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Resting metabolic rate in migratory and non-migratory geese following range expansion; go south, go low

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Summary

While many species suffer from human activities, some like geese benefit and may show range expansions. In some cases geese (partially) gave up migration and started breeding at wintering and stopover grounds. Range expansion may be facilitated and accompanied by physiological changes, especially when associated with changes in migratory behaviour. Interspecific comparisons found that migratory tendency is associated with a higher basal or resting metabolic rate (RMR). We compared RMR of individuals belonging to a migratory and a sedentary colony of barnacle geese *Branta leucopsis*. The migratory colony is situated in the traditional arctic breeding grounds (Russia), whereas the sedentary colony has recently been established in the now shared wintering area (the Netherlands). We measured RMR by oxygen consumption (\dot{V}_{O_2}) during two ontogenetic phases (juvenile growth and adult wing moult). We also investigated juvenile growth rates and adult body mass dynamics.

Mass-independent \dot{V}_{O_2} was 13.6% lower in goslings from the sedentary colony than in goslings from the migratory colony. Similarly, in adult geese, mass-independent \dot{V}_{O_2} was 15.5% lower in sedentary than in migratory conspecifics. Goslings in the Netherlands grew 36.2% slower than goslings in Russia, while we found no differences in body dimensions in adults. Adult geese from both colonies commenced wing moult with similar body stores, but whereas Russian barnacle geese maintained this level throughout moult, body stores in geese from the Netherlands fell, being 8.5% lower half-way through the moult.

We propose that the colony differences in resting metabolic rate, growth rate and body mass dynamics during moult can be explained by environmental and behavioural differences. The less stringent time constraints combined with poorer foraging opportunities allow for a smaller ‘metabolic machinery’ in non-migratory geese. Our analysis suggests that range expansion may be associated with changes in physiology, especially when paired with changes in migratory tendency.

Keywords: arctic, body mass, growth, latitude, life-history, metabolic rate, migration, moult, plasticity

Introduction

Humans are impacting the globe to such an extent that, according to some, a new geological era has started (Crutzen and Stoermer 2000). Many species with sensitive requirements suffer and show range contractions, whereas some broadly tolerant species benefit and show range expansions (McKinney and Lockwood 1999). For instance, while many bird species have declined with the intensification of agriculture (Donald et al. 2002), some herbivores like geese profit from the abundance of highly nutritious agricultural crops (Fox and Abraham 2017). Range expansions cause species to experience new abiotic and biotic environmental conditions, inducing phenotypic changes in behaviour and physiology that may arise through acclimatization, adaptation, or a combination of both (Burton et al. 2010, Colautti et al. 2010, Hendry et al. 2008, Weiss-Lehman et al. 2017).

Large-scale latitudinal range expansions will bring about differences in seasonality such as changes in propensity to be migratory or sedentary. Animals can exploit seasonally changing environments by migrating between reproductive and survival habitats. Under these circumstances, migration enhances reproduction by exploitation of food peaks and reduces mortality through avoidance of food scarcity (Holt and Fryxell 2011, Lack 1968a) and pathogens (O'Connor et al. 2018, Westerdahl et al. 2014). Although beneficial, such migratory behaviour requires certain abilities (e.g., physiological, navigational) and also bears substantial costs, such as the energetic and survival costs of the migratory journey as well as its preparatory phase (Alerstam et al. 2003, Hein et al. 2012, Hulbert et al. 2007, Klaassen et al. 2014). Arctic-breeding migratory birds, for example, can benefit from the combination of long daylight hours and superior food conditions. But the short-lasting nature of the seasonal resource pulse may put them under time pressure in order to accomplish activities like reproduction, growth, moult and deposition of body stores needed for migration. This may result in increased food intake to meet the demands for faster growth and (re)fueling. To process more food animals primarily enlarge their gastrointestinal tract and accessory organs like the liver, and studies on birds including waterfowl have shown that individuals adjust the size of such organs in relation to actual needs and feeding conditions (Battley and Piersma 2005, Karasov 1996, Van Gils et al. 2008). Moreover, hypertrophy of exercise-related organs like skeletal muscles, kidneys and heart has been observed in birds preparing for long-distance migration (Piersma et al. 1999). These food-processing and exercise-related organs have disproportionately high metabolic rates, so that maintaining them at larger size results in higher mass-specific maintenance metabolism at whole-body level (Daan et al. 1990, Konarzewski and Diamond 1995). Comparative studies of species or subspecies indeed find that migratory tendency is associated

with higher basal or resting metabolic rate as compared with a sedentary strategy (Jetz et al. 2008, Swanson 2010, Wikelski et al. 2003). Because species and subspecies that occupy different ranges with no or limited gene flow are bound to differ in other respects besides migratory tendency, intra-specific comparisons could provide a more rigorous test (Garland and Adolph 1994) of whether migratory individuals have higher resting metabolic rates, but such comparisons are largely lacking.

Goose populations in Europe and North-America have increased in response to decreased hunting pressure in combination with food subsidies provided by changes in agriculture in their wintering and stopover areas (Abraham et al. 2005, Ebbinge 1985, Fox et al. 2005). In many cases, these increases in population numbers have been accompanied by range expansions. Probably as a response to changing costs and benefits of migration, some populations of species like barnacle geese *Branta leucopsis* even partially or fully stopped migrating, and started breeding at stopover sites or even at wintering sites (Van der Jeugd et al. 2009). Aside from distance to wintering grounds, the original and new breeding environments of barnacle geese are expected to differ in other biotic and abiotic characteristics, notably temperature, photoperiod and foraging conditions. Together they yield different pressures that are expected to result in seasonal or permanent adjustments of the physiological phenotype (Wikelski and Ricklefs 2001).

