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RESEARCH ARTICLE

Seasonal variation in the thermal responses to changing environmental temperature in the world's northernmost land bird

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ABSTRACT

Arctic homeotherms counter challenges at high latitudes using a combination of seasonal adjustments in pelage/plumage, fat deposition and intricate thermoregulatory adaptations. However, there are still gaps in our understanding of their thermal responses to cold, particularly in Arctic birds. Here, we have studied the potential use of local heterothermy (i.e. tissue cooling that can contribute to significantly lower heat loss rate) in Svalbard ptarmigan (*Lagopus muta hyperborea*) – the world's northernmost land bird. We exposed birds kept under simulated Svalbard photoperiod to low ambient temperatures (T_a; between 0 and −30°C) during three seasons (early winter, late winter, summer), whilst recording resting metabolic rate (RMR), core temperature (T_c) and several cutaneous temperatures. Leg skin temperature varied the most, but still only by up to ∼15°C, whereas body trunk skin temperature changed <1°C when T_a decreased from 0 to −30°C. At the same time, T_c increased by 0.9°C, concomitant with increased RMR. This was probably driven by the triggering of cerebral thermosensors in response to cooling of the poorly insulated head, the skin of which was 5.4°C colder at −30°C than at 0°C. Thermal conductance in winter was higher in yearlings, probably because they were time/resource constrained from acquiring a high-quality plumage and sufficient fat reserves as a result of concomitant body growth. In conclusion, Svalbard ptarmigan do not employ extensive local heterothermy for cold protection but instead rely on efficient thermogenesis combined with excellent body insulation. Hence, cold defence in the world's northernmost land bird is not mechanistically much different from that of its lower latitude relatives.

KEY WORDS: Arctic, Heterothermy, Heat loss rate, Peripheral temperature, Seasonal acclimatization, Thermoregulation

INTRODUCTION

High-latitude animals must adapt to extreme seasonal variation in photoperiod, precipitation, temperature and environmental productivity. The success with which this is achieved is remarkable when considering that environmental temperatures may be >80°C below the core temperature (T_c) of resident homeotherms over extended periods (Irving and Krog, 1954), while daylight hours range between 0 and 24 h over the course of the year. Winter residency under such conditions comes with substantial energetic challenges. Some mammals overcome these by hibernating, with metabolic rate sometimes dropping to <1% of normal levels and tissue temperatures (T_t) sometimes falling below freezing (reviewed by Ruf and Geiser, 2015). This option is probably not available for birds (but see Jaeger, 1948), which instead often vacate breeding territories to winter in more thermally and nutritionally benign habitats (Newton and Dale, 1996). Non-migratory birds (and resident mammals alike) mitigate winter energy expenditure by behavioural adjustments that reduce heat loss, such as huddling (Ancel et al., 1997; Gilbert et al., 2010), shelter building (Irving et al., 1967; Marjakangas et al., 1984) and microhabitat selection (Coulianos and Johnels, 1962; Duchesne et al., 2011), and, last but not least, through a range of morphological (e.g. moulting to obtain a more insulating winter coat) and physiological adjustments (e.g. fat deposition and thermoregulatory responses such as peripheral vasoconstriction, respiratory responses, shivering thermogenesis, etc.; reviewed by Blix, 2016).

Strong selection for energy conservation is also the reason why many non-hibernating animals in seasonal biomes are not obligate homeotherms, but instead allow T_c/T_t to decrease in all (torpor, rest-phase hypothermia) or part of (local heterothermy) the body during inactivity. Reducing the thermal gradient towards the environment lowers the need for metabolic heat production: heat is lost at a slower rate and, hence, less energy is required to maintain heat balance. Colder tissues also have lower metabolic demands. Torpor and rest-phase hypothermia are frequently used by many small mammals and birds, for example in response to deteriorating environmental conditions and lower nutritional status (e.g. Nord et al., 2009, 2011). This may reduce resting energy expenditure to 10–30% of normal levels (depending on the extent of T_c decrease; Geiser, 2004), and so could substantially increase overwinter survival (Brodin et al., 2017). Larger, non-hibernating, homeotherms (>500 g) typically maintain a stable T_c during cold exposure (but see Harlow, 1981), and instead reduce the body surface-to-environment thermal gradient through local heterothermy: a substantial decrease in T_t in the extremities and/or body periphery that is under vasomotor control (e.g. Irving and Krog, 1955). This is an important avenue for energy conservation (Scholander et al., 1950), and probably explains how some well-insulated mammals can endure extreme cold without increasing metabolism above basal levels (cf. Nilssen et al., 1984; Folkow and Mercer, 1986).

Local heterothermy also occurs in birds, studied mostly in the legs of aquatic birds where elaborate counter-current heat-exchange systems (Midtgård, 1981, 1989) allow both low- and high-latitude species to regulate and maintain foot temperature at, or close to, ambient temperature (T_a) (Irving and Krog, 1955). This reduces heat loss at the same time as maintaining adequate nutritional blood supply to foot tissues. Seabirds may also display local heterothermy in appendages or the body trunk when diving (Bevan et al., 1997; Handrich et al., 1997; Ponganis et al., 2003; but see Enstipp et al., 2005). This is presumably part of their diving response, which

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includes massive peripheral vasoconstriction causing a drop in local energy expenditure (through a reduced supply of blood-borne O_2 and substrate) as well as in local T_t (as a result of lower metabolism and reduced inflow of warm blood, causing lower heat loss rates), both of which would contribute to extending dive duration (Scholander, 1940). By comparison, the occurrence and possible energetic significance of local heterothermy in land birds has received little attention, although Ekimova (2005) report that fasting pigeons (*Columba livia*) reduce leg skin temperature to near T_a.

