter-billed individuals did not (R^2 = 0.18, $F_{3,2336}$ =170.70, $P < 0.00001$; Fig. 3A). This may be due to most *Loripes* being buried out of reach for shorter-billed knots: An individual with a 40-mm bill has access to about two-thirds of all *Loripes*, whereas a bird with a 30-mm bill is able to access only one-third (Fig. 3B). Shorter-billed red knots consumed relatively more of the shallowly buried bivalve *Dosinia isocardia* (hereafter, *Dosinia*) and rhizomes of the seagrass *Zostera noltii* (hereafter, *Zostera*; Fig. 3B and fig. S5). Juvenile red knots consumed fewer *Loripes* compared with older birds ($P < 0.00001$ for the age-bill interaction; Fig. 3A). This is probably due to the fact that *Loripes* is mildly toxic; the sulphide metabolism of endosymbiotic bacteria living inside its gill causes diarrhea (*14*). In spite of its toxic effects, red knots depend on *Loripes*, especially in years with few alternatives (*15*). Juveniles may need physiological adjustments before they can digest this special type of prey efficiently (*16*). Only birds with longer bills can make this switch to eating the deeply buried *Loripes*; the shorter-billed birds are restricted to a "juvenile diet" of relatively rare *Dosinia* (*15*) and poor-quality rhizomes (*17*). Hence, for the shorter-billed birds, the inability to access the high-quality and abundant *Loripes* after the first winter may come at a cost.

Individual color-ringing of 2381 red knots during annual expeditions to Banc d'Arguin from 2002 to 2013, and subsequent resightings of these individuals (*12*), indicate that birds with shorter bills had lower apparent survival rates, primarily in the case of juveniles between their first and second winters [Fig. 4A, fig. S6, and tables S5 to S8; we use the term "apparent survival" because mortality is confounded with permanent emigration (*18*)]. The much weaker bill-length effect in adults may be attributable to the advantages of a short bill when feeding on arthropods on the tundra (*19*); juveniles do not benefit from these advantages because they stay at the Mauritanian nonbreeding grounds year-round (*20*). Because early-snowmelt years produced shorter-billed juveniles (Fig. 2C), and because shorter-billed juveniles experienced hampered survival in the tropics (Fig. 4A), overwintering juveniles thus had poor survival rates after Arctic summers with early snowmelt [proportion of variation explained by date of snowmelt (R^2_{dev}) = 0.32 (*12*); Fig. 4B]. However, with snowmelt occurring progressively earlier over the years (Pearson's r = –0.58 for 2002–2012), the temporal variation in juvenile survival was similarly well explained by a linear time trend (model 13 versus 14, ΔAIC_c=1.01; table S7). Strictly speaking, we therefore cannot distinguish an effect of snowmelt date on survival from any other potential covariate changing over time. We see this problem as inherent to any descriptive study of climate change effects.

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In the face of climate change–induced body shrinkage and the strong selection pressure against shorter-billed juveniles at the nonbreeding grounds, one would expect the adult population to maintain a relatively constant bill length or at least to show less shrinkage of the bill compared with other structural body-size components. This was the case (fig. S7): Although overall body size (PC1 on bill, tarsus, and wing) in adults decreased at a rate of 0.020 SDs per year ($R^2 = 0.26$, $F_{2,1727} = 299.20$, $P < 0.001$), their bill length decreased at a rate of only 0.010 SDs per year ($R^2 = 0.21$, $F_{2,1727} = 223.57$, $P = 0.097$), suggesting a climate change–induced directional selection on body shape.

The body shrinkage observed in juvenile red knots may be a phenotypically plastic response to an altered environment. Neonatal red knots feed on arthropods (21) that emerge from a defrosting tundra soil (22). With the rapid advancement in the seasonal appearance of high-Arctic arthropods (23), red knot chicks may face a trophic mismatch by hatching too late relative to the peak food abundance (23)—in spite of evidence for earlier nesting in high-Arctic shorebirds (24), and in spite of the observation that red knot spring migration through France is advancing [although at only 0.25 days/year, which is half the rate at which the timing of snowmelt is advancing) (25)]. In addition to advancing the timing of the arthropod peak, earlier snowmelts are also known to depress the peak's amplitude. This is because earlier snowmelts produce smaller-bodied insects (26) and cause greater soil temperature fluctuations, thereby enhancing mortality among larvae (27).

Our finding that bills and bodies are smaller in years with low breeding-ground NDVI values (Fig. 2C) hints at the importance of the food peak's amplitude, because low NDVI values are considered to reflect low insect abundances (28).