We set out to compare individuals belonging to either migratory or sedentary colonies of barnacle geese. The migratory individuals spend the summer at the traditional breeding grounds in the Russian Arctic, whereas the sedentary individuals summer at the newly established breeding grounds within the shared wintering area in Western Europe. We measured resting metabolic rate during two ontogenetic phases, namely during the growth of juvenile birds and during the wing moult of adult birds. Because of the direct relationship between metabolism and biosynthesis, we also investigated growth rates of juveniles and body mass dynamics of adults, both life-history traits with clear fitness consequences. We hypothesized that the non-migratory birds that stay for breeding in the south have a lower resting metabolic rate and slower growth rate than their Arctic migratory conspecifics.

Materials and methods

Study populations and handling of geese

Barnacle geese from the ancestral migratory population were studied in a colony at Kolokolkova Bay near the abandoned settlement of Tobseda (68°35'N, 52°20'E), situated along the Barents Sea in arctic Russia. Barnacle geese from the newly established, sedentary population were studied in a colony in the Delta

area in the southwest of the Netherlands (51°40'N, 4°14'E), within the temperate wintering range shared by the two populations. Both populations have been subject to long-term studies on various life-history aspects, and more details on study sites and populations can be found in Eichhorn et al. (2009) and Van der Jeugd et al. (2009) and references therein.

Juvenile (i.e., goslings) and wing-moulting adult geese were captured during their flightless phase, both in the Netherlands (between 31 May and 16 July 2012) and in Russia (between 27 July and 17 August 2014). Wing moult in geese comprises the simultaneous replacement of all primary and secondary flight feathers. Geese were driven into a catching pen. Immediately after capture, geese were transferred to small compartmented tents; goslings were housed separately from adults to avoid trampling. Ringing (with uniquely marked leg rings) and collection of morphometric measurements started approximately 30 min after capture. All geese except five goslings were sexed by cloacal examination. Adult geese selected for respirometry did not have unmoulted juvenile feathers, and hence most likely comprise mature birds in their third calendar year or older (Cramp and Simmons 1977). Birds were weighed with precision spring-scales (PESOLA Präzisionswaagen AG, Switzerland) at ± 5 g and ± 10 g accuracy for weights up to and above 600 g, respectively, and measured with callipers (± 0.1 mm) for tarsus length, and with a ruler (± 1 mm) for head length, wing length (maximum chord) and the length of the 9th primary feather (P9), counted inward out. Geese and other waterfowl shed and re-grow their flight feathers simultaneously; thus, measuring a single primary allows monitoring the progress of moult. Among the (re-)captured geese were also goslings that had been marked at hatch in that season with uniquely coded web-tags. Morphological measurements on goslings of known age were used to compare juvenile growth rate between colonies. Size of head and tarsus as measured in moulting adult geese during 2012-2015 seasons were used as indicators of final body size targeted by growing goslings.

Upon ringing, a subsample of geese (one to nine individuals per capture event/day) was transferred to an enclosure placed on grassland suitable for foraging, and provided with water for drinking. Geese were removed from the enclosure and kept in ventilated boxes without food and water for 2 h (juveniles) to 3 h (adults) before start of respirometry. This time was sufficient for allowing them to empty their guts, which were anyway not filled much due to restricted food intake while in captivity. All birds were released after measurements.

Respirometry

We used an open-circuit respirometry system ('Turbofox'; Sable Systems International, Las Vegas, NV, USA) installed within walking distance from the breeding colonies to measure the oxygen consumption rates (\dot{V}_{O_2}) and carbon dioxide production rate (\dot{V}_{CO_2}) of geese resting in a chamber (an opaque plastic box). Depending on goose size, chambers with a volume of 11 L (29 x 22 x 18 cm, Length x Width x Height), 18 L (31 x 24 x 24 cm) or 52 L (43 x 33 x 37 cm) were used during a trial, ensuring that geese could sit comfortably. Gas-impermeable tubing was used to make connections between the various components of the respirometry system. The O_2 -analyser was calibrated before each trial using ambient air scrubbed of water vapour and CO_2 (set to 20.95% O_2 ; the zero point was fixed and not subjected to drift). The CO_2 -analyser was calibrated daily using calibration gas (0.49% CO_2). The humidity meter was calibrated at least weekly, but usually every other day, according to manufacturer recommendations. We used wet and dried (using magnesium perchlorate) ambient air to set the span and zero water vapour pressure reading (kPa), respectively. During trials with larger geese (>0.6 kg) the primary flow control unit of the Turbofox pulled air through the chamber at a rate of 5-6 L min^{-1} (automatically corrected to STP: 273 K and 101.3 kPa). A subsample (200 ml min^{-1}) was passed through a humidity meter (RH-300), a CO_2 -analyser, and a fuel-cell oxygen-analyser (i.e., the analyser unit of the Turbofox). For trials with smaller geese, the subsample pump of the system was used as the main flow generator, pulling air at a rate of up to 1.5 L min^{-1} through the chamber, which was then passed through the analyser unit. Flowrates were chosen based on preliminary trials to ensure that O_2 concentration within the chamber remained at ~20.5% and CO_2 concentration did not exceed 0.5%. The O_2 and CO_2 concentrations within the chamber, main flow rate through the chamber, humidity of the gas sample, and barometric pressure were recorded every second onto a laptop computer using ExpeData software (1.4.15, Sable Systems). Lag time between air leaving the respiration chamber and detection by the gas analysers was found to be 25 s for the oxygen analyser and 20 s for the CO_2 analyser. These lag times were taken into account when calculating oxygen consumption rates and CO_2 production rates. The time constants of the respiration chambers were calculated to be 7.3 min for trials with small goslings (11 l chamber volume, 1.5 l min^{-1} flowrate) and 9.5 min for trials with large goslings and adult geese (52 l chamber volume, 5.5 l min^{-1} flowrate). The respirometry system was tested frequently using the N_2 dilution technique (Fedak et al. 1981). The set-up was identical in both locations with the respirometry chamber kept in a well-ventilated, separate room, to reduce disturbance from the experimenter.