Here, we have studied the potential use of local heterothermy in a bird at the extreme of its range: the Svalbard ptarmigan (*Lagopus muta hyperborea* Sundevall 1845). This rock ptarmigan (*Lagopus muta*) subspecies is a year-round resident in the High Arctic Svalbard archipelago (77–81°N) and, as such, it is the world's northernmost resident land bird. Not surprisingly, the Svalbard ptarmigan experiences an extreme environment throughout its annual cycle, where the sun does not rise above the horizon for more than 3 months in winter but is continuously above the horizon from early April until mid-August, and where average T_a is below freezing for 9 months of the year. Metabolic fuel is acquired from low-growing tundra vegetation (Mortensen et al., 1983), which is frequently deeply embedded in ice or snow in winter. Therefore, these birds display seasonal cycles in body composition, building fat stores in summer/autumn times of plenty that may be drawn upon during periods of reduced food availability (Mortensen et al., 1983; Mortensen and Blix, 1985). However, like many larger birds, the Svalbard ptarmigan (and other related species) maintain normothermic T_c even in severe cold (Irving and Krog, 1954; Mortensen and Blix, 1986). The combination of a harsh year-round environment and, presumably, lack of torpor/rest-phase hypothermia renders the Svalbard ptarmigan a suitable model for studies of local heterothermy. Accordingly, we measured T_c, T_t and metabolic responses to experimental cold exposure (between 0 and −30°C) in captive Svalbard ptarmigan, kept indoors under a simulated Svalbard photoperiod, to study the thermal responses to experimental cold exposure in this bird. In particular, we were interested to see whether Svalbard ptarmigan routinely employ extensive local heterothermy of a sufficient magnitude to significantly lower heat loss rate in the cold (here defined as marked peripheral cooling with superficial tissue/appendage temperatures approaching 0°C). Subjects were either in their first winter (when they must divide resources between growth and winter acclimatization) or in their second winter, or older (when they are physically mature). The experiment was performed at three time points spread over the birds' annual cycle, coincident with large natural variation in photoperiod, food intake, body condition and fasting resistance (Fig. 1). Specifically, birds were measured: (1) in early winter in constant darkness (DD), when they were in their prime body condition (Fig. 1B,C), but food intake was decreasing (Fig. 1D), presumably as a result of a seasonally regulated and hormonally mediated decrease in appetite (Stokkan et al., 1986; Reierth et al., 1999); (2) in late winter under 15 h light and 9 h dark (LD), when body condition was still high and appetite was on the increase (Fig. 1B–D) but summer moult had not yet begun; and (3) in summer in constant light (LL), when body condition was at its lowest and birds had moulted into their summer plumage, while food intake was near its annual peak (Fig. 1B–D; see also Stokkan et al., 1986). We predicted the greatest extent of peripheral cooling, and the largest energy costs of thermoregulation in response to experimental cold exposure, to be manifested in summer-adapted birds (measurement period 3, as defined above), which should be the least equipped to counter a cold challenge. Analogously, we predicted peripheral cooling to be used to the lowest extent under similar cold exposure in early winter-adapted birds (measurement period 1), when these were better protected from cold via the more insulating winter plumage and considerable amounts of subcutaneous fat (Mortensen et al., 1983; Mortensen and Blix, 1986; see also Fig. 1C). Finally, we predicted that the transition from early to late winter (measurement period 2) would lead to an increased extent of peripheral cooling and higher costs of thermoregulation in response to cold exposure, as a result of reduced body condition and fasting resistance (Fig. 1B,C).

MATERIALS AND METHODS

Birds and housing

Twelve male Svalbard ptarmigan were used in the study. Seven of these were captured as chicks (body mass at capture: 46–435 g depending on developmental stage) near Longyearbyen, Svalbard

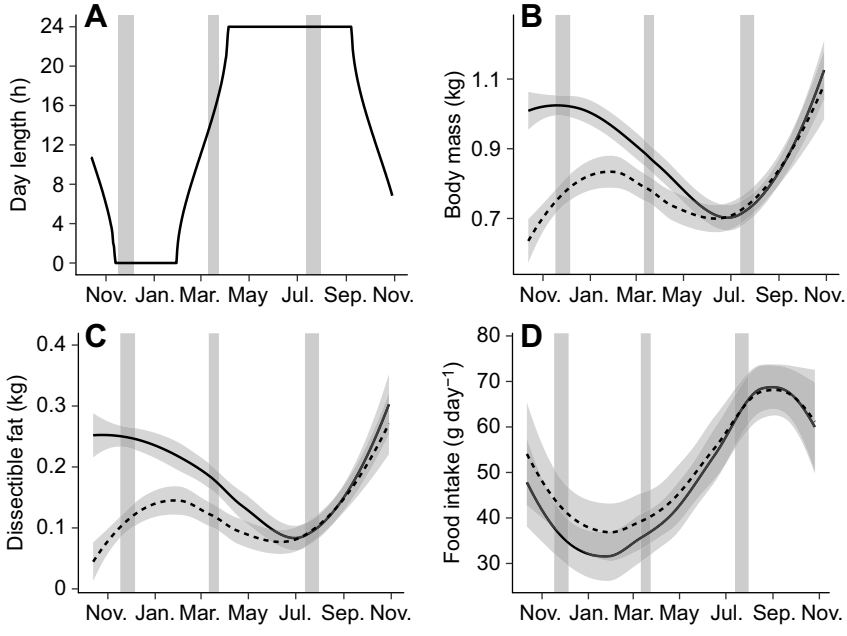

Fig. 1. Annual variation in experimental photoperiod, and body mass, dissectible fat and food intake for the Svalbard ptarmigan in this study. (A) Natural variation in photoperiod (including civil twilight) over the course of the year in Longyearbyen, Svalbard (78°13′N, 15°38′E) – experimental birds were exposed to a simulated version of this. (B–D) LOESS (locally weighted scatterplot smoothing) ±95% confidence interval. Solid lines represent birds that were in their second calendar year or older (i.e. 2CY+), and dashed lines represent birds that were in their first calendar year (i.e. 1CY) when the experiment started. The shaded vertical bars show experimental periods. Biometric and food intake data were collected from n=10–12 male Svalbard ptarmigan (1CY: n=5–7; 2CY+: n=5) over the course of the study.

(78°13′N, 15°38′E), in August 2014 (i.e. 3–4 months before the start of the experiment; age category 1CY) under permission issued by the Governor of Svalbard (permit no. 2014/00290-2 a.522-01) and the Norwegian Food Safety Authority (permit no. 2014/150134), whereas the remaining five (all ≥2 years old; age category 2CY+) originated from a captive population (founded 1997) in the approved animal research facility at the Department of Arctic and Marine Biology, University of Tromsø, Norway. Ten birds (five wild-caught, five captive) were measured during all seasons, but two wild-caught birds were measured only during early winter as they were subsequently allocated to the breeding population (Table S1). There were two sibling pairs amongst the wild-caught birds (i.e. the total of seven birds originated from five families), whereas the captive-bred birds were all unrelated. Previous work has shown that the morphological and physiological changes associated with winter acclimatization/acclimation do not differ between captive and wild-caught Svalbard ptarmigan as long as captive birds are maintained under a simulated Svalbard photoperiod (e.g. Stokkan et al., 1986; Lindgård and Stokkan, 1989). Ethical approval for experiments was issued by the Norwegian Food Safety Authority (permit no. 6639).

Birds were maintained singly in indoor cages (1.0×0.7×0.6 m) in light- and temperature-controlled rooms, at thermoneutrality (6.8±1.9°C, mean±s.d.; Mortensen and Blix, 1986) and under a natural Longyearbyen (78°13′N, 15°38′E) photoperiod (Fig. 1A). Civil twilight was added to daytime (cf. Stokkan et al., 1986). During LD periods (i.e. 30 January to 4 April, and 8 September to 11 November), lights were switched on and off abruptly by a timer (SC 28X1 Pro, Hugo Müller GmbH and Co., Schwenningen, Germany). Faint continuous light [<<1 lx at the cage door versus 766±366 lx (mean±s.d.) in LL] was provided by a red incandescent lamp during the DD period (i.e. 12 November to 29 January), to account for the fact that even the polar night is not always completely dark and to allow for bird maintenance and cage cleaning. No non-experimental light could reach the birds. Pelleted ptarmigan feed (Agrimex, Trøgstad, Norway) and water were available *ad libitum*. We weighed birds (±0.1 g) and measured food intake (±0.1 g food ingested day^{-1}, based on 48 h consumption) at least fortnightly, to monitor seasonal changes associated with winter acclimation (Fig. 1B–D). Dissectible fat mass was calculated from total body mass following Mortensen et al. (1983).

