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Gils, J. van, Lisovski, S., Lok, T., Meissner, W., Ozarowska, A., Fouw, J. de, Rakhimberdiev, E., Soloviev, M.Y., Piersma, T. & Klaassen, M. (2016). Body shrinkage due to Arctic warming reduces red knot fitness in tropical wintering range. *Science*, 352, 819-821

Published version: [dx.doi.org/10.1126/science.aad6351](https://doi.org/10.1126/science.aad6351)

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

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[Abstract:]

Reductions in body size are increasingly 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 c. canutus*), 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 where short-billed individuals have reduced survival on their tropical wintering grounds. This is associated with these molluscivores eating fewer deeply buried bivalve prey and more shallowly buried seagrass rhizomes. We suggest seasonal migrants experience reduced fitness at one end of their range due to a changing climate at the other end.

Phenological changes and geographical range shifts represent 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 micro-evolutionary response to warming due to smaller individuals being better able to dissipate body heat due to a larger body surface/volume ratio (e.g., Bergmann's rule (2)). Conversely, 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). As 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 up 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 spending the northern winter at lower latitudes (11), where the impacts of climatic change are less obvious.

Here, based on the analysis of satellite data, we show that over the past 33 years, snowmelt has occurred progressively earlier on the high-Arctic breeding grounds of the red knot (*Calidris canutus canutus*) at Taimyr Peninsula (Fig. 1; 76-78°N), changing at a rate of about half a day per year (Fig. 2A; $R^2 = .32$, $F_{1,31} = 14.77$, $P < .001$; see Table S1 and Figs. S1-S3). During these three decades, 1,990 juvenile red knots were caught and their body sizes measured in Gdańsk Bay, Poland, during their first southward migration to the West-African nonbreeding grounds (Fig. 1). These juvenile birds were smaller after Arctic summers with an early snowmelt, notably with respect to body mass (Fig. 2B; $AIC_c = 14775.24$, $P < .0005$; Table S2), bill length (Fig. 2C; $AIC_c = 7610.48$, $P < .005$; Table S3), and overall body size (PC1 on bill, tarsus, and wing; Table S4; $AIC_c = 5925.22$, $P < .05$). The models best explaining variation in bill length and overall body size additionally included breeding-ground Normalized Difference Vegetation Index (NDVI, a proxy for total primary biomass production (12)), with longer-billed, bigger birds captured after summers with high NDVI values (Fig. 2C). These size variations are still apparent once juveniles arrive at their main wintering ground on the Banc d'Arguin, Mauritania

(annual average juvenile bill length in Poland and Mauritania correlate strongly: Pearson's $r = .73$), where red knots show no signs of compensatory growth (body size dimensions, including bill length, are highly repeatable 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 2,340 birds caught at Banc d'Arguin between 2002 and 2013 shows that longer-billed birds rely mostly on the abundant bivalve prey species, *Loripes lucinalis* ('*Loripes*'), while short-billed individuals do not (Fig. 3A; $R^2 = .18$, $F_{3,2336} = 170.70$, $P < .00001$). This may be due to most *Loripes* being buried out of reach for short-billed knots: an individual with a 40-mm long bill has access to about 2/3 of all *Loripes*, while a bird with a 30-mm long bill is able to access only 1/3 (Fig. 3B). Shorter-billed red knots consumed relatively more of the shallowly buried bivalve *Dosinia isocardia* ('*Dosinia*') and rhizomes of seagrass *Zostera noltii* ('*Zostera*'; Fig. 3B and Fig. S5). Note that juvenile red knots consumed fewer *Loripes* compared with older birds ($P_{\text{age-bill interaction}} < .00001$; Fig. 3A). This is probably due to the fact that *Loripes* is mildly toxic – causing diarrhea due to the sulphide-metabolism of endosymbiotic bacteria living inside this bivalve's gill (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 include the deeply living *Loripes*, with the shorter-billed birds thus being stuck with a 'juvenile diet' of rather 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 1st winter may come at a cost.

