

1 Seasonal variation in the thermal responses to changing environmental temperature in the world's
2 northernmost landbird

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18 Running head : Thermoregulation in the world's northernmost landbird

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21 **ABSTRACT**

22 Arctic homeotherms counter challenges at high latitudes using a combination of seasonal adjustments
23 in pelage/plumage, fat deposition, and intricate thermoregulatory adaptations. However, there are still
24 gaps in our understanding of their thermal responses to cold, particularly in Arctic birds. Here, we
25 have studied the potential use of local heterothermy (i.e., tissue cooling that can contribute to
26 significantly lower heat loss rate) in Svalbard ptarmigan (*Lagopus muta hyperborea*) – the world’s
27 northernmost landbird. We exposed birds kept under simulated Svalbard photoperiod to low ambient
28 temperatures (T_a ; between 0 and -30°C) during three seasons (early winter, late winter, summer),
29 whilst recording resting metabolic rate (RMR), core temperature (T_c) and several cutaneous
30 temperatures. Leg skin temperature varied the most, but still only by up to $\sim 15^{\circ}\text{C}$, whereas body trunk
31 skin temperature changed $< 1^{\circ}\text{C}$ when T_a decreased from 0 to -30°C . At the same time, T_c increased by
32 0.9°C , concomitant with increased RMR. This was likely driven by triggering of cerebral
33 thermosensors in response to cooling of the poorly insulated head, the skin of which was 5.4°C colder
34 at -30°C than at 0°C . Thermal conductance in winter was higher in yearlings, probably because they
35 were time/resource constrained from acquiring a high-quality plumage and sufficient fat reserves due
36 to concomitant body growth. In conclusion, Svalbard ptarmigan do not employ extensive local
37 heterothermy for cold protection, but instead rely on efficient thermogenesis combined with excellent
38 body insulation. Hence, cold defence in the world’s northernmost landbird is not mechanistically
39 much different from that of lower latitude relatives.

40

41 *Keywords:* Arctic, heterothermy, heat loss rate, peripheral temperature, seasonal acclimatization,
42 thermoregulation

43

44 **Summary statement**

45 The Svalbard ptarmigan, much like low-latitude birds but unlike sympatric homeotherms, do not
46 employ extensive local heterothermy for cold protection. Instead, these birds maintain prime-quality
47 insulation; a feature shared with many other High-Arctic homeotherms.

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51 **INTRODUCTION**

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

68

69 Strong selection for energy conservation is also the reason for why many non-hibernating animals in
70 seasonal biomes are not obligate homeotherms, but instead allow T_c/T_t to decrease in the whole
71 (torpor, rest-phase hypothermia), or in parts of the body (local heterothermy) during inactivity.
72 Reducing the thermal gradient towards the environment lowers the need for metabolic heat
73 production: heat is lost at a slower rate and, hence, less energy is required to maintain heat balance.
74 Colder tissues also have lower metabolic demands. Torpor and rest-phase hypothermia are frequently
75 used by many small mammals and birds, e.g. in response to deteriorating environmental conditions
76 and lower nutritional status (e.g. Nord et al. 2009; 2011). This may reduce resting energy expenditure
77 to 10 – 30 % of normal levels (depending on the extent of T_c decrease; Geiser 2004), and so could
78 substantially increase overwinter survival (Brodin et al. 2017). Larger, non-hibernating, homeotherms
79 (> 500 g) typically maintain a stable T_c during cold exposure (but see Harlow 1981), and instead
80 reduce the body surface-to-environment thermal gradient through local heterothermy; a substantial
81 decrease in T_t in the extremities and/or body periphery that is under vasomotor control (e.g. Irving and
82 Krog 1955). This is an important avenue for energy conservation (Scholander et al. 1950), and likely
83 explains how some well-insulated mammals can endure extreme cold without increasing metabolism
84 above basal levels (cf. Nilssen et al. 1984; Folkow & Mercer 1986).

85

86 Local heterothermy also occurs in birds, studied mostly in the legs of aquatic birds where elaborate
87 counter-current heat-exchange systems (Midtgård 1981; 1989) allow both low- and high latitude

88 species to regulate and maintain foot temperature at, or close to, ambient temperature (T_a) (Irving and
89 Krog 1955). This reduces heat loss at the same time as adequate nutritional blood supply can be
90 maintained to feet tissues. Seabirds may also display local heterothermy in appendages or the body
91 trunk when diving (Bevan et al. 1997; Handrich et al. 1997; Ponganis et al. 2003; but see Enstipp et al.
92 2005). This is presumably part of their diving responses, which include massive peripheral
93 vasoconstriction causing a drop in local energy expenditure (due to reduced supply of blood-borne O_2
94 and substrate) as well as in local T_t (due to lower metabolism and reduced inflow of warm blood,
95 hence causing lower heat loss rates), both of which would contribute to extending dive duration
96 (Scholander 1940). By comparison, the occurrence and possible energetic significance of local
97 heterothermy in landbirds has received little attention, although Ekimova (2005) report that fasting
98 pigeons (*Columba livia* Gmelin, 1789) reduce leg skin temperature to near T_a .