Measurement of body temperature and experimental protocol

We measured body temperature (T_c, T_t) and metabolic responses to cold exposure (0 to −30°C) during three discrete periods (Fig. 1): (1) early winter, when birds were under DD and subcutaneous fat deposits were largest [mean±s.e. body mass: 758.0±12.9 g (1CY)/1043.7± 15.1 g (2CY+); dissectible fat: 106.5±6.5 g (1CY)/251.1 ±7.6 g (2CY+)]; (2) late winter, when birds were under LD and still carried significant fat reserves [body mass: 811.4±23.4 g (1CY)/929.1± 20.7 g (2CY+); dissectible fat: 133.5±11.8 g(1CY)/193.1 ±10.5 g (2CY+)]; and (3) summer, when birds were under LL, in summer plumage, and fat reserves were at the yearly nadir [body mass: 712.4±21.2 g (1CY)/679.8±11.6 g (2CY+); dissectible fat: 83.5± 10.7 g (1CY)/67.0±5.9 g (2CY+)].

Birds were measured during the daytime [starting at 09:51 h (±37 min s.d.) local Tromsø time]. At the start of a measurement session, birds were collected from their cages, weighed and then immediately brought to an adjacent laboratory where they were instrumented with 36-gauge type T (copper–constantan) thermocouples (Omega Engineering, Stamford, CT, USA) for temperature measurement. All thermocouples were attached by the same person (A.N.). Specifically, we measured (1) T_c in the colon by inserting the thermocouple 70 mm into the cloaca, and then equipped birds to measure cutaneous (surface) T_t at four additional sites; (2) in the dorsal scapular area (T_{back}); (3) over the breast muscle (T_{breast}), which is the main heat-producing tissue in birds (Aulie, 1976); (4) at the tibiotarsus adjacent to the intratarsal joint (T_{tarsus}), a key site for counter-current heat exchange in several bird species (Midtgård, 1981); and (5) at the scalp (T_{head}), to measure a potential proxy for temperature change in the more thinly insulated head/brain. All cutaneous thermocouples (tc2–5) were attached onto the skin surface using cyanoacrylate glue (Loctite® Power Easy gel, Henkel, Düsseldorf, Germany). A 2×7 mm rectangular piece of surgical tape was attached to the end of the thermocouple (leaving the thermosensitive junction bare) to increase the area of adhesion. The cloacal thermocouple (tc1) was covered by a blunted 10 cm polythene catheter (diameter 1.22 mm; Fortex Engineering, Lincoln, UK) and was secured to the tail feathers using surgical tape. Thermocouples were carefully threaded through the plumage and collated in a bundle contained in silicone tubing, such that no individual wires protruded from the body. All thermocouples were calibrated at 0°C (Ice point drywell model 5115) and 40°C (High precision bath model 6025, both Fluke Calibration, American Fork, UT, USA) prior to use. Instrumentation during DD was performed under illumination from a red-light head torch.

Birds were subsequently put into a 43.2 l (early winter) or 33.6 l (late winter, summer) transparent Plexiglas chamber located inside a climatic chamber (model 24/50 DU, Weiss Technik, Giessen, Germany), for measurement of T_c, T_t and resting metabolic rate (RMR; by use of respirometry) responses to different T_a. To ensure that the bird could move around freely, we attached the silicone-encased thermocouple bundle to a lightweight spring connected to a swivel in the centre of the chamber roof, from where it exited the chamber through an otherwise sealed port. Corrugated cardboard was placed on the chamber floor to make it less slippery. We subsequently subjected birds to a decreasing (starting at 0°C; n=8 birds, of which 6 were measured during all seasons as detailed above) or an increasing (starting at −30°C; n=4 birds) sliding temperature protocol, during which we collected T_c, T_t and RMR data at expected thermoneutrality [T_a: −0.2±1.3°C (mean±s.d.)], close to, but below, the lower critical temperature (T_a: −10.2±0.4°C), and far below thermoneutrality (T_a: −30.3±0.3°C) (Mortensen and Blix, 1986). Measurement order was randomized by coin tossing before the start of the experiment, and each bird was measured in the same order during all seasons. Given the size of the birds (range 595–1130 g; Fig. 1), we allowed them 1 h to equilibrate at each T_a (i.e. 0, −10, −30°C) before we started to record experimental data for 20 min. Baseline data for ambient gas composition were collected for approximately 15 min, in-between measurements of RMR. The air temperature inside the metabolic chamber was monitored with a 20-gauge type T thermocouple (Omega Engineering) positioned in the chamber ceiling, at a height at which heat produced by the bird did not affect the reading. Measurements during DD were performed in dim red light (<<1 lx). A measurement session (from collection to subsequent return to the cage) lasted 6.6±0.3 h, after which we removed (tc1) or cut the thermocouple wires at the skin surface (tc2–5), weighed the bird, and returned it to its cage. The exposure period should be adequate to detect any local heterothermy, as RMR, T_c and T_t typically stabilized within 30 min of putting the bird into the metabolic chamber and remained unaltered in a given T_a thereafter. By comparison, the much larger homeotherm reindeer (*Rangifer*

tarandus tarandus) responds with substantial local heterothermy (i.e. leg skin temperature dropping below 10°C) within 1–3 h of being subjected to T_a below their lower critical temperature (e.g. Folkow and Mercer, 1986; Johnsen et al., 1985).

Measurement of RMR

In early winter, O_2 consumption and CO_2 production were measured using a FoxBox (Sable Systems, Las Vegas, NV, USA), and flow rate was recorded with a SRT-2 volumetric flow meter (Flow Tech, Phoenix, AZ, USA). During late winter and summer, O_2 consumption was measured using a S3-A oxygen analyser (Applied Electrochemistry, Pittsburgh, PA, USA), and CO_2 production was recorded using a ML206 gas analyser (AD Instruments, Sydney, Australia). Flow rate was registered with a FMA-A2317 mass flow meter (Omega Engineering). Humidity and temperature of the sample gas were measured using a HMI32 thermometer and hygrometer (Vaisala, Vanda, Finland) throughout the experiment.