After initial disturbance, birds typically calmed down quickly inside the chamber, and the recorded O_2 and CO_2 traces stabilised within ~30 min. Respirometry trials lasted for two to three hours and were conducted throughout the 24-h day. A residual analysis indicated no effect of daytime on measured \dot{V}_{O_2}

(Supporting Information: Fig. S1). Body mass was determined by weighing the birds at the end of each respirometry trial. Adult geese were generally in a post-absorptive state, whereas some of the goslings may have been still in an absorptive state, as gauged from the respiratory exchange ratio ($RER = \dot{V}_{CO_2} / \dot{V}_{O_2}$; mean \pm sd of 0.75 ± 0.04 in adults and 0.81 ± 0.06 in juveniles). Due to their carbohydrate-rich diet a relatively high RER might be expected in geese during foraging, which may take longer to decrease and stabilize after digestion. Moreover, due to gut fermentation, a truly post-absorptive (but not yet fasting) state might be generally difficult to achieve in herbivorous geese. Chamber temperatures during respirometry ranged 10-18 °C (mean=14 °C) for adult and 12-22 °C (mean=15 °C) for juvenile geese in Russia, and 15-21 °C (mean=18 °C) for adult and 15-27 °C (mean=20 °C) for juvenile geese in the Netherlands. Although thermal relationships have not been determined specifically for the barnacle goose, we are confident that our experimental temperatures were within their thermal neutral zone. Combining t_{lc} measurements from 33 seabird species, Ellis and Gabrielsen (2001) established the allometric equation: $t_{lc} = 43.15 - 6.58 \log \text{mass} - 0.26 \text{ latitude}$, where mass is in grams and latitude in degrees. Using this formula and individually measured body mass we estimate $t_{lc} = 5.4 \pm 2.2$ °C (mean \pm sd) in the adult barnacle geese and $t_{lc} = 9.7 \pm 3.6$ °C in the juvenile geese. This inferred lower critical temperature for adults fits the one measured in the closely related black brant (*Branta bernicla orientalis*, mass=1.130 kg, $t_{lc} = 6$ °C) during the Alaskan summer (Irving et al. 1955). Moreover, when chamber temperature was included in the analysis it did not improve the model fitted for \dot{V}_{O_2} . Accordingly, a residual analysis suggests that the experienced temperatures had no effect on the measured \dot{V}_{O_2} (Supporting Information: Fig. S2). The measurements in Russia took place when arctic summer temperatures peaked and in fact often overlapped with ambient temperatures in the Netherlands during juvenile growth (Supporting Information: Fig. S3).

Data analysis

Respirometry data

Respirometry data were analysed using ExpeData, correcting for gas-analyser drift and lag time of the respirometry system. Also, main flow rate was corrected to STP dry (STPD) using equation 8.6 in Lighton (2008). Similarly, we did not scrub water vapour before gas analysis but corrected for this dilution effect during data analysis using equation 15.3 in Lighton (2008). \dot{V}_{O_2} and \dot{V}_{CO_2} were calculated using equations 11.7 and 11.8 in Lighton (2008), respectively. From each respirometry trial, a 15-min data segment encompassing the lowest stable \dot{V}_{O_2} values was selected to represent the resting metabolic

rate (RMR) of the bird for that trial. Oxygen consumption rate values are presented on a whole animal basis (ml min^{-1}).

Statistical analysis

Resting \dot{V}_{O_2} was compared between the migratory and sedentary colony while accounting for an allometric relationship of \dot{V}_{O_2} with body mass (M): $\dot{V}_{\text{O}_2} = a \text{ Col } M^b e^\varepsilon$, where a and b represent the allometric constant and scaling exponent, respectively, Col is a dimensionless factor representing colony, ε represents the error term, and e is the base of the natural logarithm. Log-log transformation linearizes the relationship between \dot{V}_{O_2} and M , so that our basic model becomes: $\ln(\dot{V}_{\text{O}_2}) = \ln(a) + b\ln(M) + \ln(\text{Col}) + \varepsilon$.

In contrast to goslings, which usually continued foraging while held in captivity, adult geese showed a much more wary behaviour. They likely compromised foraging activity, and some may have fasted to a variable extent during captivity. Time since capture (i.e., time elapsed between capture and \dot{V}_{O_2} measurement, $t_{\text{catch}} - \dot{V}_{\text{O}_2}$, centred to its mean) was, therefore, included in our models as controlling covariate. Additionally, capture date was included as random effect, in a more conservative approach that accounts for potential correlation among individuals that were caught and processed together. Sex, respirometry chamber temperature during \dot{V}_{O_2} measurements and, for adult geese, progress of wing moult (expressed by the length of the 9th primary, P_9) were added as further explanatory variables. For further details see Supporting Information: Appendix 1.

Juvenile growth and adult body mass dynamics were analysed from cross-sectional data from the same colonies and seasons, using simple linear ANCOVA models. For juvenile geese, length of wing, head, tarsus and body mass were combined in a principal component analysis (PCA) to obtain the first principal component (PC1) that was then related to gosling age and colony. For adult geese, a single size-variable PC1 was obtained from a PCA of tarsus and head length, which was included as covariate in the model relating body mass to moult stage (length of P_9) and colony. All statistical analyses were performed in IBM SPSS Statistics 24.0 (Armonk, NY: IBM Corp.).

Results

Metabolic rates

Metabolic rate was studied in a total of 62 juvenile and 39 adult barnacle geese ranging in mass 0.122-1.555 kg and 1.270-2.250 kg, respectively (Fig. 1), and was modelled separately for juvenile and adult

geese. Sample sizes and summary statistics of variables used to model oxygen consumption rates are given in Supporting Information: Tables S1-S2.