The negative effects of climate change on the growth of red knots may thus be due to a trophic mismatch. The fitness-related consequences of this growth inhibition are that smaller, shorter-billed individuals have, on average, reduced apparent survival rates at their tropical wintering grounds. This mechanism may be one of the drivers of the steep and ongoing population decline of the *C. c. canutus* red knots (15, 29). The discovery of rapid body shrinkage and its downstream effects on population size may extend to other Arctic migrants.
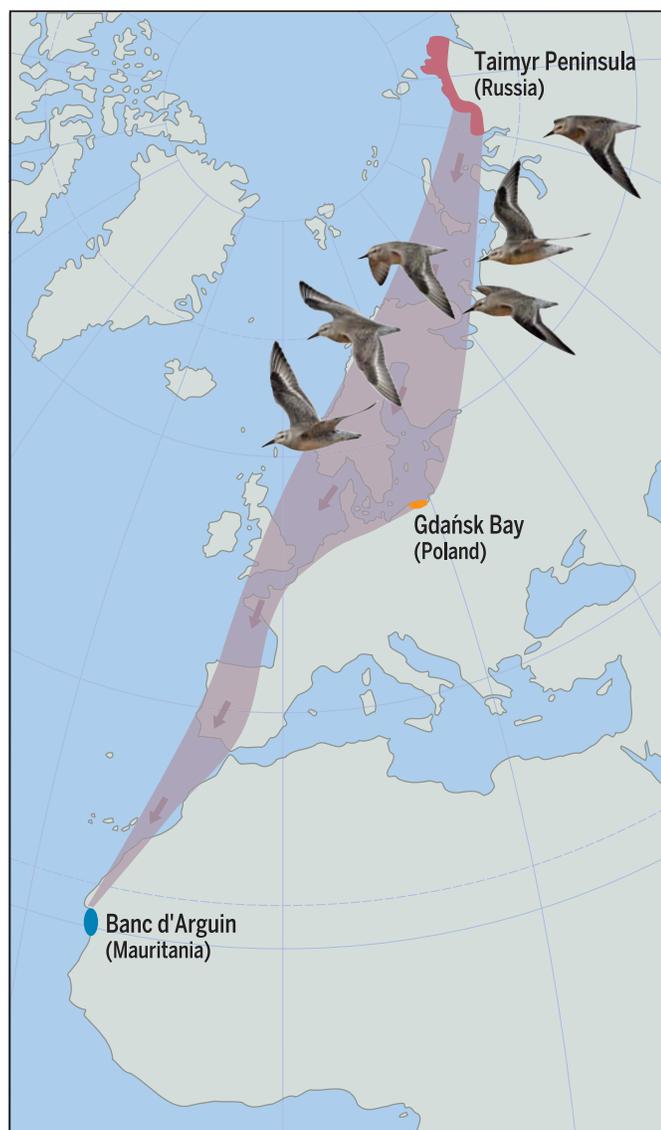

Fig. 1. Red knots breed during summer in the high Arctic at Taimyr Peninsula and spend the long nonbreeding season at Banc d'Arguin, Mauritania, West Africa. On their first southward migration to West Africa, many juvenile red knots make a stopover on the Baltic coast of Poland.
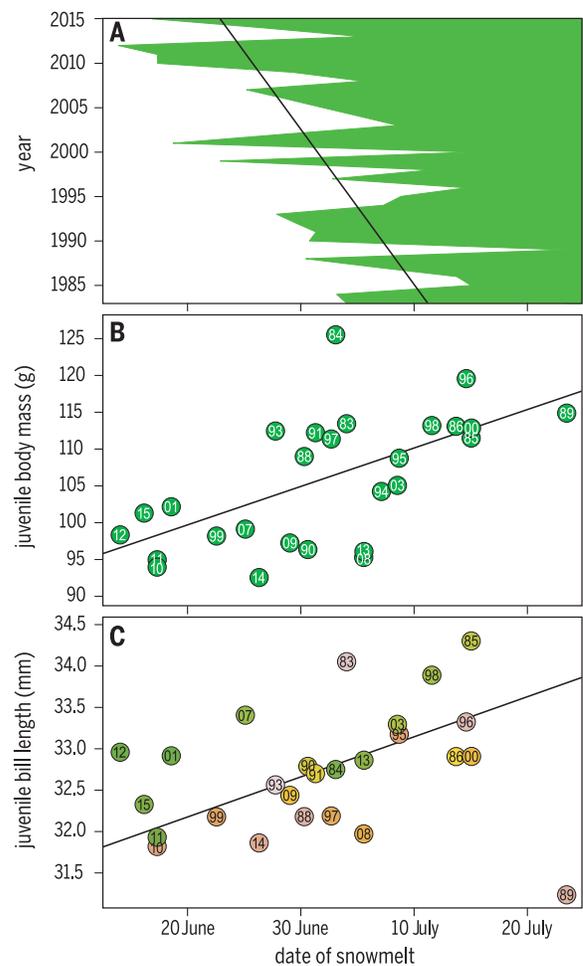