99

100 Here, we have studied the potential use of local heterothermy in a bird at the extreme of its range; the
101 Svalbard ptarmigan (*Lagopus muta hyperborea* Sundevall, 1845). This rock ptarmigan (*L. muta*
102 Montin, 1781) subspecies is a year-round resident in the High Arctic Svalbard archipelago (77 –
103 81°N) and, as such, it is the world's northernmost resident landbird. Not surprisingly, the Svalbard
104 ptarmigan experiences an extreme environment throughout its annual cycle, where the sun does not
105 rise above the horizon for more than three months in winter but is continuously above the horizon
106 from early April until mid-August, and where average T_a is below freezing for nine months of the
107 year. Metabolic fuel is acquired from low-growing tundra vegetation (Mortensen et al. 1983), which is
108 frequently deeply embedded in ice or snow in winter. Therefore, these birds display seasonal cycles in
109 body composition, building fat stores in summer/autumn times of plenty that may be drawn upon
110 during periods of reduced food availability (Mortensen *et al.* 1983; Mortensen and Blix 1985).
111 However, like many larger birds, the Svalbard ptarmigan (and other related species) maintain
112 normothermic T_c even in severe cold (Irving and Krog 1954; Mortensen and Blix 1986). The
113 combination of a harsh year-round environment and presumable lack of torpor/rest-phase hypothermia
114 renders the Svalbard ptarmigan a suitable model for studies of local heterothermy. Accordingly, we
115 measured T_c , T_t and metabolic responses to experimental cold exposure (between 0 and -30°C) in
116 captive Svalbard ptarmigan, kept indoors under a simulated Svalbard photoperiod, to study the thermal
117 responses to experimental cold exposure in this bird. In particular, we were interested to see if
118 Svalbard ptarmigan routinely employ extensive local heterothermy of a sufficient magnitude to
119 significantly lower heat loss rate in the cold (here defined as marked peripheral cooling with
120 superficial tissue/appendage temperatures approaching 0 °C). Subjects were either in their first winter
121 (when they must divide resources between growth and winter acclimatization), or in their second
122 winter, or older (when they are physically mature). The experiment was performed at three time-points
123 spread over the birds' annual cycle, coincident with large natural variation in photoperiod, food intake,
124 body condition and fasting resistance (Fig. 1). Specifically, birds were measured: 1) in early winter in

125 constant darkness (DD), when they were in their prime body condition (Figs. 1B-C), but food intake
126 was decreasing (Fig. 1D), presumably as a result of a seasonally regulated and hormonally mediated
127 decrease in appetite (Stokkan et al. 1986; Reiherth et al. 1999); 2) in late winter under 15 h light and 9
128 h dark (LD), when body condition was still high and appetite was on the increase (Figs. 1B-D), but
129 summer moult had not yet begun; and 3) in summer in constant light (LL), when body condition was
130 at its lowest and birds had moulted into their summer plumage, while food intake was near its annual
131 peak (Figs. 1B-D; see also Stokkan et al. 1986). We predicted the greatest extent of peripheral cooling,
132 and the largest energy costs of thermoregulation in response to experimental cold exposure, to be
133 manifested in summer-adapted birds (measurement period 3), which should be the least equipped to
134 counter a cold challenge. In analogy, we predicted peripheral cooling to be used to the lowest extent
135 under similar cold exposure in early winter-adapted birds (measurement period 1, as defined above),
136 when these were better protected from cold *via* the more insulating winter plumage and considerable
137 amounts of subcutaneous fat (Mortensen et al. 1983; Mortensen and Blix 1986; see also Fig. 1C). We,
138 finally, predicted that transition from early to late winter (measurement period 2) would lead to an
139 increased extent of peripheral cooling and higher costs of thermoregulation in response to cold
140 exposure, due to reduced body condition and fasting resistance (Fig 1B-C).

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143 **MATERIALS AND METHODS**

144 **Birds and housing**

145 Twelve male Svalbard ptarmigan were used in the study. Seven of these were captured as chicks (body
146 mass at capture: 46 to 435 g depending on developmental stage) near Longyearbyen, Svalbard (78°13'
147 N, 15°38' E), in August 2014 (i.e., 3 to 4 months before the start of the experiment; age category
148 1CY) under permissions issued by the Governor of Svalbard (permit no. 2014/00290-2 a.522-01) and
149 the Norwegian Food Safety Authority (permit no. 2014/150134) , whereas the remaining five (all \geq 2
150 years old; age category 2CY+) originated from a captive population (founded 1997) in the approved
151 animal research facility at the Department of Arctic and Marine Biology, University of Tromsø,
152 Norway. Ten birds (wild-caught: 5; captive: 5) were measured during all seasons, but 2 wild-caught
153 birds were measured only during early winter as they were subsequently allocated to the breeding
154 population (Table S1). There were two sibling pairs amongst the wild-caught birds (i.e., the total of
155 seven birds originated from five families), whereas the captive bred birds were all unrelated. Previous
156 work has shown that the morphological and physiological changes associated with winter
157 acclimatization/acclimation do not differ between captive and wild-caught Svalbard ptarmigan as long
158 as captive birds are maintained under a simulated Svalbard photoperiod (e.g. Stokkan et al. 1986;
159 Lindgård and Stokkan 1989). Ethical approval of experiments was issued by the Norwegian Food
160 Safety Authority (permit no. 6639).

161

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

175

176 **Measurement of body temperature and experimental protocol**

177 We measured body temperature- (T_c , T_t) and metabolic responses to cold exposure (0 to $-30^\circ C$) during
178 three discrete periods (Fig. 1): 1) early winter, when birds were under DD and subcutaneous fat
179 deposits were the largest (body mass: 758.0 ± 12.9 g [1CY] / 1043.7 ± 15.1 g [2CY+]; dissectible fat:
180 106.5 ± 6.5 g [1CY] / 251.1 ± 7.6 g [2CY+]); 2) late winter, when birds were under LD 15:9 and still
181 carried significant fat reserves (body mass: 811.4 ± 23.4 g [1CY] / 929.1 ± 20.7 g [2CY+]; dissectible
182 fat: 133.5 ± 11.8 g [1CY] / 193.1 ± 10.5 g [2CY+]); and 3) summer, when birds were under LL, in
183 summer plumage, and fat reserves were at the yearly nadir (body mass: 712.4 ± 21.2 g [1CY] / $679.8 \pm$
184 11.6 g [2CY+]; dissectible fat: 83.5 ± 10.7 g [1CY] / 67.0 ± 5.9 g [2CY+]).