In juvenile geese, the final model of resting metabolic rate (\dot{V}_{O_2}) retained the significant fixed effects of body mass and colony (model I in Table 1, Fig. 2). \dot{V}_{O_2} scaled with body mass at an exponent of 0.68 and was 13.6% lower in goslings in the sedentary colony in the Netherlands than in goslings in the migratory colony in arctic Russia (or, vice versa, \dot{V}_{O_2} in Russian goslings was 15.5% higher than in Netherlands goslings). \dot{V}_{O_2} mean estimates for goslings at 1 kg body mass were 18.9 ml min⁻¹ in Russia (RU) and 16.3 ml min⁻¹ in the Netherlands (NL).

In adult geese, the final resting metabolic rate (\dot{V}_{O_2}) model retained the significant fixed effects of body mass, colony, a curvilinear effect of moult stage, and time since capture (model II in Table 1, Fig. 3). \dot{V}_{O_2} scaled with body mass at an exponent of 0.71 and was 15.5% lower in sedentary geese in the Netherlands than in migratory conspecifics in Russia (or, vice versa, \dot{V}_{O_2} in Russian geese was 18.2% higher than in Netherlands geese). \dot{V}_{O_2} estimates at mean adult body mass were 24.7 ml min⁻¹ (RU) and 20.9 ml min⁻¹ (NL) at the start of wing moult (i.e., P9=0). It increased by 10.0% to peak with 27.2 ml min⁻¹ (RU) and 23.0 ml min⁻¹ (NL) at P9=95 mm, 13 days into moult (Fig. 3). Extrapolated to 1 kg body mass, adult mean \dot{V}_{O_2} is estimated at 16.6 ml min⁻¹ (RU) and 14.0 ml min⁻¹ (NL) at the start of moult, and expected to peak with 18.2 ml min⁻¹ (RU) and 15.4 ml min⁻¹ (NL) during moult.

Juvenile growth and adult body mass dynamics

There was a clear difference in growth trajectories of goslings raised in the sedentary and migratory colony (interaction colony × age, $P < 0.001$; Fig. 4, Supporting Information: Table S3). Over the studied body size range, which was comparable across colonies, goslings in the Netherlands grew 36.2% slower than goslings in arctic Russia. It took Netherlands' goslings 63 days to attain a body size that their Russian conspecifics attained in only 40 days. Goslings from both colonies, however, apparently reach a similar final body size at adult age, as is indicated by head and tarsus length of adult barnacle geese (n=315 in RU, n=301 in NL): estimated marginal means (±SE) accounting for sex-differences were 83.7±0.2 mm (RU) and 84.1±0.2 mm (NL) for head (mean difference n.s., $P = 0.10$), and 82.9±0.2 mm (RU) and 82.6±0.2 mm (NL) for tarsus length (mean difference n.s., $P = 0.18$).

Adult geese from both colonies commenced wing moult with similar body stores (i.e., body mass corrected for size) which were maintained by migratory geese (RU) but decreased in sedentary geese (NL) during the moult (interaction P9 × colony, $P = 0.005$; Fig. 5, Supporting Information: Table S4).

Estimated marginal mean body mass half-way through the moult (at P9=132 mm) amounts to 1.801±0.016 (±SE) kg in Russian barnacle geese and to 1.648±0.023 kg in their conspecifics from the Netherlands (i.e., a mass difference of 8.5%).

Discussion

Our analysis of resting metabolic rates revealed that, when corrected for body mass, barnacle geese from the newly established temperate-breeding, sedentary colony in the Netherlands exhibit lower metabolic rates than their migratory conspecifics from an arctic-breeding (Russian) colony. This was the case during post-natal growth of juveniles as well as during post-breeding wing moult of adults. The magnitude of the differences between the sedentary and migratory individuals were similar for both age groups. Moreover, juvenile growth was slower, and adult body mass loss during moult was larger in individuals from the sedentary colony in the Netherlands.

Two main, non-mutually exclusive factors may explain these patterns, namely differences in environment (often characterized by latitude) and in life-style (migratory or not). Comparing bird species from different latitudes, metabolic rates of adults were found to decrease towards lower latitudes, both in terms of maintenance metabolism (i.e., basal metabolic rate, BMR) (Jetz et al. 2008, Londoño et al. 2015, McNab 2009, Wiersma et al. 2007) and in total daily energy expenditure (i.e., field metabolic rate, FMR) (Anderson and Jetz 2005, Piersma et al. 2003). Similar latitudinal metabolic differences across species have been reported for hatchlings (Klaassen and Drent 1991) and during post-natal growth (Ton and Martin 2016). Comparing subspecies from different latitudes, a lower BMR (Wikelski et al. 2003) or FMR (Tieleman et al. 2006) has been reported in tropical-sedentary versus temperate-migratory songbirds. Comparing migratory life-styles, Jetz *et al.* (2008) found a lower BMR in non-migrant than in migrant bird species, but they found an even stronger correlation of BMR with annual temperature. They suggested that the higher BMR of migratory species is, at least in part, the result of acclimatization to colder breeding areas at higher latitudes. This hypothesis of an overriding temperature effect was put to the test by comparing tropical bird species living at different altitudes (as opposed to latitudes), but no association between BMR and altitude was found (Londoño et al. 2015). Moreover, in the tropics migratory bird species have a higher BMR during overwintering than tropical sedentary bird species that share the same habitat (Bushuev et al. 2018). These findings indicate that a low BMR in tropical sedentary birds is not merely the result of acclimatization to warm stable temperatures, but rather associated with the sedentary lifestyle.