Fig. 2. Changes in Arctic climate and red knot body size over the past three decades. (**A**) Snow at the red knots' breeding ground at Taimyr Peninsula has been melting progressively earlier at an average rate of 0.5 days/year. (**B**) Juvenile red knots, captured during brief stopovers in Poland on their first southward migration from the Arctic, had lower body masses after breeding seasons in which snow had disappeared early (each circle denotes the annual mean, with number inside the circle giving the year). (**C**) They also had shorter bills after breeding seasons in which the Arctic snow melted earlier [circles denote annual means as in (B)], especially in years when breeding-ground NDVI [as a proxy for total primary biomass production (12)] was low [NDVI is indicated by the color range of the circles (green, high; pink, low)].
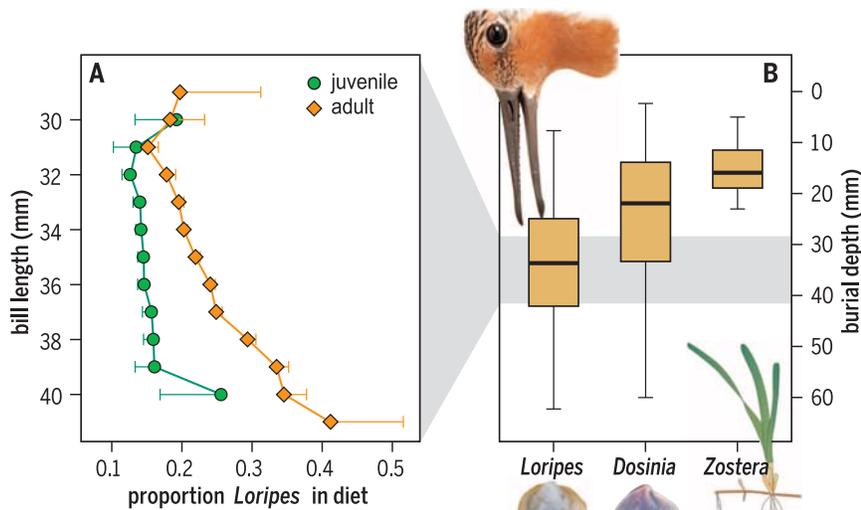
Fig. 3. Prey choice and prey availability at the Mauritanian wintering grounds. (**A**) Analysis of stable isotopes of blood samples shows that juvenile red knots (n = 676 birds) largely ignored the most abundant but mildly toxic prey, *Loripes*. However, with an increase in age, adult red knots (n = 1664) added substantial amounts of *Loripes* to their diet, but only if they had long bills. Plotted are means ± SE. (**B**) This bill length–dependent diet shift may be explained by the depth distribution of *Loripes*. The majority of these bivalves live between 30 and 40 mm below the seafloor, which is precisely the range of the bill lengths. The other two food sources, *Dosinia* bivalves and *Zostera* rhizomes, are found at shallower depths and are accessible to all red knots. Bars indicate medians, boxes indicate 25th to 75th percentiles, and whiskers indicate ranges.
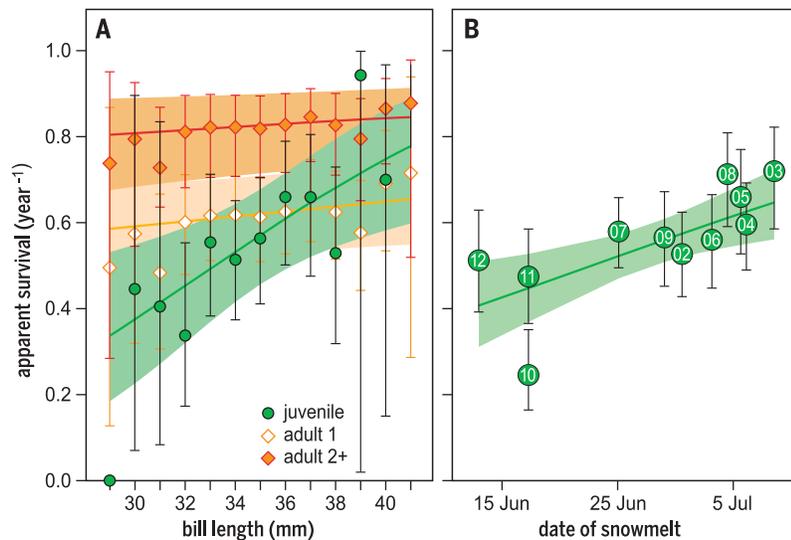
Fig. 4. Annual survival rates of individually marked red knots. (**A**) Annual apparent survival rates [± 95% confidence intervals (CIs)] increase significantly as a function of bill length in juveniles (the slope β of the relationship of logit-transformed values = 0.30; 95% CI, 0.08 to 0.51; n = 690 birds), whereas this relation is not significant for adults [β = 0.05; 95% CI, −0.02 to 0.11; n = 1691 birds; distinguishing between survival in the first year after capture (adult 1) and later (adult 2+)]. Symbols show apparent survival rates of juveniles born in 2009 (a year with average survival; model 11, table S7); lines show these data as a linear function of bill length [model 1 (the best-supported model), table S7]. Shaded areas are 95% CIs of the linear functions. Bill-length effect is assumed to be the same in all years. (**B**) Annual apparent survival rates (± 95% CIs) of juveniles increase with the date of snowmelt in their year of birth (the year is indicated inside the circle). Symbols show juvenile apparent survival rates estimated per year (model 8, table S7); lines show these data as a linear function of the date of snowmelt (model 14, table S7). Time dependence in both the apparent survival and resighting makes the survival estimate for the final year (i.e., for juveniles born in 2013) unreliable; hence, this estimate was excluded.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S7
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