185

186 Birds were measured during daytime (starting at $09:51$ am ± 37 min (SD); local Tromsø time). At the
187 start of a measurement session, birds were collected from their cages, weighed, and then immediately
188 brought to an adjacent laboratory where they were instrumented with 36-gauge type T (copper-
189 constantan) thermocouples (Omega Engineering, Stamford, CT, USA) for temperature measurement.
190 All thermocouples (tc) were attached by the same person (AN). Specifically, we measured 1) T_c in the
191 colon by inserting the tc 70 mm into the cloaca, and then equipped birds to measure cutaneous
192 (surface) T_t 's at four additional sites. *viz.*: 2) in the dorsal scapular area (T_{back}); 3) over the breast
193 muscle (T_{breast}), which is the main heat-producing tissue in birds (Aulie 1976); 4) at the tibiotarsus
194 adjacent to the intratarsal joint (T_{tarsus}); a key venue for counter-current heat exchange in several bird
195 species (Midtgård 1981); and 5) at the scalp (T_{head}), to measure a potential proxy for temperature
196 change in the more sparsely insulated head/brain. All cutaneous thermocouples (2-5) were attached
197 onto the skin surface using cyanoacrylate glue (Loctite[®] Power Easy gel, Henkel, Düsseldorf,
198 Germany). A 2×7 mm rectangular piece of surgical tape was attached to the end of the thermocouple

199 (leaving the thermosensitive junction bare) to increase the area of adhesion. The cloacal thermocouple
200 (tc 1) was covered by a blunted 10 cm polythene catheter (\varnothing 1.22 mm; Fortex Engineering, Lincoln,
201 UK) and was secured to the tail feathers using surgical tape. Thermocouples were carefully threaded
202 through the plumage and collated in a bundle contained in silicone tubing, such that no individual
203 wires protruded from the body. All thermocouples were calibrated at 0°C (Ice point drywell model
204 5115) and 40°C (High precision bath model 6025, both Fluke Calibration, American Fork, UT, USA)
205 prior to use. Instrumentation during DD was performed under illumination from a red-light head torch.

206

207 Birds were subsequently put into a 43.2 l (early winter) or 33.6 l (late winter, summer) transparent
208 Plexiglas chamber located inside a climatic chamber (model 24/50 DU, Weiss Technik, Giessen,
209 Germany), for measurement of T_c , T_t and resting metabolic rate (RMR; by use of respirometry)
210 responses to different T_a 's. To ensure that the bird could move around freely, we attached the silicone-
211 encased thermocouple bundle to a lightweight spring connected to a swivel in the centre of the
212 chamber roof, from where it exited the chamber through an otherwise sealed port. The chamber floor
213 was sheeted with corrugated cardboard to reduce slickness. We subsequently subjected birds to a
214 decreasing (starting at 0°C; $n = 8$ birds, of which 6 were measured during all seasons as detailed
215 above) or an increasing (starting at -30°C; $n = 4$ birds) sliding temperature protocol, during which we
216 collected T_c , T_t and RMR data at expected thermoneutrality (T_a : $-0.2 \pm 1.3^\circ\text{C}$ (SD)), close to, but
217 below, the lower critical temperature (T_a : $-10.2 \pm 0.4^\circ\text{C}$), and far below thermoneutrality (T_a : $-30.3 \pm$
218 0.3°C)(Mortensen and Blix 1986). Measurement order was randomized by coin tossing before the start
219 of the experiment, and each bird was measured in the same order during all seasons. Given the size of
220 the birds (range 595 to 1130 g; Fig. 1), we allowed them 1 h to equilibrate at each T_a (i.e., 0°C, -10°C,
221 -30°C) before we started to record experimental data for 20 min. Baseline data for ambient gas
222 composition were collected for approximately 15 min at the time, in-between measurements of RMR.
223 The air temperature inside the metabolic chamber was monitored with a 20-gauge type T
224 thermocouple (Omega Engineering) positioned in the chamber ceiling, at a height at which heat
225 produced by the bird did not affect the reading. Measurements during DD were performed in dim red
226 light ($\ll 1$ lx). A measurement session (from collection in, to subsequent return to, the cage) lasted 6.6
227 ± 0.3 h, after which we removed (tc 1) or cut the thermocouple wires at the skin surface (tc 2-5),
228 weighed the bird, and returned it to its cage. The exposure period should be adequate to detect any
229 local heterothermy, as RMR and tissue temperatures typically stabilized within 30 min of putting the
230 bird into the metabolic chamber and remained unaltered in a given T_a thereafter. By comparison, the
231 much larger, homeotherm, reindeer (*Rangifer tarandus tarandus* L. 1758) responds with substantial
232 local heterothermy (i.e., leg skin temperature dropping below 10°C) within 1-3 hour after being
233 subjected to T_a 's below their lower critical temperature (e.g., Folkow and Mercer 1986; Johnsen et al.
234 1985).

235

236

237 **Measurement of resting metabolic rate**

238 In early winter, O₂ consumption and CO₂ production were measured using a FoxBox (Sable Systems,
 239 Las Vegas, NV, USA), and flow rate was recorded with a SRT-2 mechanical flow meter (Flow Tech,
 240 Phoenix, AR, USA). During late winter and summer, O₂ consumption was measured using a S3-A
 241 oxygen analyser (Applied Electrochemistry, Pittsburgh, PA, USA), and CO₂ production was recorded
 242 using a ML206 gas analyser (AD Instruments, Sydney, Australia). Flow rate was registered with a
 243 FMA-A2317 mass flow meter (Omega Engineering). Humidity and temperature of the sample gas was
 244 measured using a HMI32 thermometer and hygrometer (Vaisala, Vanda, Finland) throughout the
 245 experiment.

246

247 We calibrated the O₂ analysers against ambient air (20.95% O₂) and 100% N₂ (i.e., 0% O₂), and also
 248 using the N₂-dilution technique (Fedak et al. 1981), the latter forming the basis for correcting for
 249 between-instrument variation in the accuracy of O₂ measurement, as outlined in Supplementary
 250 Material 1. The CO₂ analysers were calibrated against 100% N₂ and 1% CO₂. We calibrated all
 251 analysers daily, and used day-specific calibration values to convert the input signal to gas
 252 concentrations. The SRT-2 flow meter was calibrated against a DTM-325 gas meter (Elster American
 253 Meter, Nebraska City, NE, USA), whereas the FMA-A2317 mass flow meter was factory calibrated
 254 immediately prior to use. All data were recorded and digitized from raw signals using a ML796
 255 PowerLab/16SP A-D converter (AD Instruments, Sydney, Australia).