Correspondingly, we believe that the differences in RMR between our study colonies were not or only to a minor extent due to acclimatization to different ambient temperatures. We measured RMR during adult wing moult and growth of young, which both take place during the warmest period of the year when ambient temperature differences between the arctic and temperate colonies are minor (Supporting Information: Fig. S3). At other times of the breeding season thermoregulatory costs may be higher in the arctic site than in the temperate site. For instance, adult geese may pay such costs temporarily early in the breeding season, and goslings during the early post-natal phase shortly after hatching. For this reason, we selected only larger/older goslings (> 2 weeks) well after they had reached thermal independence from (brooding) parents (own obs.). Outside breeding, geese from both colonies share common wintering grounds for half of the year (November to May), where they experience similar ambient temperatures including the lowest in the annual cycle. Thus, overall, rather than climate-driven thermoregulatory effects, a combination of other environmental and behavioural differences seem more plausible explanations for the lower RMR and growth rates in sedentary versus migratory geese. The less stringent time constraints for growth and lack of migratory disposition combined with poorer foraging opportunities allow for a smaller 'metabolic machinery' and hence reduction in maintenance costs in non-migratory geese (Swanson et al. 2017, Williams and Tieleman 2000).

Juvenile growth and energetics

Post-natal growth rate can influence offspring survival during pre- and post-fledging periods and, moreover, if growth rate affects final body size, it can also affect fecundity later in life (Gebhardt-Henrich and Richner 1998, Sedinger et al. 1995). In the present study, we did not link growth rate to final body size at the individual level, nor did we account for potential cohort effects. Nevertheless, our data suggest that goslings in the sedentary colony in the Netherlands grow slower but finally reach a similar adult body size as their migratory conspecifics in the Russian Arctic colony. Hence, the growth phase appears to be shorter in the Russian Arctic than in the Netherlands. This may be the effect of differences in predation pressure, season length, day length, foraging conditions and/or parasite pressure.

A flightless state and small body size makes goslings vulnerable to predation. Thus, time-dependent mortality could be an important selection pressure for fast growth towards reducing the pre-fledging period (Lack 1968b). We did frequently observe goslings being killed in the Arctic study site by various predators (glaucous gull *Larus hyperboreus*, Heuglin's gull *L. heuglini*, arctic skua *Stercorarius parasiticus*, white-tailed eagle *Haliaeetus albicilla*, arctic fox *Vulpes lagopus*). In many temperate goose colonies, including our study colony in the Netherlands, these predators or their local equivalents (e.g.,

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red fox *V. vulpes*) are either not present or have been largely reduced in number by human intervention. Depression of natural predators (besides reduced persecution by man) has likely supported the colonization of temperate breeding areas, and may thus also have reduced the selection pressure on fast juvenile growth.

With regard to season length, Van der Jeugd et al. (2009) analysed timing of breeding and post-fledging survival of barnacle geese including the same study colonies as in the present study. Not only is the time window for successful breeding much wider for geese in the temperate breeding areas, their fledglings also enjoy higher survival that, importantly, shows no decline with hatch date. In contrast, survival of fledglings from the arctic-migratory birds drops steeply with date of hatch, likely because for late-born chicks, the season becomes too short to prepare for autumn migration. This suggests that both breeding adults (who determine hatch date of their offspring) as well as their developing young are under less time pressure in the sedentary colony (Van der Jeugd et al. 2009).

However, lower growth rate in the sedentary birds of the Netherlands may also be constrained due to poorer foraging conditions. Small avian herbivores such as geese depend on high-quality food (graminoids with low fibre and high protein content), and food abundance and food quality are known to be important determinants of gosling growth and survival as well as final body size (Cooch et al. 1991, Larsson et al. 1998, Richman et al. 2015). During the southwest expansion of the breeding area into temperate regions, barnacle geese preferred, and probably relied upon, managed grassland. Grazing or mowing regimes and direct or indirect input of fertilizers at these sites had created foraging and brood-rearing sites of improved food quality that may rival the food quality available at the arctic foraging grounds (Van der Jeugd et al. 2009). However, the arctic and temperate sites differ in potential daily foraging time. We observed that broods in the Dutch colony interrupted their daytime foraging activity for a nocturnal roost of approximately 6 hours on predator-free islands without foraging opportunities, whereas broods in the Russian colony continued foraging throughout 24 hours of daylight. Accounting for differences in daylight hours experienced during growth largely reduces colony differences in growth rate (Supporting Information: Fig. S4 and Table S5).

Lower parasite pressure in arctic than in temperate breeding grounds (Piersma 1997) could be another factor that may explain part of the observed variation in growth rate. Parasites divert nutrients and energy away from their hosts or may incur costs through immune system activation (Hanssen et al. 2004, Hasselquist and Nilsson 2012, Schmid-Hempel 2011).

The lower growth rate of the goslings from the sedentary (NL) colony was associated with a lower RMR. The RMR of growing organisms reflects the metabolic turnover for biosynthesis and for

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maintenance. Part of the lower RMR in the goslings from the Netherlands is likely a direct consequence of slower biosynthesis (Fig. 4). But we also suspect that they have a slower maintenance metabolism, because food-processing organs can be maintained at smaller size or used less intensively (McKechnie 2008, Swanson et al. 2017, Van Leeuwen et al. 2012, Williams and Tieleman 2000). The direction of control, i.e., whether metabolic rate drives growth or vice versa, is not easy or perhaps not even meaningful to tease apart as these processes are clearly intertwined (Burton et al. 2011, Glazier 2015).

Adult wing moult

We found a curvilinear pattern of RMR over the course of wing moult, with a peak at approximately 2 weeks after old flight feathers were shed, which may reflect variation in instantaneous overall moult intensity caused by partially overlapping growth periods of different feather tracts (e.g. flight feathers and wing coverts; Hohman et al. 1992). Our findings are consistent with previous findings in captive-bred barnacle geese as well as with studies of other species showing RMR to reflect moult intensity (Lindström et al. 1993, Portugal et al. 2007). Aside from varying moult intensity, a changing body composition due to the dynamic breakdown and rebuilding of breast and leg muscles may also contribute to varying RMR during wing moult in geese (Portugal et al. 2009).

