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 (Ta between 0 and −30°C) during three seasons (early winter, late winter, summer), whilst recording resting metabolic rate (RMR), core temperature (Tc) 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 Ta decreased from 0 to −30°C. At the same time, Tc 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 −15°C than at 0°C. Thermal conductance in winter was higher in yearlings, 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 −15°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 (Tc) 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 (Tt) 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 Tc/Tt 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 Tc decrease; Geiser, 2004), and so could substantially increase overwinter survival (Brodin et al., 2017). Larger, non-hibernating, homeotherms (>500 g) typically maintain a stable Tc during cold exposure (but see Harlow, 1981), and instead reduce the body surface-to-environment thermal gradient through local heterothermy: a substantial decrease in Tc 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 (Ta) (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 O2 and substrate) as well as in local Tc (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 Tc.

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 Td 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 Tc 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 Tc, Td 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.
(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., Schweningen,
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 food (Agrimex, Trøstad, 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)
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 (Tc, Ti) 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) Tc in the colon
by inserting the thermocouple 70 mm into the cloaca, and then
equipped birds to measure cutaneous (surface) Ti at four additional
sites; (2) in the dorsal scapular area (Tback); (3) over the breast
muscle (Tbreast), which is the main heat-producing tissue in birds
(Aulie, 1976); (4) at the tibiotarsus adjacent to the intratarsal joint
(Ttarsus), a key site for counter-current heat exchange in several
bird species (Midtgård, 1981); and (5) at the scalp (Tscalp) 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
polyethylene 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 51115) 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 Tc, Ti and resting metabolic rate
(RMR; by use of respirometry) responses to different Tc. 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 (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 Tc, Ti and RMR
data at expected thermoneutrality [Tc: −0.2±1.3°C (mean±s.d.)],
close to, but below, the lower critical temperature (Tc: −10.2±0.4°C),
and far below thermoneutrality (Tc: −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 Tc
(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
before the start of the experiment, and each bird was measured
as detailed above
Measurement of RMR

In early winter, O2 consumption and CO2 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, O2 consumption was measured using a S3-A oxygen analyser (Applied Electrochemistry, Pittsburgh, PA, USA), and CO2 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 O2 analysers against ambient air (20.95% O2 and 100% N2 (i.e. 0% O2), and also using the N2-dilution technique (Fedak et al., 1981), the last forming the basis for correcting for between-instrument variation in the accuracy of O2 measurement, as outlined below. The CO2 analysers were calibrated against 100% N2 and 1% CO2. 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 O2 measurement

We used the N2 dilution technique (Fedak et al., 1981), with a N2 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 O2 measurement, and derived adjusted RMR values according to:

$$RMR_{adj} = \frac{RMR}{\sum_{i=1}^{n} \frac{\Delta O_2_{obs,i}}{\Delta O_2_{pred,i}}} / N,$$

where RMR$adj$ is RMR adjusted for between-instrument variation, \(\Delta O_2\) is the measured (\(\Delta O_2_{obs}\)) or predicted (\(\Delta O_2_{pred}\)) change in fractional O2 during N2 dilution, and N is the total number of N2 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):

$$f_{STP} = f_s \times \frac{T_{gas} \times 760}{273.15 \times BP},$$

where \(f_s\) 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):

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

where RH is relative humidity of the sample gas and $T_{gas}$ is gas temperature in °C. We then calculated the rate of O2 consumption and CO2 production following Eqs 4 and 5, respectively (Lighton, 2008):

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

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

where $\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$ are O2 consumption and CO2 production rate in ml min$^{-1}$, $F_{I_{O_2}}$ and $F_{E_{O_2}}$ are the fractional O2 concentration in influent and effluent air, and $F_{E_{CO_2}}$ and $F_{I_{CO_2}}$ are the fractional CO2 concentration in effluent and influent air, respectively. O2 consumption was converted to energy consumption (W) assuming an oxygoule equivalent of 20 J ml$^{-1}$ O2 (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 $T_a$: 2; $T_{back}$: 0; $T_{breast}$: 5; $T_{head}$: 14; $T_{anus}$: 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:

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

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 $T_a$, $T_a$ 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 $T_a \times season \times age$ (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 $T_a \times measurement$ 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.
criterion (AIC) (Zuur et al., 2009). The simplest random structure, i.e. a random intercept for bird id, was preferred in all cases (mean ΔAICalternative-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 LMERConvenienceFunctions; https://CRAN.R-project.org/package=LMERConvenienceFunctions). 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 ⁰Tₐ or age groups, or within seasons within age groups between ⁰Tₐ 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 ⁰Tₐ (41.71±0.14°C) across seasons and ⁰Tₐ was consistently higher than peripheral ⁰Tₐ (⁰Tback: 37.44±0.27°C; ⁰Tbreast: 37.26±0.24°C; ⁰Thead: 31.04±0.80°C; ⁰Ttarsus: 28.66±1.85°C) (Fig. 2). Accordingly, on average, birds maintained ⁰Tₐ: 4.65±0.22°C above body trunk skin (i.e. ⁰Tback and ⁰Tbreast), 10.78±0.57°C above ⁰Thead, and 13.30±1.32°C above ⁰Ttarsus (Fig. 2).

⁰Tₐ was about 0.2°C lower in summer than in winter, and consistently increased with decreasing ⁰Tₐ (Table 1; Fig. 3A). On average, ⁰Tₐ 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× ⁰Tₐ: P<0.003; Table 1). ⁰Tₐ 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 ⁰Tₐ 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, ⁰Tₐ was significantly different between all ⁰Tₐ when birds were exposed to the increasing ⁰Tₐ 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, ⁰Tback 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 ⁰Tₐ (Table 1). ⁰Tback also varied between seasons depending on bird age (season×age: P=0.007) (Table 1). In 1CY birds, mean ⁰Tback 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 ⁰Tback in early and late winter (37.17±0.38°C and 36.96±0.39°C, respectively), but increased ⁰Tback by 1°C in summer (Table 1).

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

⁰Tₐ was markedly affected by ⁰Tₐ 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). ⁰Thead 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 ⁰Thead in early winter (1CY: 29.61±0.44°C; 2CY+: 31.42±0.42°C), such that the seasonal increase in ⁰Thead was larger in this group (Table 1).

⁰Ttarsus decreased with ⁰Tₐ 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×⁰Tₐ: P<0.001) (Table 1; Fig. 3C). ⁰Ttarsus 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 (32.09±1.71°C). In contrast, there was no significant effect of ⁰Tₐ in late winter (Table 1; Fig. 3C). ⁰Ttarsus 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).

Mass-specific RMR, total RMR and thermal conductance

Mass-specific RMR (across age categories) at ⁰Tₐ 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 ⁰Tₐ in early and late winter, but not in summer (Fig. 4). Moreover, the proportional response to a drop in ⁰Tₐ from 0°C to −30°C, differed between the age groups in a season-dependent manner (season×⁰Tₐ×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 (4.10±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 ⁰Tₐ 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)
### Table 1. Test statistics, degrees of freedom (Satterthwaite approximation) and P-values for final models of core ($T_c$) and peripheral cutaneous tissue ($T_h$) temperature measured in Svalbard ptarmigan at each of three ambient temperatures ($T_a$) during early winter, late winter and summer.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate (±s.e.)</th>
<th>d.f.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_c$ (°C)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Early winter$^a$</td>
<td>41.71±0.10</td>
<td>2, 75.53</td>
<td>3.29</td>
<td>0.043</td>
</tr>
<tr>
<td>Late winter$^a$</td>
<td>41.78±0.10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer$^a$</td>
<td>41.54±0.10</td>
<td></td>
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<td>Measurement order</td>
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</tr>
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<tr>
<td>Measurement order=0 to −30°C</td>
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<td>0°C$^a$</td>
<td>41.41±0.12</td>
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<tr>
<td>Measurement order=−30 to 0°C</td>
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<td>−10°C$^a$</td>
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</tr>
<tr>
<td>Measurement order=−30 to 0°C</td>
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<td>−30°C$^b$</td>
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<tr>
<td>$T_h$ (°C)</td>
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<td></td>
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<tr>
<td>Season</td>
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<td></td>
</tr>
<tr>
<td>Early winter$^a$</td>
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<td>2, 72.77</td>
<td>6.32</td>
<td>0.003</td>
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<tr>
<td>Late winter$^a$</td>
<td>41.40±0.16</td>
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<tr>
<td>Summer$^a$</td>
<td>42.40±0.16</td>
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<tr>
<td>$T_{head}$ (°C)</td>
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<tr>
<td>Season</td>
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</tr>
<tr>
<td>Early winter$^a$</td>
<td>37.83±0.26</td>
<td>2, 79.07</td>
<td>17.05</td>
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<tr>
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<tr>
<td>Summer$^a$</td>
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<tr>
<td>$T_{breast}$ (°C)</td>
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<tr>
<td>Season</td>
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</tr>
<tr>
<td>Early winter$^a$</td>
<td>36.27±0.36</td>
<td>2, 77.12</td>
<td>17.01</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Late winter$^a$</td>
<td>36.96±0.39</td>
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</tr>
<tr>
<td>Summer$^a$</td>
<td>38.07±0.38</td>
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<tr>
<td>$T_{tarsus}$ (°C)</td>
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<td></td>
<td></td>
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<tr>
<td>Season</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Early winter$^a$</td>
<td>31.93±0.46</td>
<td>2, 67.23</td>
<td>6.71</td>
<td>0.002</td>
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<tr>
<td>Late winter$^a$</td>
<td>31.48±0.44</td>
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### Table 1. Continued