256

257 **Data handling and statistical analyses**

258 We STP-corrected flow rates from the SRT-2 flow meter according to Lighton (2008):

259
$$\text{flow}_{\text{stp}} = \text{flow}_{\text{a}} \times \frac{T_{\text{gas}} \times 760}{273.15 \times \text{BP}} \quad \text{Eqn. 1}$$

260 where flow_a is the uncorrected flow rate (ml·min⁻¹), T_{gas} is gas temperature in °K and BP is barometric
 261 pressure in mmHg (Tromsø data provided by the Norwegian Meteorological Institute). We then
 262 STPD-corrected all flow rates by subtracting flow_{H₂O} from flow_{stp}, where flow_{H₂O} was calculated
 263 following Eqn. 2 (Vaisala 2013):

264
$$\text{flow}_{\text{H}_2\text{O}} = \text{flow}_{\text{stp}} \times \frac{(\text{RH}/100) \times 4.588 \times 10^{(7.59 \times T_{\text{gas}})/(240.73 + T_{\text{gas}})}}{\text{BP}} \quad \text{Eqn. 2}$$

265 where RH is relative humidity of the sample gas, and T_{gas} is gas temperature in °C. We then calculated
 266 O₂ consumption and CO₂ production following Eqns. 3 and 4, respectively (Lighton 2008).

267
$$V_{\text{O}_2} = \text{flow}_{\text{stpd}} \times \frac{(F_{\text{iO}_2} - F_{\text{eO}_2}) - F_{\text{iO}_2} \times (F_{\text{eCO}_2} - F_{\text{iCO}_2})}{1 - F_{\text{iO}_2}} \quad \text{Eqn. 3}$$

268
$$V_{\text{CO}_2} = \text{flow}_{\text{stpd}} \times \frac{(F_{\text{eCO}_2} - F_{\text{iCO}_2}) + F_{\text{iCO}_2} \times (F_{\text{iO}_2} - F_{\text{eO}_2})}{1 + F_{\text{iCO}_2}} \quad \text{Eqn. 4}$$

269 where V_{O_2} and V_{CO_2} are O_2 consumption and CO_2 production in $ml\ min^{-1}$, F_iO_2 and F_eO_2 are the
270 fractional O_2 concentration in influent and effluent air, and F_eCO_2 and F_iCO_2 are the fractional CO_2
271 concentration in effluent and influent air. O_2 consumption was converted to energy consumption (W)
272 assuming an oxyjoule equivalence of $20\ J \cdot (ml\ O_2)^{-1}$ (Kleiber 1961).

273

274 We only used data from periods when the birds were at full rest and had completed their thermal
275 equilibration periods. If a bird did not meet the ‘rest’ requirements, we used resting data collected at
276 the relevant T_a , but outside the dedicated 20-min measurement period. Such data were used in 12 (out
277 of 95) cases. We also dismissed data from thermocouples that fell out (tc1)/off (tc 2-5) or broke (tc 1-
278 5)(for T_c : 2; T_{back} : 0; T_{breast} : 5; T_{head} : 14; T_{tarsus} : 8; respectively, out of 95 recording periods). Final
279 sample sizes for each parameter, season, T_a , and age category, are reported in Table S1.

280

281 Whole-animal thermal conductance (Aschoff 1981) was calculated in $W\ kg^{-1}\ ^\circ C^{-1}$ as:

$$282 \quad C = \frac{RMR}{m_b} / (T_c - T_a) \quad \text{Eqn. 5}$$

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

285

286 All statistical analyses were performed in R 3.3.1 (R Development Core Team 2016). We analysed all
287 bird T_c 's/ T_t 's, mass-specific RMR (i.e., RMR / body mass), total RMR, and C , with linear mixed
288 effects models (lme4 package; Bates et al. 2015). All original models included experimental period
289 (early winter, late winter, summer), T_a ($0^\circ C$, $-10^\circ C$, $-30^\circ C$), bird age (first winter [1CY], or older
290 [2CY+]), and measurement order (i.e., increasing or decreasing T_a ; see above), as main effects. The
291 original model for total RMR also included body mass as a covariate. We did not account for body
292 mass in any other models, because it co-varied with bird age in two out of three seasons (Fig. 1) but
293 varied relatively little within age classes. ‘Age’ and body mass, therefore, conveyed largely the same
294 statistical information, so adding the latter to our models was not warranted. We included the three-
295 way interaction ‘ $T_a \times$ season \times age’ (and all of its lower level interactions), to account for any
296 potential age-related differences in the seasonal effects of cold exposure on thermoregulation. In
297 addition, original models included the two-way interaction ‘ $T_a \times$ measurement order’, to account for
298 possible variation introduced by the order of temperature exposures. To account for repeated
299 sampling, we fitted four alternative random structures to the original models: 1) a random intercept for
300 ‘bird id’; 2) a random intercept (‘bird id’) and slope (T_a); 3) a random intercept for ‘bird id’ and a
301 random intercept for ‘family’ (to account for any genetic effects pertaining to the relatedness of some
302 of the birds); or 4) a random intercept/slope (‘bird id’ and T_a , respectively) and a random intercept for
303 ‘family’. We then selected the most appropriate random structure based on the Akaike Information
304 Criterion (AIC)(Zuur et al. 2009). The simplest random structure, i.e. a random intercept for ‘bird id’,

305 was preferred in all cases (mean $\Delta AIC_{\text{alternative-best fit}}$: 7.6) We derived final models by sequentially
306 excluding the model term with the lowest P -value and comparing AIC values for the full and reduced
307 models (fitted with maximum likelihood) starting with the highest order interactions and retaining
308 parameters for which $\Delta AIC > 5$ (package LMER Convenience Functions; Tremblay and Ransijn
309 2015). We then re-fitted the final model using restricted maximum likelihood (Zuur et al. 2009), and
310 calculated degrees of freedom for this model using the Satterthwaite approximation (lmerTest
311 package; Kuznetsova et al. 2016). Multiple comparisons for final models were performed on predicted
312 marginal means within 'seasons' between T_a 's or 'age groups', or within 'seasons' within 'age groups'
313 between T_a 's, as applicable (lsmeans package; Lenth 2016). We adjusted P -values for multiple
314 comparisons using the Holm-Bonferroni correction (Holm 1979). Data in tables and text are predicted
315 marginal means \pm SE, and all significances are two-tailed.