We calibrated the O_2 analysers against ambient air (20.95% O_2) and 100% N_2 (i.e. 0% O_2), and also using the N_2-dilution technique (Fedak et al., 1981), the last forming the basis for correcting for between-instrument variation in the accuracy of O_2 measurement, as outlined below. The CO_2 analysers were calibrated against 100% N_2 and 1% CO_2. We calibrated all analysers daily, and used day-specific calibration values to convert the input signal to gas concentrations. The SRT-2 flow meter was calibrated against a DTM-325 gas meter (Elster American Meter, Nebraska City, NE, USA), whereas the FMA-A2317 mass flow meter was factory calibrated immediately prior to use. All data were recorded and digitized from raw signals using a ML796 PowerLab/16SP A-D converter (AD Instruments).

Adjustment for between-instrument variation in O_2 measurement

We used the N_2 dilution technique (Fedak et al., 1981), with a N_2 flow of 125–900 ml min^{-1} (n=61 dilutions over the course of the study), as measured with a FMA5512A mass flow meter (Omega Engineering), to control for between-instrument variation in the accuracy of O_2 measurement, and derived adjusted RMR values according to:

$$\mathrm{RMR_{adj}} = \frac{\mathrm{RMR}}{\left(\Sigma_{i=1}^{n} \frac{\Delta O_{2,\mathrm{obs},i}}{\Delta O_{2,\mathrm{pred},i}}\right)/N}, \quad (1)$$

where RMR_{adj} is RMR adjusted for between-instrument variation, ΔO_2 is the measured ($\Delta O_{2,obs}$) or predicted ($\Delta O_{2,pred}$) change in fractional O_2 during N_2 dilution, and N is the total number of N_2 dilutions during each experimental period.

Data handling and statistical analyses

We calculated standard temperature and pressure-corrected flow rates (f_{STP}) from the SRT-2 flow meter according to Lighton (2008):

$$f_{STP} = f_a \times \frac{T_{gas} \times 760}{273.15 \times BP}, \quad (2)$$

where f_a is the uncorrected flow rate (ml min^{-1}), T_{gas} is gas temperature in K and BP is barometric pressure in mmHg (Tromsø data provided by the Norwegian Meteorological Institute). We then standard temperature and pressure dry (STPD)-corrected all flow rates by subtracting f_{H_2O} from f_{STP}, where f_{H_2O} was calculated following Eqn 3 (Vaisala, 2013):

$$f_{H_2O} = f_{STP} \times \frac{(RH/100) \times 4.588 \times 10^{(7.59 \times T_{gas})/(240.73 + T_{gas})}}{BP}, \quad (3)$$

where RH is relative humidity of the sample gas and T_{gas} is gas temperature in °C. We then calculated the rate of O_2 consumption and CO_2 production following Eqns 4 and 5, respectively (Lighton, 2008):

$$\dot{V}_{O_2} = f_{STPD} \times \frac{(F_{I_{O_2}} - F_{E_{O_2}}) - F_{I_{O_2}} \times (F_{E_{CO_2}} - F_{I_{CO_2}})}{1 - F_{I_{O_2}}}, \quad (4)$$

$$\dot{V}_{CO_2} = f_{STPD} \times \frac{(F_{E_{CO_2}} - F_{I_{CO_2}}) + F_{I_{CO_2}} \times (F_{I_{O_2}} - F_{E_{O_2}})}{1 + F_{I_{CO_2}}}, \quad (5)$$

where $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ are O_2 consumption and CO_2 production rate in ml min^{-1}, $F_{I_{O_2}}$ and $F_{E_{O_2}}$ are the fractional O_2 concentration in influent and effluent air, and $F_{E_{CO_2}}$ and $F_{I_{CO_2}}$ are the fractional CO_2 concentration in effluent and influent air, respectively. O_2 consumption was converted to energy consumption (W) assuming an oxyjoule equivalence of 20 J ml^{-1} O_2 (Kleiber, 1961).

We only used data from periods when the birds were at full rest and had completed their thermal equilibration periods. If a bird did not meet the 'rest' requirements, we used resting data collected at the relevant T_a, but outside the dedicated 20 min measurement period. Such data were used in 12 (out of 95) cases. We also dismissed data from thermocouples that fell out (tc1) or off (tc2–5), or broke (tc1–5) (for T_c: 2; T_{back}: 0; T_{breast}: 5; T_{head}: 14; T_{tarsus}: 8; out of 95 recording periods). Final sample sizes for each parameter, season, T_a and age category are reported in Table S1.

Whole-animal thermal conductance (Aschoff, 1981) was calculated in W kg^{-1} °C^{-1} as:

$$C = \frac{\mathrm{RMR}}{m_b}/(T_c - T_a), \quad (6)$$

where C is thermal conductance, m_b is body mass and T_a is ambient temperature inside the metabolic chamber.

All statistical analyses were performed in R 3.3.1 (http://www.R-project.org/). We analysed all bird T_c, T_t, mass-specific RMR (i.e. RMR/body mass), total RMR and C with linear mixed effects models (lme4 package; Bates et al., 2015). All original models included experimental period (early winter, late winter, summer), T_a (0, −10, −30°C), bird age [first winter (1CY), or older (2CY+)] and measurement order (i.e. increasing or decreasing T_a; see above) as main effects. The original model for total RMR also included body mass as a covariate. We did not account for body mass in any other models, because it co-varied with bird age in two out of three seasons (Fig. 1) but varied relatively little within age classes. Age and body mass, therefore, conveyed largely the same statistical information, so adding the latter to our models was not warranted. We included the three-way interaction T_a×season×age (and all of its lower level interactions), to account for any potential age-related differences in the seasonal effects of cold exposure on thermoregulation. In addition, original models included the two-way interaction T_a×measurement order, to account for possible variation introduced by the order of temperature exposures. To account for repeated sampling, we fitted four alternative random structures to the original models: (1) a random intercept for bird id; (2) a random intercept (bird id) and slope (T_a); (3) a random intercept for bird id and a random intercept for family (to account for any genetic effects pertaining to the relatedness of some of the birds); or (4) a random intercept/slope (bird id and T_a, respectively) and a random intercept for family. We then selected the most appropriate random structure based on the Akaike information

Journal of Experimental Biology (2018) 221, jeb171124. doi:10.1242/jeb.171124

criterion (AIC) (Zuur et al., 2009). The simplest random structure, i.e. a random intercept for bird id, was preferred in all cases (mean $\Delta AIC_{alternative\text{-}best\ fit}$: 7.6). We derived final models by sequentially excluding the model term with the lowest *P*-value and comparing AIC values for the full and reduced models (fitted with maximum likelihood) starting with the highest order interactions and retaining parameters for which ΔAIC >5 (package LMERConvenience Functions; https://CRAN.R-project.org/package=LMERConvenience Functions). We then re-fitted the final model using restricted maximum likelihood (Zuur et al., 2009), and calculated degrees of freedom for this model using the Satterthwaite approximation (lmerTest package; https://CRAN.R-project.org/package=lmerTest). Multiple comparisons for final models were performed on predicted marginal means within seasons between T_a or age groups, or within seasons within age groups between T_a, as applicable (lsmeans package; Lenth, 2016). We adjusted *P*-values for multiple comparisons using the Holm–Bonferroni correction (Holm, 1979). Data in the tables and text are predicted marginal means±s.e., and all significances are two-tailed.