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<th>d.f.</th>
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<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season×late winter</td>
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<td></td>
</tr>
<tr>
<td>$0°C^a$</td>
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</tr>
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<td>$-10°C^a$</td>
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<td>$-30°C^a$</td>
<td>29.98±1.77</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Season×summer</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>$0°C^a$</td>
<td>32.04±1.84</td>
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<td></td>
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<tr>
<td>$-10°C^a$</td>
<td>26.41±1.92</td>
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<td></td>
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</tr>
<tr>
<td>$-30°C^a$</td>
<td>16.73±1.92</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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 to −30°C. Different superscript letters denote statistically significant ($P$<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. $T_h$ and cutaneous $T_c$ (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 $T_h$ at each $T_a$ and during each season, are given in Table S1. Statistics are reported in Table 1.
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. $T_{\text{tarsus}}$; 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 $T_{\text{tarsus}}$ 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 $T_{\text{tarsus}}$ 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. Ludik, 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).

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

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**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.**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Estimate (s.e.)</th>
<th>d.f.</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
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<tr>
<td>Mass-specific RMR (W kg$^{-1}$)</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>early winter/age=1CY</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0°C</td>
<td>5.99±0.39</td>
<td>220.0</td>
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<td></td>
</tr>
<tr>
<td>−10°Ca</td>
<td>5.99±0.39</td>
<td>209.33</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>−30°Cb</td>
<td>8.64±0.39</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season×age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0°Ca</td>
<td>5.98±0.45</td>
<td>7.66±0.45</td>
<td>0.008</td>
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</tr>
<tr>
<td>−10°Cb</td>
<td>7.66±0.45</td>
<td>10.54±0.45</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>−30°Ce</td>
<td>10.54±0.45</td>
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<tr>
<td>Season=late winter/age=1CY</td>
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<tr>
<td>0°Ca</td>
<td>8.14±0.45</td>
<td>9.42±0.45</td>
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<tr>
<td>−10°Cb</td>
<td>9.42±0.45</td>
<td>13.26±0.45</td>
<td>&lt;0.001</td>
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<tr>
<td>−30°Cc</td>
<td>13.26±0.45</td>
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<tr>
<td>Season=late winter/age=2CY+</td>
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<tr>
<td>0°Ca</td>
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<td>Total RMR (W)</td>
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<tr>
<td>Season</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>early winter</td>
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<td>0°C</td>
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<tr>
<td>−30°Cb</td>
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</tr>
<tr>
<td>late winter</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0°Ca</td>
<td>4.71±0.23</td>
<td>6.00±0.22</td>
<td>0.001</td>
<td></td>
</tr>
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<td>8.08±0.22</td>
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<tr>
<td>−30°Cc</td>
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</tr>
<tr>
<td>summer</td>
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<td>0°Ca</td>
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<td>Conductance (W kg$^{-1}$°C$^{-1}$)</td>
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<td>Season</td>
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<td></td>
</tr>
<tr>
<td>early winter</td>
<td></td>
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</tr>
<tr>
<td>Age=1CY</td>
<td>0.123±0.005</td>
<td>0.093±0.006</td>
<td>0.001</td>
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</tr>
<tr>
<td>Age=2CY+</td>
<td>0.145±0.005</td>
<td>0.119±0.006</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>late winter</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age=1CY</td>
<td>0.187±0.005</td>
<td>0.187±0.006</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>Age=2CY+</td>
<td>0.187±0.006</td>
<td></td>
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</tbody>
</table>

$T_a$ was 0, −10 or −30°C. Different superscript letters denote statistically significant ($P$<0.05) pairwise differences within each respective contrast.
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 $T_a$ 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 $T_{\text{head}}$ 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 $T_{\text{head}}$ 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 ($T_p$). 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

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

Supplementary information
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