316

317

318 **RESULTS**

319 **Deep and peripheral tissue temperatures**

320 Average T_c ($41.71 \pm 0.14^\circ\text{C}$) across seasons and T_a 's was consistently higher than peripheral T_t 's
321 (T_{back} : $37.44 \pm 0.27^\circ\text{C}$; T_{breast} : $37.26 \pm 0.24^\circ\text{C}$; T_{head} : $31.04 \pm 0.80^\circ\text{C}$; T_{tarsus} : $28.66 \pm 1.85^\circ\text{C}$)(Fig. 2).
322 Accordingly, on average, birds maintained T_c $4.65 \pm 0.22^\circ\text{C}$ above body trunk skin (i.e. T_{back} and
323 T_{breast}), $10.78 \pm 0.57^\circ\text{C}$ above T_{head} , and $13.30 \pm 1.32^\circ\text{C}$ above T_{tarsus} (Fig. 2).

324

325 T_c was about 0.2°C lower in summer than in winter, and consistently increased with decreasing T_a
326 (Table 1; Fig. 3A). On average, T_c was 0.26°C higher in -10°C than in 0°C , and 0.64°C higher in -
327 30°C than in -10°C (Fig. 3A). The effect size varied with measurement order (measurement order \times
328 T_a : $P < 0.001$; Table 1). T_c did not change between 0°C ($41.41 \pm 0.12^\circ\text{C}$) and -10°C ($41.68 \pm 0.12^\circ\text{C}$)
329 when birds were subjected to the decreasing T_a protocol, and was 0.55°C ($42.10 \pm 0.12^\circ\text{C}$) higher in -
330 30°C compared to the other two temperatures (Table 1). In contrast, T_c was significantly different
331 between all T_a 's when birds were exposed to the increasing T_a protocol (-30°C : $42.40 \pm 0.16^\circ\text{C}$; -10°C :
332 $41.40 \pm 0.16^\circ\text{C}$; 0°C : $41.09 \pm 0.17^\circ\text{C}$)(Table 1).

333

334 When averaged over seasons, T_{back} did not differ between 0°C ($37.83 \pm 0.15^\circ\text{C}$) and -10°C ($37.64 \pm$
335 0.26°C), but was 1.12°C lower at -30°C ($36.62 \pm 0.26^\circ\text{C}$) relative to the other T_a 's (Table 1). T_{back} also
336 varied between seasons depending on bird age (season \times age: $P = 0.007$)(Table 1). In 1CY birds,
337 mean T_{back} was relatively similar in early winter ($37.92 \pm 0.32^\circ\text{C}$) and summer ($37.80 \pm 0.36^\circ\text{C}$), but
338 ca. 1.6°C lower in late winter ($36.27 \pm 0.36^\circ\text{C}$). In contrast, 2CY+ birds maintained a relatively stable
339 average T_{back} in early and late winter ($37.17 \pm 0.38^\circ\text{C}$ and $36.96 \pm 0.39^\circ\text{C}$, respectively), but increased
340 T_{back} by 1°C in summer (Table 1).

341

342 T_{breast} was stable across seasons and age categories, but decreased with decreasing T_a , such that T_{breast} at
343 0°C ($37.58 \pm 0.45^\circ\text{C}$) and -10°C ($37.33 \pm 0.44^\circ\text{C}$) was 1.08°C higher than T_{breast} at -30°C ($36.38 \pm$
344 0.44°C)(Table 1).

345

346 T_{head} was markedly affected by T_a , decreasing by 1.79°C between 0°C ($33.43 \pm 0.31^\circ\text{C}$) and -10°C
347 ($31.64 \pm 0.32^\circ\text{C}$), and a further 3.63°C during the transition to -30°C ($28.01 \pm 0.32^\circ\text{C}$)(Fig. 3B). T_{head}
348 also varied with season, being 0.50°C higher in late compared to early winter, and 0.66°C higher in
349 summer compared to late winter (Table 1; Fig. 3B). The seasonal effect differed between age
350 categories: 1CY maintained a significantly lower average T_{head} in early winter (1CY: $29.61 \pm 0.44^\circ\text{C}$;
351 2CY+: $31.42 \pm 0.42^\circ\text{C}$), such that the seasonal increase in T_{head} was larger in this group (Table 1).

352

353 T_{tarsus} decreased with T_a , from $32.21 \pm 1.39^\circ\text{C}$ in 0°C to $29.82 \pm 1.38^\circ\text{C}$ and $23.27 \pm 1.37^\circ\text{C}$ in -10°C
354 and -30°C , respectively. This effect differed between seasons (i.e., season $\times T_a$: $P = 0.001$)(Table 1;
355 Fig. 3C). T_{tarsus} did not differ between 0°C ($32.12 \pm 1.71^\circ\text{C}$) and -10°C ($30.35 \pm 1.71^\circ\text{C}$) in early
356 winter, but was significantly lower at -30°C ($23.09 \pm 1.71^\circ\text{C}$). In contrast, there was no significant
357 effect of T_a in late winter (Table 1; Fig. 3C). T_{tarsus} in summer was relatively similar to early and late
358 winter values in thermoneutrality ($32.04 \pm 1.92^\circ\text{C}$), but subsequently dropped by 5.63°C and 15.31°C
359 when birds were measured in -10°C ($26.41 \pm 1.92^\circ\text{C}$) and -30°C ($16.73 \pm 1.84^\circ\text{C}$), respectively (Fig.
360 3C).

361

362 **Mass-specific RMR, total RMR, and thermal conductance**

363 Mass-specific RMR (across age categories) at T_a 0°C (corresponding to expected thermoneutrality,
364 according to Mortensen & Blix 1986) increased 13% between early ($4.94 \pm 0.31 \text{ W kg}^{-1}$) and late (5.59
365 $\pm 0.30 \text{ W kg}^{-1}$) winter, and 40% between late winter and summer ($7.81 \pm 0.25 \text{ W kg}^{-1}$). Mass-specific
366 RMR was higher in 1CY than in 2CY+ birds at all T_a 's in early and late winter, but not in summer
367 (Fig. 4). Moreover, the proportional response to a drop in T_a , from 0°C to -30°C , differed between the
368 age-groups in a season-dependent manner (season $\times T_a \times$ age: $P = 0.008$)(Table 2). The proportional
369 response in 1CY birds was stronger in late winter ($+4.56 \text{ W kg}^{-1} / +77\%$) than at other times of the
370 year (early winter: $+3.05 \text{ W kg}^{-1} / +55\%$; summer: $+5.12 \text{ W kg}^{-1} / +63\%$). By contrast, the proportional
371 response in 2CY+ birds was relatively similar in early and late winter (early winter: $+2.65 \text{ W kg}^{-1} /$
372 $+66\%$; late winter: $+3.20 \text{ W kg}^{-1} / +63\%$), but considerably stronger in summer ($+7.69 \text{ W kg}^{-1} /$
373 $+103\%$)(Fig. 4). Total RMR at expected thermoneutrality (i.e., at 0°C) differed between seasons, being
374 relatively similar in early ($4.21 \pm 0.20 \text{ W}$) and late ($4.71 \pm 0.23 \text{ W}$) winter, but some 21% higher in
375 summer ($5.39 \pm 0.22 \text{ W}$). The total RMR response to a drop in T_a , from 0 to -30°C , largely followed
376 patterns in mass-specific RMR (although there was no age effect). Accordingly, total RMR in early
377 winter was 2.47 W (59%) higher at -30°C compared to at 0°C ; a difference that had increased to 3.37