Individual color-ringing of 2,381 red knots during annual expeditions to Banc d'Arguin from 2002 to 2013, and subsequent resightings of these individuals (12), show that birds with short bills indeed had lower apparent survival, primarily so from the 1st to the 2nd winter (Fig. 4A; Fig. S6; Tables S5-S8; note that we use the term apparent survival because mortality is confounded with permanent emigration (18)). The much weaker bill-length effect in adults may indicate the advantages of a short bill when feeding on arthropods on the tundra (19) – juveniles lack these advantages as they stay at the Mauritanian

nonbreeding grounds year-round (20). Since early-snowmelt years produce short-billed juveniles (Fig. 2C), and since short-billed juveniles show hampered survival in the tropics (Fig. 4A), overwintering juveniles showed poor survival after Arctic summers with early snowmelt (Fig. 4B; $R^2_{\text{dev}} = 0.32$). Note, however, that with snowmelt occurring progressively earlier over the years (Pearson's $r = -.58$ for years 2002-2012), the temporal variation in juvenile survival was similarly well explained by a linear time trend (Table S7, model 13 vs. 14, $\Delta\text{AIC}_c=1.01$). 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.

In the face of climate-change induced body shrinkage and the strong selection pressure at the nonbreeding grounds against short-billed juveniles, one would expect the adult population to maintain a rather constant bill length, or at least to show less shrinkage of the bill compared to other structural body size components. This was indeed the case (Fig. S7): while overall body size (PC1 on bill, tarsus, and wing) in adults decreased at a rate of 0.020 SD per year ($R^2 = .26$, $F_{2,1727} = 299.20$, $P < .001$), their bill length decreased at a rate of only 0.010 SD per year ($R^2 = .21$, $F_{2,1727} = 223.57$, $P = .097$), suggesting climate-change induced directional selection on body shape.

The body shrinkage as 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). This would then happen 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 actually advancing (although at 0.25 day/yr, i.e., half of the rate at which timing of snowmelt advances; 25). In addition to advancing 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, since low NDVI values are considered to reflect low insect abundances (28).

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

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Acknowledgments: This paper was conceptualized during JAVG's sabbatical at the Centre for Integrative Ecology at Deakin University and benefitted greatly from discussions with Y. Aharon-Rotman and B.J. Hoye at DU, A.I. Bijleveld, S. Duijns, E.M.A. Kok and T. Oudman at NIOZ, and from comments by three anonymous referees. We thank W. Bouma and F. Sanders for wordsmithing and D. Visser for graphical support. Field support was provided by the KULING group in the Polish Baltic, and the Banc d'Arguin teams led by B. Spaans, J. Leyrer, M. Brugge, A. Dekinga and J. ten Horn, while hosted at Iwik by PBNA staff (notably M. Camara). We thank the Directors of the PNBA for access to the study area. Stable-isotope analyses were conducted by T. Leerink, J. Ossebaar and K. Donkers. Financial support was provided by NWO-VIDI grant (864.09.002) to JAVG, by NWO-Rubicon to TL, by a suite of grants to TP (Waddenfonds project 'Metawad' (WF209925), research support from BirdLife Netherlands and WWF-Netherlands, the Prins Bernhard Cultuurfondsprijs voor Natuurbehoud, NWO-WOTRO Integrated Programme grant (W.01.65.221.00) and MAVA-grant (Switzerland)), and ARC (DP130101935) to MK. Data are available at Dryad at: <http://dx.doi.org/10.5061/dryad.n1m8d>.

[Figure captions:]

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 day/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 dot denotes annual mean with number inside dot giving year). (C) They also had shorter bills when the Arctic snow melted earlier (each dot denotes annual mean), especially in years when local vegetation greenness was low (taking breeding-ground NDVI, indicated by greenness of the symbols, as a proxy).

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 ($n = 1,664$) added significant amounts of *Loripes* to their diet, but only so in birds with long bills. Plotted are means \pm SE. (B) This bill-length dependent diet shift may be explained by the depth distribution of *Loripes*, with the majority of these bivalves living between 30-40 mm, i.e., precisely the range of bill lengths. The other two food sources, *Dosinia* and *Zostera* rhizomes, are found at shallower depths and are accessible to all red knots.

