

Phenotypic compromises in a long-distance migrant during the transition from migration to reproduction in the High Arctic

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Summary

1. Seasonal carry-over effects may be important structuring components of avian life-history cycles. However, little is known on physiological transitions between stages and on phenotypic compromises that may be made at such time to improve fitness.
2. We studied postmigratory body remodelling in red knots (*Calidris canutus islandica*) arriving on the Arctic breeding grounds. Our objectives were to determine the effects of body reconstruction and preparation for breeding on maintenance energy costs and to determine whether weather conditions can force compromises between functions required for postmigration recovery of body composition, thermoregulation and breeding.
3. During two consecutive springs at the northernmost land on Earth (Alert, Ellesmere Island, Canada, 8230N), we monitored changes in knots post-arrival body stores. Using ultrasonography, we also tracked changes in gizzard size, an indicator of gut size, and pectoral muscle thickness, not only an endogenous protein source but also a thermogenic organ. We measured basal metabolic rate (BMR) throughout reconstruction and compared it with BMR of nonbreeding red knots wintering in the Dutch Wadden Sea.
4. Arriving knots faced temperatures up to 13 C lower than during midwinter. Birds arrived

Introduction

Seasonal carry-over effects, where events or activities occurring during specific life-history stages influence fitness through long-lasting consequences at later stages, are increasingly recognized as important components of the cyclic aspects of avian life histories (Harrison et al. 2011). A simple mechanism for carry-over effects is that individuals make the transition between seasons or stages in altered condition, that is, with different or reduced levels of resources (macro- or micronutrients), which then directly affect subsequent performance (Harrison et al. 2011). However, little attention has been given to physiological adjustments occurring during transitions between stages (Ramenofsky & Wingfield 2006; Wingfield 2008) and little is known about how phenotypic flexibility (reversible adjustment of adult phenotype to prevailing ecological constraints: Piersma & Drent 2003; Piersma & van Gils 2011) may influence recovery from physiological challenges. Therefore, the physiological basis of carry-over effects remains poorly understood (Harrison et al. 2011).

Among vertebrates, the red knot (*Calidris canutus islandica*, Fig. 1), an Arctic-breeding long-distance migratory shorebird, has provided remarkable examples of such phenotypic flexibility (Piersma 2002). For example, islandic knots winter on west European mudflats (Piersma & Davidson 1992; Quaintance et al. 2011) where they feed on bivalves containing large amounts of indigestible shell matter (van Gils et al. 2005; Quaintance et al. 2010) and where they are thought to face peak thermoregulatory demands owing to cold and windy conditions (Wiersma & Piersma 1994; Piersma 2002). Knots respond to these constraints by increasing their body mass (Vézina et al. 2006; Vézina, Dekinga & Piersma 2006).

arriving male red knots, while female ovaries, although still immature, grew by 69% over the first 11 days post-arrival. Maintaining large, functioning reproductive organs in females involves energy costs |

size again to study intra-individual change in organ size (average time between measurements = 9 days, range 2...19 days). This also allowed for calculating within-year repeatability in body mass and organ size (according to Lessells & Boag 1987). Six red knots were also recaptured and measured in both years. To prevent problems associated with pseudoreplication, all analyses using data at the inter-individual level are based on the "rst intrayear measurement per bird.

Wintering knots

All wintering birds were captured during a bird-banding expedition to the island of Griend (53 15N, 5 15E) in the Dutch Wadden Sea in 2008. 2(v00(d77-24)3(su)19.4(218942b)2(T)0(h)2F7 1 Ti)0(n(at)-198.50(h)2)-249.1O(d)f0(d771(e)0(a)19.4g)-200

1991; van der Meer & Piersma 1994). In BMR analyses, we replaced covariate •PC1• by •body mass• to account for the effect of mass on BMR. As birds feed throughout the day, their mass may increase over time. Therefore, we also included •capture time• in the analysis on body mass variations to account for this effect.