378 W (72%) and 4.41 W (82%) by late winter and summer, respectively (Table 2). Body mass changes
379 throughout the study period were too small to affect total RMR ($P > 0.3$).

380

381 Average mass-specific thermal conductance across ages, C , reached its minimum average value in
382 early winter ($0.110 \pm 0.004 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$) and subsequently increased by 20% ($+0.022 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$)
383 during late winter measurements (Fig. 5). Summer values ($0.187 \pm 0.003 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$) were 70%
384 ($+0.077 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$) and 41% ($+0.055 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$) higher than in early and late winter, respectively.
385 C developed differently over seasons for 1CY and 2CY+ birds (season \times age: $P < 0.001$; Table 2).
386 Specifically, C was significantly higher in 1CY birds than in 2CY+ birds during both early (+32%;
387 1CY: $0.123 \pm 0.005 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$; 2CY+: $0.093 \pm 0.004 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$) and late (+22%; 1CY: $0.145 \pm$
388 $0.004 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$; 2CY+: $0.119 \pm 0.004 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$) winter, but both age categories attained identical
389 C in summer (Table 2; Fig. 5).

390

391

392 **DISCUSSION**

393 We found no evidence for substantial local heterothermy in the Svalbard ptarmigan. Even during
394 exposure to severe cold, we observed only a relatively modest drop in leg skin temperature (i.e., T_{tarsus} ;
395 Fig. 3C), which was likely not substantial enough to significantly reduce the birds' heat loss rate. This
396 implies that counter-current vascular arrangements are not prominent in the legs of Svalbard
397 ptarmigan. This corroborates studies of the vascular anatomy of the rock ptarmigan leg (Midtgård
398 1981). It follows that the stronger T_{tarsus} response in summer than in winter birds likely reflected a
399 combination of the inferior insulation, the thermally unfavourable shape, and the low heat production
400 rate of this structure. Yet, it is possible that our measurements of T_{tarsus} did not capture the full
401 biophysical relevance of counter-current heat exchange since the foot/substrate interface (i.e., the foot
402 pad) could be a key avenue for leg heat loss. In line with this, foot pad temperatures in willow
403 ptarmigan (*L. lagopus* Linnaeus, 1758) roosting at -10°C were $6\text{-}8^\circ\text{C}$ (Mercer and Simon 1987), which
404 is well below the tibiotarsal temperatures recorded by us. Even so, the appendage heterothermic
405 response to cold is much smaller in ptarmigan than in other sympatrically breeding species with
406 unfeathered legs, such as glaucous gulls (*Larus hyperboreus* Gunnerus, 1767) and brent geese (*Branta*
407 *bernicle* Linnaeus, 1758)(Irving and Krog 1955). It is, thus, possible that the ca. tenfold increase in
408 feet plumage weight and fourfold increase in feet plumage thickness (and resultant complete covering
409 of the foot pads) in winter-acclimated Svalbard ptarmigan (Nord et al., unpublished data.), reduces the
410 need for specialized vascular adaptations in this structure.

411

412 In comparison, body trunk skin temperature was remarkably stable, varying by less than 1°C when T_a
413 decreased to -30°C . As a result, the skin-to-environment temperature gradient was maintained near
414 70°C at this T_a , irrespective of time of the year or plumage (Fig. 2). This was possible because the

415 seasonal increase in thermal conductance (C) was fully compensated by increased thermogenesis, such
416 that mass-specific RMR at -30°C rose (relative to RMR at 0°C) in roughly 10% increments between
417 study periods, from +60% in early winter, *via* +70% in late winter, to +80% in summer (Table 2).

418

419 T_c at thermoneutrality was largely stable over the year, and within the range of T_c 's found in other
420 galliformes (i.e., $38.2\text{-}42.5^{\circ}\text{C}$; Prinzinger et al. 1991). Increased T_c with decreasing T_a (Fig. 3A) has
421 previously been observed in other medium-to-large (> 500 g) birds (e.g. Schwan and Williams 1978;
422 Bech 1980; Rintamäki et al. 1983). This is not normally seen in smaller (< 400 g) birds (Saarela and
423 Heldmaier 1987; Saarela et al. 1995; Saarela and Hohtola 2003), presumably because their more
424 unfavourable surface-area-to-volume-ratio renders body insulation insufficient to allow their T_c to rise
425 despite increased heat production. We believe that increased thermogenesis during cold exposure was
426 proximately driven by brain (hypothalamic) temperature sensors that were cooled below set-point
427 (Mercer and Simon 1987), as judged from the significant reduction in T_{head} during cold exposure in our
428 birds (Fig. 3B). Aside from preserving thermal balance, increased thermogenesis in the cold is likely
429 also important to reducing predation risk, because temperature reduction in the head could come at the
430 cost of reduced vigilance and escape speed (Rashotte et al. 1998; Carr and Lima 2013). In line with
431 this, minimum T_{head} was largely stable between seasons (Fig. 3B), even in summer when the head
432 plumage was only one third in mass, and half in thickness, compared to winter conditions (Nord *et al.*,
433 unpublished data).