In contrast to colony differences of juvenile growth rates observed by us, van der Jeugd et al. (2009) reported similar growth rates of the 9th primary suggesting similar rates of feather synthesis in moulting adult barnacle geese from arctic and temperate populations. However, the different body mass trends observed throughout moult in the present study (Fig. 5) indicate different turnover rates of other tissues. Although the relatively low sample sizes underlying the estimates of adult primary feather growth rates in van der Jeugd et al. (2009) may call for a re-examination of potential population differences, their conclusions are not necessarily in conflict with present results, because body mass changes and the progress of moult are regulated by different hormones (Jenni-Eiermann et al. 2002). Our present findings are in line with and extend to previous findings about the regulation of body stores during incubation (preceding wing moult): sedentary, temperate (NL) barnacle geese spent more time on the nest thereby accepting a higher body mass loss, whereas migratory, arctic (RU) breeders took more foraging recesses and conserved their lean (protein) mass (Eichhorn et al. 2010). Migratory barnacle geese increase their lean mass during the pre-migratory period (Eichhorn et al. 2012) presumably to strengthen their flight capabilities. Overall, we suspect that differences in body composition and size of organs involved in exercise and digestion may have contributed to the observed colony differences in whole organism metabolic rate.

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Due to inferior foraging conditions (especially less foraging time, see above) temperate geese are more limited in the potential rate of tissue accretion during moult. However, due to a sedentary lifestyle that removes the pressure of depositing body stores for autumn migration, temperate geese may also simply not aim to maximize food intake. This additional explanation is supported by the finding that captive barnacle geese with *ad libitum* access to food showed even greater body mass loss during wing moult than the wild geese studied here (Portugal et al. 2007). In captivity, the rate of mass loss was larger in individuals that initiated moult with larger body stores and spent more time resting and less time foraging (Portugal et al. 2011). Portugal et al. (2007) concluded that the reduction of food intake and concomitant mass loss during the flightless period is a behavioural response of ‘innate nature’, with the adaptive value of reducing predation risk in the wild. Our additional findings on geese in the wild, however, suggest that foraging behaviour and mass loss during moult are plastic and depend on the environmental context such as future needs.

Finally, as evoked for growing juveniles, differences in (human-induced) predation risk and parasitemia in the temperate and arctic colony are further factors worth exploring to explain the observed differences in body mass dynamics.

Perspectives

Within thirty years after the establishment of a sedentary population of barnacle geese in the Netherlands, we found individuals from a temperate and arctic colony to differ in metabolic rate, growth rate, and adult body mass dynamics. The considerable logistic challenges of conducting respirometry trials in the (remote) field have limited our analyses to two study colonies we deem representative for the two populations. Clearly, for a solid and more general conclusion about differences between temperate and arctic breeding geese, we would need to include individuals from more than one colony at both breeding areas, or include another breeding population. We were able to investigate this with respect to gosling growth rates by combining measurements taken in the Russian and Dutch study colony over several years with measurements taken in the short-distance migratory Baltic breeding population (i.e., in the island of Gotland) which is located within the flyway at intermediate latitude (unpublished data). As would be expected from our analysis presented here, the growth rate of Baltic goslings was intermediate between that of goslings from arctic Russia and the Netherlands.

Studies of heritability in RMR and growth performance (body mass and mass gain) suggest that there is generally potential for a response to selection on these traits in birds (Nilsson et al. 2009, Sadowska et al. 2009, Van Noordwijk and Marks 1998). In our study system, however, there might be

little scope for a genetic response, apart from a founder effect perhaps, given the relatively recent split (ca. 30 years). There is also continuing exchange of individuals and genetic material between the migratory and non-migratory populations. These populations still share their wintering range, and sometimes pairs are formed between birds from either population (Jonker et al. 2013, Van der Jeugd and Litvin 2006). Thus, phenotypic plasticity may be a more likely explanation for our results, because RMR as well as growth rate are highly flexible traits, and metabolic adjustments related to migration can be short-lasting and reversible (McKechnie 2008, Swanson 2010). Also, the aforementioned intermediate growth rate of goslings from the Baltic population is more in line with predictions from a migratory or latitude driven explanation than with an explanation favouring genetic (founder) effects. As a next step, we suggest that it would also be interesting to investigate if our colony differences in RMR also persist during other life-cycle stages, in particular when individuals from both populations experience the same environment, either in a common-garden experiment or in the field on their shared wintering grounds. Similarly, in order to investigate whether genetic differences play a role, one should try and rear goslings from eggs of both populations under the same conditions.

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Author contributions - GE conceived the study, collected and analysed the data; ME analysed raw respirometry records; JYG provided scientific equipment; DH hosted and supported GE during his Marie Curie fellowship; GE and BN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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The following **Supporting Information** is available for this article online:

Appendix 1: Statistical method details;

Supporting Tables: Table S1 – Table S5;

Supporting Figures: Fig. S1 – Fig. S4.

Figure Legends

Fig. 1. Resting rate of oxygen consumption (\dot{V}_{O_2}) versus body mass as measured in growing juvenile (circles) and wing-moulting adult (triangles) barnacle geese from a migratory and a sedentary colony in arctic Russia (RU) and the Netherlands (NL), respectively.