We used *ANCOVA* to compare BMR of red knots measured at Alert and in the Wadden Sea. This analysis tested for an effect of •site• (Alert $n = 28$, or Wadden Sea, $n = 17$) on BMR while controlling for •body mass• as a covariate. The interaction •site*body mass• was also included to test whether slopes of the relationships differed among sites. To control for the effect of time on BMR in the Arctic (see Results), we restrained our Alert data set to birds measured •early• (“rst 5 days after arrival, $n = 14$) and •late• (15th day after arrival or later, $n = 14$). We did not include the variable •year• in the model as birds from the Wadden Sea were measured only in 2008. Differences between least square means were tested with *post hoc* Tukey test.

To investigate whether loss of pectoral muscle was related to gizzard development within individuals while in the Arctic, we computed •change in gizzard• width and height from one measure to the next in birds for which we had repeated measurements, and tested for a relationship with •change in pectoral muscle• thickness using regression analyses. We used the same approach to examine whether variations in pectoral muscle thickness were related to changing ambient temperatures.

Dissection data by Morrison, Davidson & Piersma (2005) and our

$F_{1,91} = 3.8$, $P = 0.054$, controlling for body size; $F_{1,91} = 3.3$, $P = 0.07$) and muscle size decreased with date of capture ($F_{1,91} = 7.6$, $P < 0.01$). Excluding marginally significant covariates confirmed the reduction of muscle size over time (Fig. 3b). Repeated measures analysis of birds captured and measured several times within a year confirmed the decrease in muscle thickness within individuals ($F_{2,22,1} = 3.9$, $P < 0.05$; -6.3% between first and third measurement over mean 84 days, Fig. 3c). Muscle thickness was not repeatable when controlling for body size ($r = 0.18$, $P = 0.1$).

CHANGE IN GIZZARD SIZE

Gizzard size was only influenced by date of capture (Fig. 4). Both gizzard width and height followed a growth curve significantly explained by a Gompertz model (width: $r^2 = 0.31$, $n = 98$, $P < 0.0001$; height: $r^2 = 0.21$, $n = 98$, $P < 0.0001$, Fig. 4a,b). Growth was not particularly fast, as 99% of the asymptotic height and width were reached at 166 and 197 days, respectively. Within individuals, gizzard width increased over time ($F_{2,33,1} = 4.3$, $P < 0.05$, Fig. 4c) and gizzard height followed the same development pattern as observed at the population level although the time effect did not reach significance (Fig. 4d, $F_{2,33,4} = 2.3$, $P = 0.1$). Repeatability of gizzard size was not significant (height $r = -0.23$, $P = 0.9$; width $r = -0.20$, $P = 0.8$).

There was no relationship between the change in gizzard size (width or height) and the change in pectoral muscle thickness within individuals ($P = 0.4$). However, the change in pectoral muscle thickness was negatively correlated with the change in mean ambient temperature. ($r^2 = 0.26$, $n = 20$, $P < 0.05$). In other words, the more temperature had risen from one measure to the next, the more muscle thickness was lost by the birds.

POSTMIGRATORY CHANGES IN BMR

Controlling for body mass ($F_{1,40} = 26.3$, $P < 0.0001$), BMR was 149% higher in 2007 (116 ± 0.04 W) than in 2008 (1.01 ± 0.05 W; year $F_{1,40} = 5.9$, $P < 0.05$) and increased linearly over time (date $F_{1,40} = 23.2$, $P < 0.0001$). However, the time effect differed between years (date year: $F_{1,40} = 7.8$, $P < 0.01$), and the mass effect differed between sexes (sex mass: $F_{1,40} = 4.5$, $P < 0.05$). We therefore reran the analysis for each sex. There was no year effect for male BMR, but their BMR still increased over time (Fig. 5a, date $F_{1,22} = 5.4$, $P < 0.05$, controlling for body mass $F_{1,22}$

Size-independent body mass was repeatable ($r = 0.32$, $F_{17,18} = 4.9$, $P < 0.001$).