434

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

445

446 Minimum C was $0.093 \pm 0.004 \text{ W kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ in 2CY+ birds in early winter (Fig. 5), which is
447 comparable to the $0.091 \pm 0.003 \text{ W kg}^{-1} \text{ }^{\circ}\text{C}^{-1}$ recorded for Svalbard ptarmigan at the same time of the
448 year by Mortensen and Blix (1986). C subsequently increased 20% from early to late winter, which is
449 lower than the 39% increase estimated by Mortensen and Blix (1986). Different seasonal responses in
450 these studies might be explained by the lower reduction of subcutaneous fat reserves in our study (5 g;
451 0.6% of total body mass) compared to that reported by Mortensen and Blix (80 g; 11% of total body

452 mass). Continued depletion of fat reserves (Fig. 1C) might also explain why we observed a subsequent
453 41% increase in C between late winter and summer (Fig. 5), whereas Mortensen and Blix (1986)
454 observed no significant difference between fat-free birds in winter- and summer plumages ($0.127 \pm$
455 $0.004 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$ and $0.120 \pm 0.007 \text{ W kg}^{-1} \text{ }^\circ\text{C}^{-1}$ for late winter and summer, respectively).
456 Nevertheless, since body coat weight and plumage thickness in summer-acclimated Svalbard
457 ptarmigan is considerably lower than in winter (Nord et al., unpublished data), inferior plumage
458 insulation most likely also contributed to increased C in summer birds.

459

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

479

480

481 CONCLUSIONS

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

489

490

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494

495

496 **COMPETING INTERESTS**

497 The authors have no competing or financial interests.

498

499

500 **AUTHORS' CONTRIBUTIONS**

501 AN and LPF jointly conceived the study, designed the experiment, performed the laboratory work, and
502 analysed the respirometry data. AN performed the statistical analyses and drafted the manuscript,
503 which was then critically evaluated by LPF.

504

505

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509

510

511 **DATA AVAILABILITY**

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

513

514

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652 TABLES

653 **Table 1.** Test statistics, degrees of freedom (Satterthwaite approximation), and *P*-values for final
 654 models of core (T_c) and peripheral tissue (T_{back} , T_{breast} , T_{head} , T_{tarsus}) temperature measured in Svalbard
 655 ptarmigan at each of three ambient temperatures (T_a ; 0°C, -10°C, -30°C) during early winter, late
 656 winter, and summer. Different letters within brackets denote statistically significant ($P \leq 0.05$)
 657 pairwise differences within each respective contrast.

Parameter	Estimate (SE)	df	F	P
<u>T_c (°C)</u>				
Season		2, 75.53	3.29	0.043
Early winter [A]	41.71 (0.10)			
Late winter [A]	41.78 (0.10)			
Summer [AB]	41.54 (0.10)			
Measurement order		1, 7.31	0.33	0.583
T_a		2, 72.77	54.35	< 0.001
Measurement order $\times T_a$		2, 72.78	6.32	0.003
<i>Measurement order = 0°C to -30°C</i>				
0°C [A]	41.41 (0.12)			
-10°C [A]	41.68 (0.12)			
-30°C [B]	42.10 (0.12)			
<i>Measurement order = -30°C to 0°C</i>				
0°C [A]	41.09 (0.17)			
-10°C [A]	41.40 (0.16)			
-30°C [B]	42.40 (0.16)			
<u>T_{back} (°C)</u>				
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 \times Age		2, 79.07	5.29	0.007
<i>Season = Early winter</i>				
Age = 1CY [A]	37.92 (0.32)			
Age = 2CY+ [A]	37.17 (0.38)			
<i>Season = Late winter</i>				
Age = 1CY [A]	36.27 (0.36)			
Age = 2CY+ [A]	36.96 (0.39)			
<i>Season = Summer</i>				
Age = 1CY [A]	37.80 (0.36)			
Age = 2CY+ [A]	38.07 (0.38)			
<u>T_{breast} (°C)</u>				
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)			
<u>T_{head} (°C)</u>				

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
<i>Season = Early winter</i>				
Age = 1CY [A]	29.61 (0.44)			
Age = 2CY+ [B]	31.42 (0.42)			
<i>Season = Late winter</i>				
Age = 1CY [A]	30.46 (0.48)			
Age = 2CY+ [A]	31.22 (0.47)			
<i>Season = Summer</i>				
Age = 1CY [A]	31.93 (0.46)			
Age = 2CY+ [A]	31.48 (0.44)			
<hr/>				
$T_{\text{tarsus}} (°C)$				
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
<i>Season = Early winter</i>				
0°C [A]	32.12 (1.71)			
-10°C [A]	30.35 (1.71)			
-30°C [B]	23.09 (1.71)			
<i>Season = Late winter</i>				
0°C [A]	32.46 (1.84)			
-10°C [A]	32.70 (1.77)			
-30°C [A]	29.98 (1.77)			
<i>Season = Summer</i>				
0°C [A]	32.04 (1.84)			
-10°C [B]	26.41 (1.92)			
-30°C [C]	16.73 (1.92)			

658

659 **Table 2.** Test statistics, degrees of freedom (Satterthwaite approximation), and *P*-values for final
660 models of mass-specific resting metabolic rate RMR and thermal conductance, measured at each of
661 three ambient temperatures (T_a ; 0°C, -10°C, -30°C) in Svalbard ptarmigan during early winter, late
662 winter, and summer. Different letters within brackets denote statistically significant ($P \leq 0.05$)
663 pairwise differences within each respective contrast.