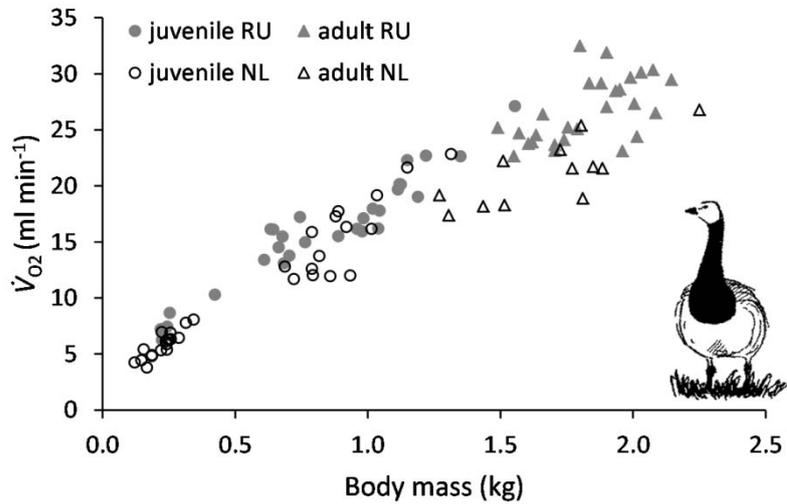


Fig. 2. Resting rate of oxygen consumption (\dot{V}_{O_2}) versus body mass as estimated from model I (Table 1) for growing juvenile barnacle geese from a migratory and a sedentary colony in arctic Russia (RU, grey lines) and the Netherlands (NL, black lines), respectively; dashed lines are 95% CIs about mean estimates shown as solid lines. The original data values are plotted as filled and open circles.

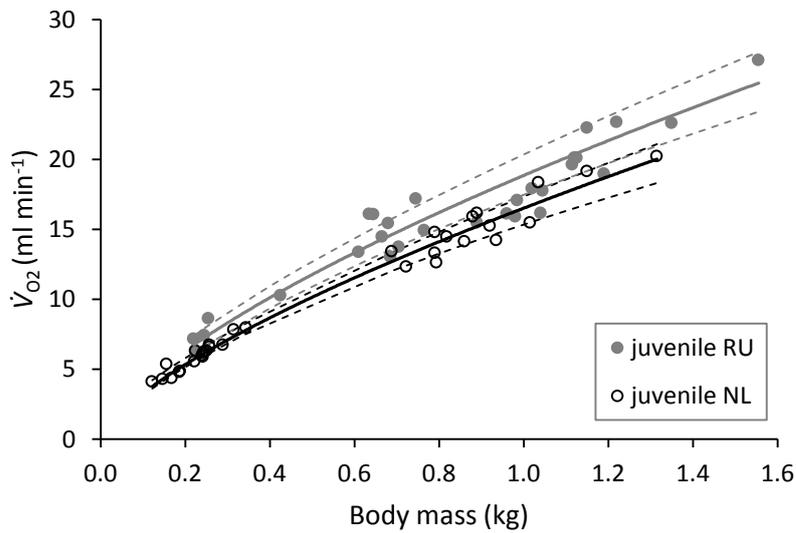


Fig. 3. Resting rate of oxygen consumption (\dot{V}_{O_2}) versus body mass (a), and versus the length of the 9th primary feather (b), as estimated from model II (Table 1) for wing-moulting adult barnacle geese from arctic Russia (grey lines) and the Netherlands (black lines), respectively; dashed lines are 95% CIs about mean estimates shown as solid lines. For the illustration of the instantaneous effect of body mass on \dot{V}_{O_2} in panel (a) P_9 was held at zero, and time since capture was held at its mean. In panel (b) both time since capture and body mass were held at their mean values for modelling the instantaneous effect of P_9 on \dot{V}_{O_2} . The original \dot{V}_{O_2} data were corrected accordingly, and are plotted as filled (Russia) and open triangles (Netherlands). Flight feathers are moulted simultaneously, and it takes approximately 5 weeks to grow P_9 to a full length of 264 mm (average of females and males; own obs.) (Van der Jeugd et al. 2009).

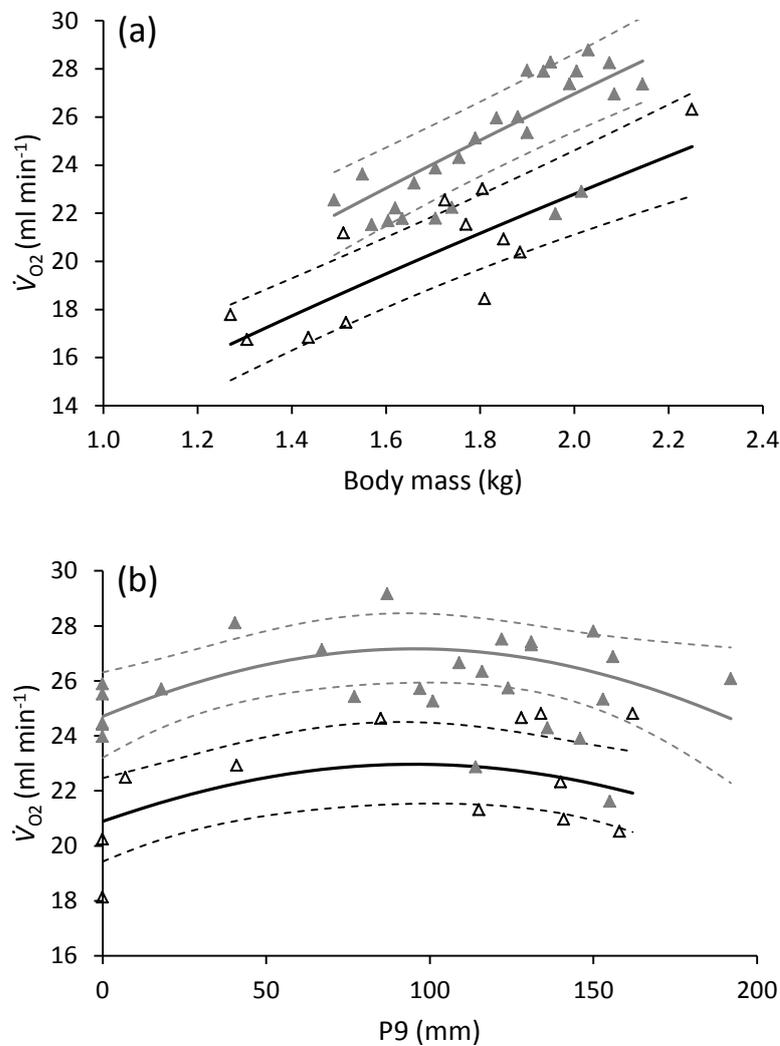


Fig. 4. Growth of body size (PC1 of wing, head and tarsus length, and body mass) in juvenile barnacle geese from a migratory and a sedentary colony in arctic Russia (RU, grey line and filled symbols, slope=0.086) and the Netherlands (NL, black line and open symbols, slope=0.055), respectively. Data were collected during same seasons when \dot{V}_{O_2} was measured, and cross symbols mark subjects that were also measured for \dot{V}_{O_2} in this study. Growth rate was 36.2% slower in the sedentary (NL) colony. See Supporting Information Table S3 for details of the statistical model.