RESULTS

Deep and peripheral tissue temperature

Average T_c (41.71±0.14°C) across seasons and T_a was consistently higher than peripheral T_t (T_{back}: 37.44±0.27°C; T_{breast}: 37.26±0.24°C; T_{head}: 31.04±0.80°C; T_{tarsus}: 28.66±1.85°C) (Fig. 2). Accordingly, on average, birds maintained T_c 4.65±0.22°C above body trunk skin (i.e. T_{back} and T_{breast}), 10.78±0.57°C above T_{head}, and 13.30±1.32°C above T_{tarsus} (Fig. 2).

T_c was about 0.2°C lower in summer than in winter, and consistently increased with decreasing T_a (Table 1; Fig. 3A). On average, T_c was 0.26°C higher at −10°C than at 0°C, and 0.64°C higher at −30°C than at −10°C (Fig. 3A). The effect size varied with measurement order (measurement order×T_a: $P<0.003$; Table 1). T_c did not change between 0°C (41.41±0.12°C) and −10°C (41.68±0.12°C) when birds were subjected to the decreasing T_a protocol, and was 0.55°C (42.10±0.12°C) higher at −30°C than at the other two temperatures (Table 1). In contrast, T_c was significantly different between all T_a when birds were exposed to the increasing T_a protocol (−30°C: 42.40±0.16°C; −10°C: 41.40±0.16°C; 0°C: 41.09±0.17°C) (Table 1).

When averaged over seasons, T_{back} did not differ between 0°C (37.83±0.15°C) and −10°C (37.64±0.26°C), but was 1.12°C lower at −30°C (36.62±0.26°C) relative to the other T_a (Table 1). T_{back} also varied between seasons depending on bird age (season×age: $P=0.007$) (Table 1). In 1CY birds, mean T_{back} was fairly similar in early winter (37.92±0.32°C) and summer (37.80±0.36°C), but ca. 1.6°C lower in late winter (36.27±0.36°C). In contrast, 2CY+ birds maintained a relatively stable average T_{back} in early and late winter (37.17±0.38°C and 36.96±0.39°C, respectively), but increased T_{back} by 1°C in summer (Table 1).

T_{breast} was stable across seasons and age categories, but decreased with decreasing T_a, such that T_{breast} at 0°C (37.58±0.45°C) and −10°C (37.33±0.44°C) was 1.08°C higher than T_{breast} at −30°C (36.38±0.44°C) (Table 1).

T_{head} was markedly affected by T_a, decreasing by 1.79°C between 0°C (33.43±0.31°C) and −10°C (31.64±0.32°C), and by a further 3.63°C during the transition to −30°C (28.01±0.32°C) (Fig. 3B). T_{head} also varied with season, being 0.50°C higher in late compared with early winter, and 0.66°C higher in summer than in late winter (Table 1; Fig. 3B). The seasonal effect differed between age categories: 1CY maintained a significantly lower average T_{head} in early winter (1CY: 29.61±0.44°C; 2CY+: 31.42±0.42°C), such that the seasonal increase in T_{head} was larger in this group (Table 1).

T_{tarsus} decreased with T_a, from 32.21±1.39°C at 0°C to 29.82±1.38°C and 23.27±1.37°C at −10 and −30°C, respectively. This effect differed between seasons (i.e. season×T_a: $P=0.001$) (Table 1; Fig. 3C). T_{tarsus} did not differ between 0°C (32.12±1.71°C) and −10°C (30.35±1.71°C) in early winter, but was significantly lower at −30°C (23.09±1.71°C). In contrast, there was no significant effect of T_a in late winter (Table 1; Fig. 3C). T_{tarsus} in summer was relatively similar to early and late winter values in thermoneutrality (32.04±1.92°C), but subsequently dropped by 5.63 and 15.31°C when birds were measured at −10°C (26.41±1.92°C) and −30°C (16.73±1.84°C), respectively (Fig. 3C).

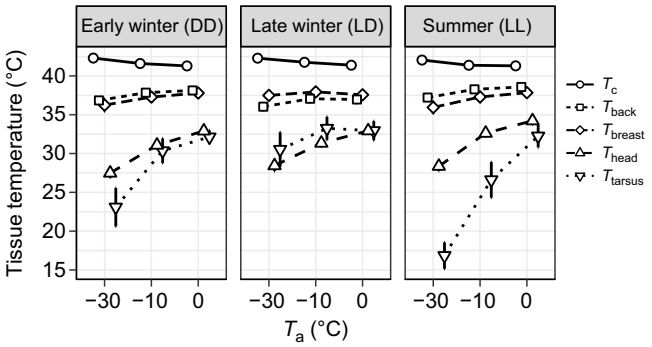

Fig. 2. Overview of variation in tissue temperature (T_t) in captive Svalbard ptarmigan at different ambient temperatures (T_a) and seasons. Data are mean±s.e.m. core (T_c) and cutaneous T_t measured at the back (T_{back}), breast (T_{breast}), head (T_{head}) and tibiotarsus (T_{tarsus}). DD, continuous darkness; LD, 15 h light:9 h dark; LL, continuous light. Data were averaged over age categories and measurement order. Sample sizes for each tissue, at each T_a and season, are reported in Table S1.

Mass-specific RMR, total RMR and thermal conductance

Mass-specific RMR (across age categories) at T_a 0°C (corresponding to expected thermoneutrality, according to Mortensen and Blix, 1986) increased 13% between early (4.94±0.31 W kg^{-1}) and late (5.59±0.30 W kg^{-1}) winter, and 40% between late winter and summer (7.81±0.25 W kg^{-1}). Mass-specific RMR was higher in 1CY than in 2CY+ birds at all T_a in early and late winter, but not in summer (Fig. 4). Moreover, the proportional response to a drop in T_a, from 0°C to −30°C, differed between the age groups in a season-dependent manner (season×T_a×age: $P=0.008$) (Table 2). The proportional response in 1CY birds was stronger in late winter (+4.56 W kg^{-1}/+77%) than at other times of the year (early winter: +3.05 W kg^{-1}/+55%; summer: +5.12 W kg^{-1}/+63%). By contrast, the proportional response in 2CY+ birds was relatively similar in early and late winter (early winter: +2.65 W kg^{-1}/+66%; late winter: +3.20 W kg^{-1}/+63%), but considerably stronger in summer (+7.69 W kg^{-1}/+103%) (Fig. 4). Total RMR at expected thermoneutrality (i.e. at 0°C) differed between seasons, being relatively similar in early (4.21±0.20 W) and late (4.71±0.23 W) winter, but some 21% higher in summer (5.39±0.22 W). The total RMR response to a drop in T_a, from 0 to −30°C, largely followed patterns in mass-specific RMR (although there was no age effect). Accordingly, total RMR in early winter was 2.47 W (59%) higher at −30°C than at 0°C, a difference that had increased to 3.37 W (72%) and 4.41 W (82%) by late winter and summer, respectively (Table 2). Body mass changes throughout the study period were too small to affect total RMR ($P>0.3$).