In contrast with body mass, birds had thicker muscles in 2007 (136 ± 0.1 mm) than in 2008 (133 ± 0.1 mm);

size (separately for width or height) to the models. BMR was not related to organ size in females ($P = 0.1$). In males, while muscle thickness and gizzard height were not significantly related to BMR ($P = 0.1$ and 0.7 respectively), gizzard

because this approach also considers convective and radiative heat transfer. However, their data (see table 1 in Wiersma & Piersma 1994) showed that convective heat loss because of wind speed is similar or higher on the Arctic tundra than on the Wadden Sea mudflats. Furthermore, the summer data used for the Canadian Arctic (including Alert) in their study were obtained during June-July and excluded arrival time. Wiersma & Piersma's (1994) estimates were also calculated for birds spending up to 75% of their time sheltered from the wind in dense or open vegetation (birds assumed to be on their nest, which is not the case in arriving individuals) and thus were calculated using reduced convective heat loss. Clearly, ambient temperatures at arrival can be much colder than at peak of winter in the Wadden Sea (Fig. 2), and this may last up to 24 days (in 2007) after first arrival. Given that summer plumage in knots and other shorebirds offers less thermal insulation than winter plumage (Piersma, Cade & Daan 1995; Williamson, Williams & Nol 2006; Vézina

Thermoregulatory costs may be at their yearly peak on arrival in the Arctic, but knots seem well adapted for the challenge. Indeed, they arrive at Alert with pectoral muscles 13-30% larger on average (81...4 g lean dry mass $n = 3$, see

& McWilliams 2010). Therefore, comparable gizzard growth in both studies suggests that knots consistently rebuild this organ at maximal rate and that "nal gizzard size is context speci"c (Bauchinger & McWilliams 2010). While knots need a large gizzard for bivalve crushing and shell processing during winter (van Gils et al. 2003, 2005), in the Arctic they feed on insects (spiders and tipulids) (Morrison 1992; Morrison & Hobson 2004; Tulp & Schekkerman 2008). In fact, asymptotic fresh gizzard mass for birds at Alert is estimated at 5 g (F. Vézina, T. Piersma unpublished calibration data from dissections). This is comparable to gizzards of knots feeding on

Piersma 2002; Lindström & Klaassen 2003; Williamson, Williams & Nol 2006), lowest in tropical wintering ranges (Piersma, Drent & Wiersma 1991, Piersma et al. 1996; Lindström 1997, Kersten et al. 1998; Kvist & Lindström 2001; Piersma 2002) and may be intermediate during stop-over in temperate areas (Piersma, Drent & Wiersma 1991; Lindström 1997; Kvist & Lindström 2001). Here we found no differences between BMR of knots wintering in the cold temperate Wadden Sea and those that had just arrived on the breeding grounds. We are not aware of other empirical BMR measurements for red knots in the Arctic. Therefore, as there was no plateau in BMR, our average values may underestimate summer BMR if it kept rising after the end of measurements. However, if reproductive function is adding energy costs to body remodelling, BMR likely declined following clutch completion as a result of reproductive organ regression (see the studies by Vézina & Williams 2003; Vézina & Salvante 2010). Thermoregulatory demand has been suggested as a cause for the high BMR of shorebirds in the Arctic (Lindström & Klaassen 2003), but our recent findings suggest that a high BMR is not a prerequisite for cold acclimation in red knots (Vézina, Dekinga & Piersma 2011). Rather, because birds faced completely different sets of constraints in these contrasted life-history stages, and because BMR is an integrated metabolic measure reflecting the sum of all physiological components, we believe that physiological adjustments to specific life-history stages is the main cause for seasonal BMR variations in shorebirds. More data are needed to explain the mechanisms underlying changes in BMR during the critical period that is the

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