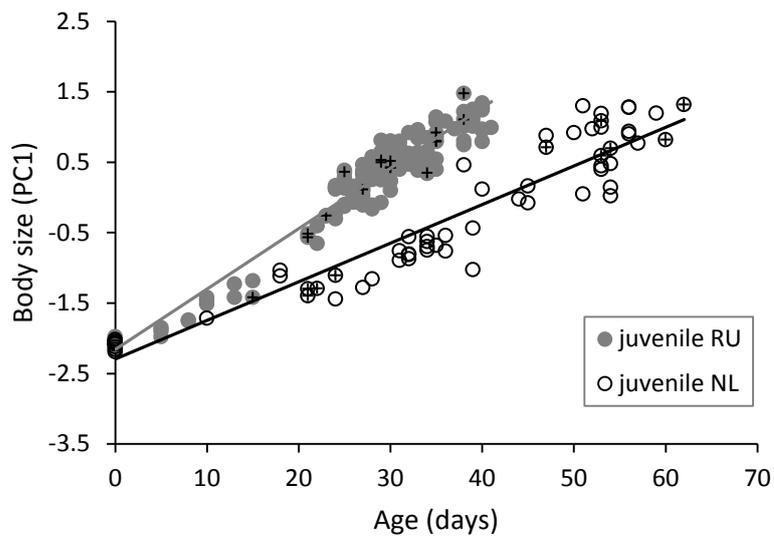


Fig. 5. Body mass (corrected for size, PC1 of head and tarsus length) versus length of the 9th primary feather in wing-moulting adult barnacle geese from a migratory and a sedentary colony in arctic Russia (RU, grey dashed line and filled symbols) and the Netherlands (NL, black solid line and open symbols), respectively. Data were collected during same seasons when \dot{V}_{O_2} was measured, and cross symbols mark subjects that were also measured for \dot{V}_{O_2} in this study. The slope is statistically significant different from zero for NL but not for RU, and slopes differ significantly from each other (Supporting Information: Table S4).

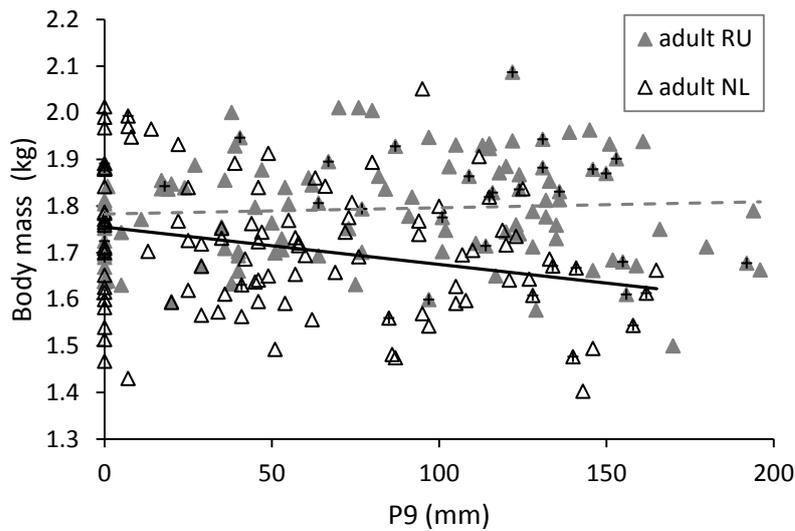


Table Legends

Table 1. Parameter estimates of fixed effects in final models of resting rate of oxygen consumption $\ln(\dot{V}_{O_2})$ in juvenile (model I) and adult (model II) barnacle geese from a migratory and a sedentary colony (*Col*) in arctic Russia (reference level, included in estimate for the intercept) and the Netherlands, respectively. The variance estimate for the random effect of capture date was 0.007 ± 0.003 (Wald $Z= 2.363$, $P= 0.018$) in juveniles, and 0.001 ± 0.001 (Wald $Z= 1.217$, $P= 0.224$) in adults. M – body mass [kg]; $P9$ (moult stage) – 9th primary feather length [mm] indicating the progress of moult; $t_{catch}-\dot{V}_{O_2}$ – time since capture [hours]; SE - standard error; \pm 95% CI – lower and upper bound of 95% confidence intervals.

Parameter	Estimate	SE	P	-95% CI	+95% CI
I. Juvenile geese					
Intercept	2.935	0.039		2.853	3.017
$\ln(Col)$	-0.145	0.046	0.005	-0.241	-0.048
$\ln(M)$	0.680	0.024	<0.001	0.632	0.729
II. Adult geese					
Intercept	2.804	0.071		2.660	2.948
$\ln(Col)$	-0.168	0.035	<0.001	-0.243	-0.093
$\ln(M)$	0.705	0.096	<0.001	0.510	0.899
$P9$ (moult stage)	0.0020	0.0008	0.013	0.0004	0.0035
$P9^2$	-0.000010	0.000004	0.023	-0.000019	-0.000002
$t_{catch}-\dot{V}_{O_2}$	-0.0050	0.0022	0.028	-0.0094	-0.0006