Mass-specific thermal conductance, *C*, across ages reached its minimum average value in early winter (0.110±0.004 W kg^{-1} °C^{-1})

Journal of Experimental Biology (2018) 221, jeb171124. doi:10.1242/jeb.171124

Table 1. Test statistics, degrees of freedom (Satterthwaite approximation) and *P*-values for final models of core (T_c) and peripheral cutaneous tissue (T_t) temperature measured in Svalbard ptarmigan at each of three ambient temperatures (T_a) during early winter, late winter and summer

Parameter	Estimate (±s.e.)	d.f.	*F*	*P*
T_c (°C)				
Season		2, 75.53	3.29	**0.043**
Early winter[a]	41.71±0.10			
Late winter[a]	41.78±0.10			
Summer[a,b]	41.54±0.10			
Measurement order		1, 7.31	0.33	0.583
T_a		2, 72.77	54.35	**<0.001**
Measurement order×T_a		2, 72.78	6.32	**0.003**
Measurement order=0 to −30°C				
0°C[a]	41.41±0.12			
−10°C[a]	41.68±0.12			
−30°C[b]	42.10±0.12			
Measurement order=−30 to 0°C				
0°C[a]	41.09±0.17			
−10°C[a]	41.40±0.16			
−30°C[b]	42.40±0.16			
T_{back} (°C)				
Season		2, 79.07	17.05	**<0.001**
T_a		2, 77.12	17.01	**<0.001**
0°C[a]	37.83±0.26			
−10°C[a]	37.64±0.26			
−30°C[b]	36.62±0.26)			
Age		1, 9.70	0.03	0.876
Season×age		2, 79.07	5.29	**0.007**
Season=early winter				
Age=1CY[a]	37.92±0.32)			
Age=2CY+[a]	37.17±0.38			
Season=late winter				
Age=1CY[a]	36.27±0.36			
Age=2CY+[a]	36.96±0.39			
Season=summer				
Age=1CY[a]	37.80±0.36			
Age=2CY+[a]	38.07±0.38			
T_{breast} (°C)				
T_a		2, 75.14	4.98	**0.009**
0°C[a]	37.58±0.45			
−10°C[a]	37.33±0.44			
−30°C[b]	36.38±0.44			
T_{head} (°C)				
T_a		2, 65.43	150.91	**<0.001**
0°C[a]	33.43±0.25			
−10°C[b]	31.94±0.25			
−30°C[c]	28.70±0.26			
Age		1, 9.33	1.85	0.206
Season		2, 67.23	7.75	**0.001**
Season×age		2, 67.23	6.71	**0.002**
Season=early winter				
Age=1CY[a]	29.61±0.44			
Age=2CY+[b]	31.42±0.42			
Season=late winter				
Age=1CY[a]	30.46±0.48			
Age=2CY+[a]	31.22±0.47			
Season=summer				
Age=1CY[a]	31.93±0.46			
Age=2CY+[a]	31.48±0.44			
T_{tarsus} (°C)				
T_a		2, 67.18	32.93	**<0.001**
Season		2, 68.82	15.26	**<0.001**
Season×T_a		2, 67.18	4.97	**0.001**
Season=early winter				
0°C[a]	32.12±1.71			
−10°C[a]	30.35±1.71			
−30°C[b]	23.09±1.71			
Season=late winter				
0°C[a]	32.46±1.84			
−10°C[a]	32.70±1.77			
−30°C[a]	29.98±1.77			
Season=summer				
0°C[a]	32.04±1.84			
−10°C[b]	26.41±1.92			
−30°C[c]	16.73±1.92			

Peripheral tissue temperature was measured on skin at the back (T_{back}), breast (T_{breast}), head (T_{head}) and tibiotarsus (T_{tarsus}). T_a was 0, −10 or −30°C. Different superscript letters denote statistically significant ($P \leq 0.05$) pairwise differences within each respective contrast.

and subsequently increased by 20% (+0.022 W kg^{-1} °C^{-1}) during late winter measurements (Fig. 5). Summer values (0.187± 0.003 W kg^{-1} °C^{-1}) were 70% (+0.077 W kg^{-1} °C^{-1}) and 41% (+0.055 W kg^{-1} °C^{-1}) higher than those in early and late winter, respectively. *C* developed differently over seasons for 1CY and 2CY+ birds (season×age: $P<0.001$; Table 2). Specifically, *C* was significantly higher in 1CY birds than in 2CY+ birds during both

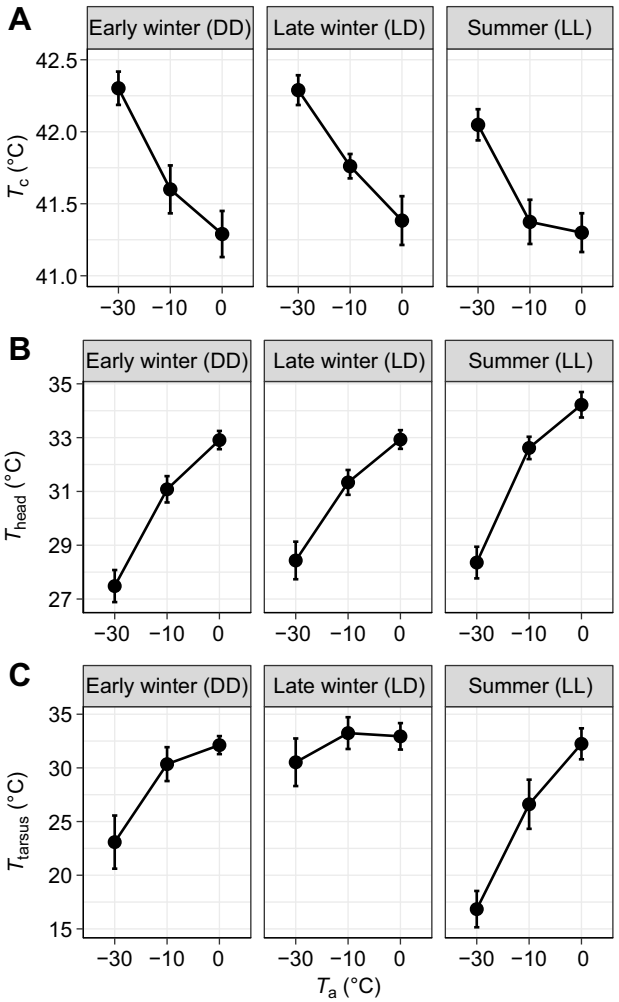

Fig. 3. T_c and cutaneous T_t (head and tibiotarsus) in relation to T_a in captive Svalbard ptarmigan in each of the three seasons. (A) T_c, (B) T_{head} and (C) T_{tarsus}. Data are means±s.e.m. Sample sizes for each T_t, at each T_a and during each season, are given in Table S1. Statistics are reported in Table 1.