Fig. 4. Annual survival rates of individually marked red knots. (A) Annual apparent survival rate (\pm 95% CI) increases significantly as a function of bill length in juveniles (β on logit-transformed values = 0.30, 95% CI: 0.08 – 0.51, $n = 690$ birds), while this relation is not significant for adults ($\beta = 0.05$, 95% CI: -0.02 – 0.11, $n = 1,691$ birds; distinguishing between survival in the first year after capture (adult 1)

and later (adult 2+)). Symbols and lines show apparent survival of juveniles born in 2009 (a year with average survival; model 11, Table S7) and as a linear function of bill length (the best-supported model 1, Table S7), respectively. Note that bill length effect is assumed to be the same in all years. (B) Annual apparent survival rate (\pm 95% CI) of juveniles increases with date of snowmelt in their year of birth (the latter indicated inside symbol). Symbols and lines show juvenile apparent survival estimated per year (model 8, Table S7) and as a linear function of date of snowmelt (model 14, Table S7), respectively. Time dependence in both Φ and p makes the survival estimate for the last year (i.e., for juveniles born in 2013) unreliable, hence this estimate was excluded.

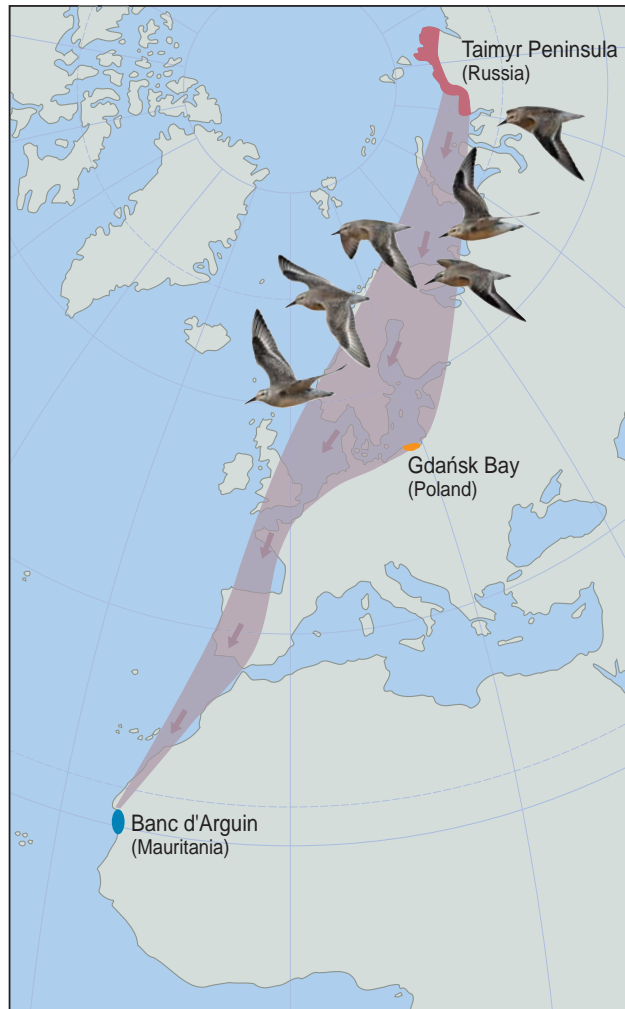


Fig. 1

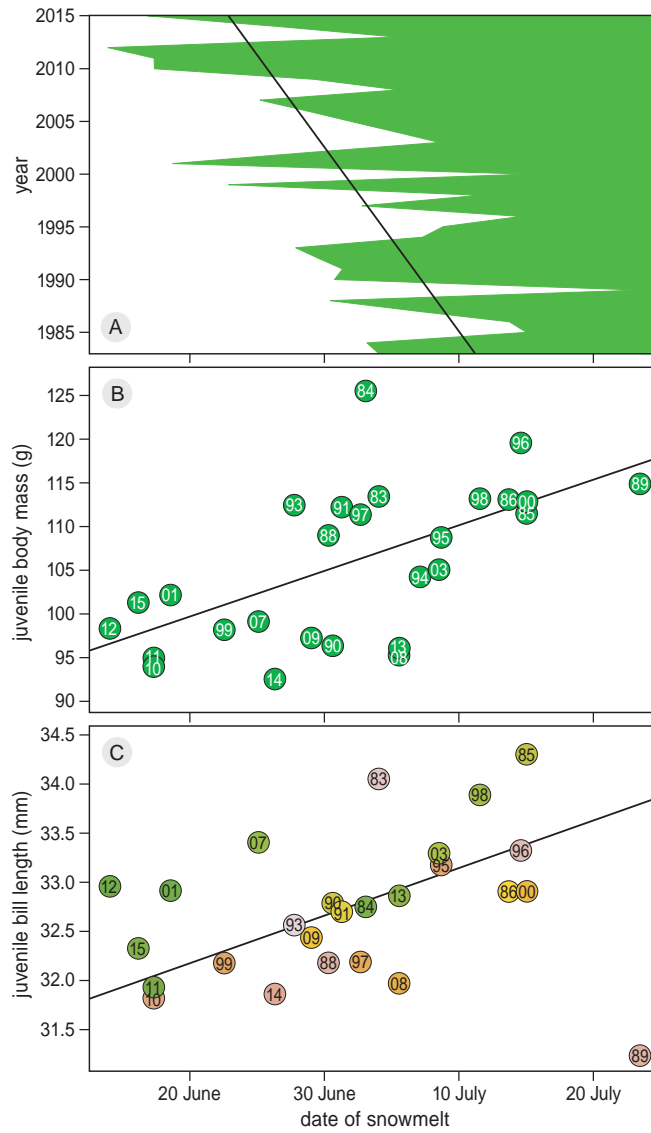


Fig. 2

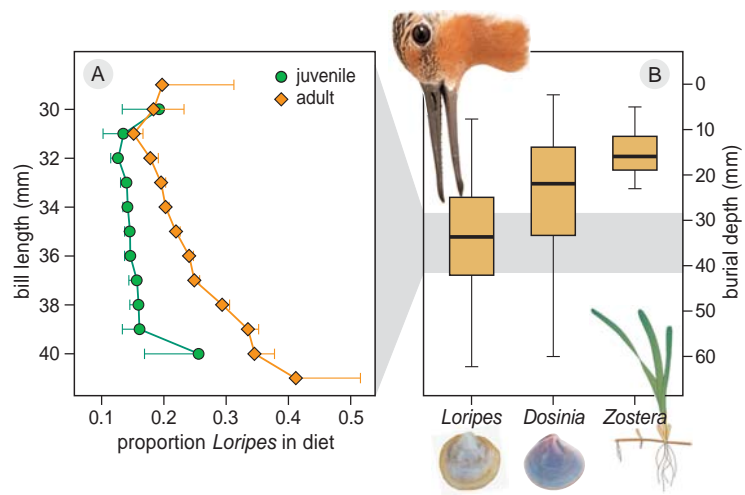


Fig. 3

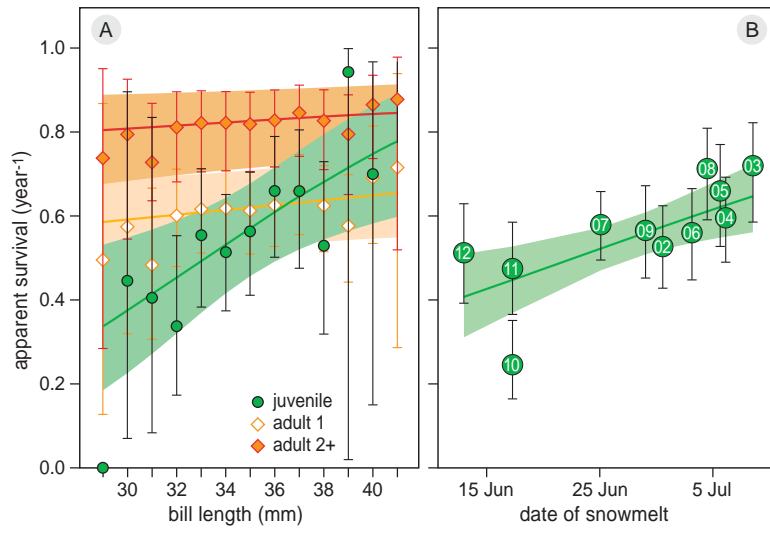


Fig. 4