Journal of Experimental Biology (2018) 221, jeb171124. doi:10.1242/jeb.171124

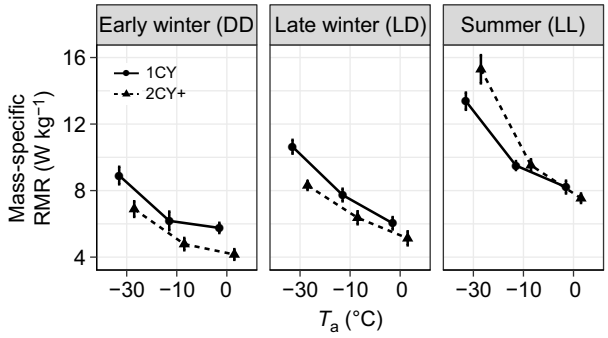

Fig. 4. Mass-specific resting metabolic rate (RMR) at different T_a in 1CY and 2CY+ captive Svalbard ptarmigan in each of the three seasons. Data are means±s.e.m. Sample sizes and statistics are reported in Table S1 and Table 2, respectively.

early (+32%; 1CY: 0.123±0.005 W kg^{-1} °C^{-1}; 2CY+: 0.093±0.004 W kg^{-1} °C^{-1}) and late (+22%; 1CY: 0.145±0.004 W kg^{-1} °C^{-1}; 2CY+: 0.119±0.004 W kg^{-1} °C^{-1}) winter, but the two age categories attained identical C in summer (Table 2, Fig. 5).

DISCUSSION

We found no evidence for substantial local heterothermy in the Svalbard ptarmigan. Even during exposure to severe cold, we observed only a relatively modest drop in leg skin temperature (i.e. T_{tarsus}; Fig. 3C), which was probably not substantial enough to significantly reduce the birds' heat loss rate. This implies that counter-current vascular arrangements are not prominent in the legs of Svalbard ptarmigan. This corroborates studies of the vascular anatomy of the rock ptarmigan leg (Midtgård, 1981). It follows that the stronger T_{tarsus} response in summer than in winter birds probably reflected a combination of the inferior insulation, the thermally unfavourable shape and the low heat production rate of this structure. Yet, it is possible that our measurements of T_{tarsus} did not capture the full biophysical relevance of counter-current heat exchange as the foot/substrate interface (i.e. the foot pad) could be a key avenue for leg heat loss. In line with this, foot pad temperatures in willow ptarmigan (*L. lagopus*) roosting at −10°C were 6–8°C (Mercer and Simon, 1987), which is well below the tibiotarsal temperatures recorded by us. Even so, the appendage heterothermic response to cold is much smaller in ptarmigan than in other sympatrically breeding species with unfeathered legs, such as glaucous gulls (*Larus hyperboreus*) and brent geese (*Branta bernicla*) (Irving and Krog, 1955). It is, thus, possible that the ca. tenfold increase in feet plumage mass and fourfold increase in feet plumage thickness (and resultant complete covering of the foot pads) in winter-acclimated Svalbard ptarmigan (A.N., B. Iudik, L.P.F. and P. L. Pap, unpublished data), reduces the need for specialized vascular adaptations in this structure.

In comparison, body trunk skin temperature was remarkably stable, varying by less than 1°C when T_a decreased to −30°C. As a result, the skin-to-environment temperature gradient was maintained near 70°C at this T_a, irrespective of the time of the year or plumage (Fig. 2). This was possible because the seasonal increase in thermal conductance (C) was fully compensated by increased thermogenesis, such that mass-specific RMR at −30°C rose (relative to RMR at 0°C) in roughly 10% increments between study periods, from +60% in early winter, via +70% in late winter, to +80% in summer (Table 2).

T_c at thermoneutrality was largely stable over the year, and was within the range of T_c found in other Galliformes (i.e. 38.2–42.5°C; Prinzinger et al., 1991). Increased T_c with decreasing T_a (Fig. 3A)

Table 2. Test statistics, degrees of freedom (Satterthwaite approximation) and *P*-values for final models of mass-specific resting metabolic rate RMR and thermal conductance, measured at each of three T_a in Svalbard ptarmigan during early winter, late winter and summer

Parameter	Estimate (s.e.)	d.f.	*F*	*P*
Mass-specific RMR (W kg^{-1})				
Season		2, 67.94	220.00	**<0.001**
T_a		2, 65.68	209.332	**<0.001**
Age		1, 8.27	6.00	**0.039**
T_a×age		2, 65.68	0.19	0.831
Season×T_a		4, 65.68	13.03	**<0.001**
Season×age		2, 67.94	13.28	**<0.001**
Season×T_a×age		4, 65.68	3.78	**0.008**
Season=early winter/age=1CY				
0°C^a	5.59±0.39			
−10°C^a	5.99±0.39			
−30°C^b	8.64±0.39			
Season=early winter/age=2CY+				
0°C^a	4.04±0.46			
−10°C^a	4.64±0.46			
−30°C^b	6.69±0.46			
Season=late winter/age=1CY				
0°C^a	5.98±0.45			
−10°C^b	7.66±0.45			
−30°C±^{c}	10.54±0.45			
Season=late winter/age=2CY+				
0°C^a	5.04±0.50			
−10°C^b	6.31±0.46			
−30°C^c	8.24±0.46			
Season=summer/age=1CY				
0°C^a	8.14±0.45			
−10°C^b	9.42±0.45			
−30°C^c	13.26±0.45			
Season=summer/age=2CY+				
0°C^a	7.48±0.46			
−10°C^b	9.44±0.46			
−30°C^c	15.17±0.46			
Total RMR (W)				
Season		2, 76.90	83.75	**<0.001**
T_a		2, 73.50	241.41	**<0.001**
Season×T_a		4, 73.50	7.39	**<0.001**
Season=early winter				
0°C^a	4.21±0.20			
−10°C^a	4.63±0.20			
−30°C^b	6.68±0.20			
Season=late winter				
0°C^a	4.71±0.23			
10°C^b	6.00±0.22			
−30°C^c	8.08±0.22			
Season=summer				
0°C^a	5.39±0.22			
10°C^b	6.52±0.22			
−30°C^c	9.80±0.22			
Conductance (W kg^{-1}°C^{-1})				
Season		2, 79.28	194.10	**<0.001**
Age		1, 9.06	8.94	**0.015**
Season×age		2, 79.28	7.70	**0.001**
Season=early winter				
Age=1CY^a	0.123±0.005			
Age=2CY+^{b}	0.093±0.006			
Season=late winter				
Age=1CY^a	0.145±0.005			
Age=2CY+^{b}	0.119±0.006			
Season=summer				
Age=1CY^a	0.187±0.005			
Age=2CY+^{a}	0.187±0.006			

T_a was 0, −10 or −30°C.
Different superscript letters denote statistically significant (P≤0.05) pairwise differences within each respective contrast.

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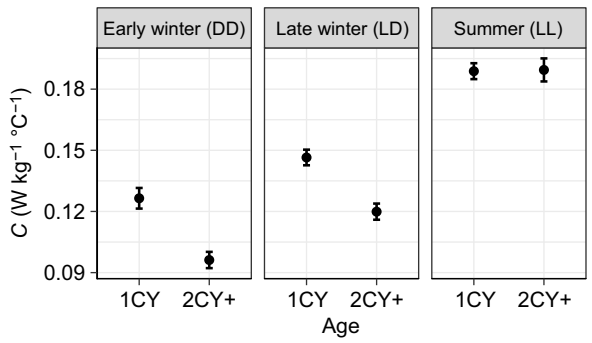

Fig. 5. Mass-specific thermal conductance (*C*) in 1CY and 2CY+ captive Svalbard ptarmigan in each of the three seasons. Data are means±s.e.m. Sample sizes for each age group and season are given in Table S1. Statistics are reported in Table 2.

has previously been observed in other medium-to-large (>500 g) birds (e.g. Schwan and Williams, 1978; Bech, 1980; Rintamäki et al., 1983). This is not normally seen in smaller (<400 g) birds (Saarela and Heldmaier, 1987; Saarela et al., 1995; Saarela and Hohtola, 2003), presumably because their more unfavourable surface area to volume ratio renders body insulation insufficient to allow their T_c to rise despite increased heat production. We believe that increased thermogenesis during cold exposure was proximately driven by brain (hypothalamic) temperature sensors that were cooled below the set point (Mercer and Simon, 1987), as judged from the significant reduction in T_{head} during cold exposure in our birds (Fig. 3B). Aside from preserving thermal balance, increased thermogenesis in the cold is probably also important to reducing predation risk, because temperature reduction in the head could come at the cost of reduced vigilance and escape speed (Rashotte et al., 1998; Carr and Lima, 2013). In line with this, minimum T_{head} was largely stable between seasons (Fig. 3B), even in summer when the head plumage was only one-third the mass and half the thickness of winter values (A.N. et al., unpublished data).

Specific RMR at 0°C, assumed to represent thermoneutrality (Mortensen and Blix, 1986), was consistently higher than the predicted phylogeny-corrected specific basal metabolic rate (*sensu* Reynolds and Lee, 1996) (early winter: +19%; late winter: +34%; summer: +74%). Previous measurements of specific thermoneutral RMR in the Svalbard ptarmigan fall closer to predicted values (range: −7% to +20%; Mortensen and Blix, 1986). These differences might be explained if our birds were, in fact, below their lower critical temperature at 0°C. The 40% increase in specific RMR at 0°C from late winter to summer (Fig. 4) could, thus, be a thermogenic response as a result of the inferior insulation of the summer plumage (A.N. et al., unpublished data), perhaps in combination with a general upregulation of metabolic activity due to increased food processing (Fig. 1D), and preparation for reproduction and for the approaching onset of winter moult.

Minimum C was 0.093±0.004 W kg^{-1} °C^{-1} in 2CY+ birds in early winter (Fig. 5), which is comparable to the 0.091± 0.003 W kg^{-1} °C^{-1} recorded for Svalbard ptarmigan at the same time of the year by Mortensen and Blix (1986). C subsequently increased 20% from early to late winter, which is lower than the 39% increase estimated by Mortensen and Blix (1986). Different seasonal responses in these studies might be explained by the lower reduction of subcutaneous fat reserves in our study (5 g; 0.6% of total body mass) compared with that reported by Mortensen and Blix (1986) (80 g; 11% of total body mass). Continued depletion of fat reserves (Fig. 1C) might also explain why we observed a subsequent 41% increase in C between late winter and summer (Fig. 5), whereas Mortensen and Blix (1986) observed no significant difference between fat-free birds in winter and summer plumages (0.127±0.004 W kg^{-1} °C^{-1} and 0.120± 0.007 W kg^{-1} °C^{-1} for late winter and summer, respectively). Nevertheless, as body coat mass and plumage thickness in summer-acclimated Svalbard ptarmigan are considerably lower than in winter (A.N. et al., unpublished data), inferior plumage insulation most probably also contributed to increased C in summer birds.

First-winter (1CY) birds had higher C than 2CY+ birds in both early and late winter (Fig. 5). As C is directly proportional to RMR (Eqn 6), this difference is probably related to the higher mass-specific RMR in 1CY winter birds (at all T_a; Fig. 4). The higher RMR of 1CY in part reflects that they were still in growth in winter, as judged from their lower body masses compared with those of 2CY+ birds (Fig. 1B), as it is well established that immature, growing, homeotherms generally maintain higher specific metabolic rates compared with mature conspecifics (Kleiber, 1961). The difference in C between age classes could also partly be explained by the considerably higher levels of subcutaneous fat in 2CY+ birds (Fig. 1C; see also Mortensen et al., 1983), which fits the observation of converging C between age groups coincident with seasonally converging fat levels (Figs 1C, 5). Yet, the age-wise difference in C increased only 10% between early and late winter, at the same time as differences in fat reserves between the age classes decreased by 59% (Fig. 1C). This indicates that there are inherent differences in insulation between 1CY and 2CY+ birds. We propose that this can be explained by differences in plumage properties, because 1CY birds must first approach adult size before commencing winter preparations, which is supported by the later timing of prime body condition in these birds (Fig. 1B,C). This may leave less time and resources for moulting into a high-quality winter coat (cf. Broggi et al., 2011), which may constrain plumage development (Lindström et al., 1993) and increase metabolic maintenance costs in winter (Nilsson and Svensson, 1996). In line with this, we observed no variation in C between age categories in summer (Fig. 5), when there were no differential time constraints on moult and when both age categories appeared to be physically mature.

Conclusions

We have shown that the Svalbard ptarmigan does not use extensive local heterothermy to limit the energy requirements for thermoregulation. Instead, this bird seems to rely on effective thermogenesis and excellent body insulation for maintaining a close to invariable body temperature over a wide range of T_a, both centrally (T_c) and in peripheral tissues (T_t). This thermoregulatory strategy more closely resembles that of lower latitude relatives (e.g. Rintamäki et al., 1983; Marjakangas et al., 1984) than that of high-latitude mammals and (some) seabirds. Nevertheless, the Svalbard ptarmigan, much like other polar animals, is extremely well adapted to 'life on the edge' (Blix, 2005; 2016).

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.N., L.P.F.; Methodology: A.N., L.P.F.; Software: A.N., L.P.F.; Validation: A.N.; Formal analysis: A.N., L.P.F.; Investigation: A.N., L.P.F.; Data

curation: A.N.; Writing - original draft: A.N.; Writing - review & editing: A.N., L.P.F.; Visualization: A.N., L.P.F.; Project administration: A.N.; Funding acquisition: A.N.

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Data availability
Data are deposited in figshare (https://doi.org/10.6084/m9.figshare.5537281.v1).

Supplementary information
Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.171124.supplemental

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