Parameter	Estimate (SE)	df	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
$T_a \times$ Age		2, 65.68	0.19	0.831
Season \times T_a		4, 65.68	13.03	< 0.001
Season \times Age		2, 67.94	13.28	< 0.001
Season \times $T_a \times$ Age		4, 65.68	3.78	0.008
<i>Season = Early winter / Age = 1CY</i>				
0°C [A]	5.59 (0.39)			
-10°C [A]	5.99 (0.39)			
-30°C [B]	8.64 (0.39)			
<i>Season = Early winter / Age = 2CY+</i>				
0°C [A]	4.04 (0.46)			
-10°C [A]	4.64 (0.46)			
-30°C [B]	6.69 (0.46)			
<i>Season = Late winter / Age = 1CY</i>				
0°C [A]	5.98 (0.45)			
-10°C [B]	7.66 (0.45)			
-30°C [C]	10.54 (0.45)			
<i>Season = Late winter / Age = 2CY+</i>				
0°C [A]	5.04 (0.50)			
-10°C [B]	6.31 (0.46)			
-30°C [C]	8.24 (0.46)			
<i>Season = Summer / Age = 1CY</i>				
0°C [A]	8.14 (0.45)			
-10°C [B]	9.42 (0.45)			
-30°C [C]	13.26 (0.45)			
<i>Season = Summer / Age = 2CY+</i>				
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 \times T_a		4, 73.50	7.39	< 0.001
<i>Season = Early winter</i>				
0°C [A]	4.21 (0.20)			
-10°C [A]	4.63 (0.20)			
-30°C [B]	6.68 (0.20)			
<i>Season = Late winter</i>				
0°C [A]	4.71 (0.23)			

10°C [B]	6.00 (0.22)		
-30°C [C]	8.08 (0.22)		
<i>Season = Summer</i>			
0°C [A]	5.39 (0.22)		
10°C [B]	6.52 (0.22)		
-30°C [C]	9.80 (0.22)		
Conductance ($W\ kg^{-1}\ ^\circ C^{-1}$)			
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
<i>Season = Early winter</i>			
Age = 1CY [A]	0.123 (0.005)		
Age = 2CY+ [B]	0.093 (0.006)		
<i>Season = Late winter</i>			
Age = 1CY [A]	0.145 (0.005)		
Age = 2CY+ [B]	0.119 (0.006)		
<i>Season = Summer</i>			
Age = 1CY [A]	0.187 (0.005)		
Age = 2CY+ [A]	0.187 (0.006)		

664
665

666 **FIGURE LEGENDS**

667 **Fig. 1. Annual variation in experimental photoperiod (A), and body mass (B), dissectible fat (C),**
668 **and food intake (D) for the Svalbard ptarmigan included in the study.** Panel A shows natural
669 variation in photoperiod (including civil twilight) over the course of the year in Longyearbyen,
670 Svalbard (78°13' N, 15°38' E), a simulated version of which birds in the experiment were exposed to.
671 Panels B-D show loess smoothers \pm 95% CI). Solid lines represent birds that were in their second
672 calendar year, or older (i.e., 2CY+), and dashed lines represent birds that were in their first calendar
673 year (i.e., 1CY) when the experiment started. The shaded vertical bars show experimental periods.
674 Biometric- and food intake data were collected from $n = 10$ -12 male Svalbard ptarmigan (1CY: $n = 5$ -
675 7; 2CY+: $n = 5$) over the course of the study.

676
677 **Fig. 2. Overview of variation in tissue temperatures in captive Svalbard ptarmigan at different**
678 **ambient temperatures (T_a) and seasons.** Data are mean (\pm SE) core (T_c) and cutaneous tissue
679 temperatures at the back (T_{back}), breast (T_{breast}), head (T_{head}), and tibiotarsus (T_{tarsus}). Data were averaged
680 over age categories and measurement order. Sample sizes for each tissue, at each T_a and season, are
681 reported in Table S1.

682
683 **Fig. 3. Mean (\pm SE) core temperature (T_c ; A), head skin temperature (T_{head} ; B) and tibiotarsus**
684 **skin temperature (T_{tarsus} ; C), in relation to ambient temperature (T_a) in captive Svalbard**
685 **ptarmigan in each of three seasons.** Sample sizes for each T_c , in each of the T_a 's and during each
686 seasons, are available in Table S1. Statistics are reported in Table 1.

687
688 **Fig. 4. Mean (\pm SE) mass-specific resting metabolic rate (RMR) at different ambient**
689 **temperatures (T_a) in first winter (1CY), and second winter or older (2CY+) captive Svalbard**
690 **ptarmigan during three different times of the year.** Sample sizes and statistics are reported in Table
691 S1 and Table 2, respectively.

692
693 **Fig. 5. Mean (\pm SE) mass-specific thermal conductance (C) in first winter (1CY), and second**
694 **winter or older (2CY+), captive Svalbard ptarmigan during early winter, late winter, and**
695 **summer.** Sample sizes for each age group and season are given in Table S1. Statistics are reported in
696 Table 2.

697

698 **FIGURES**

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700

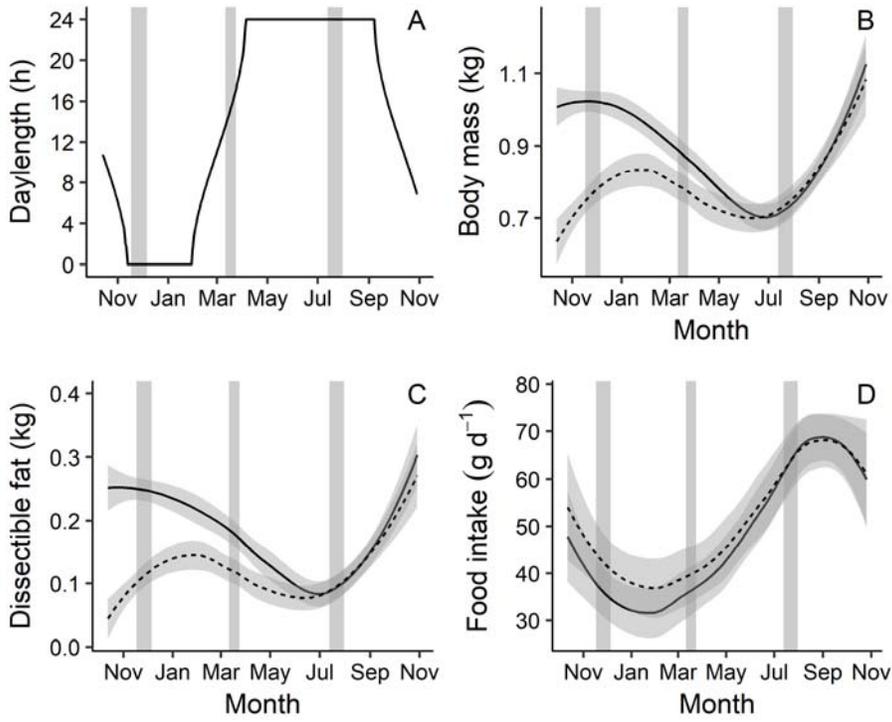


Fig. 1.

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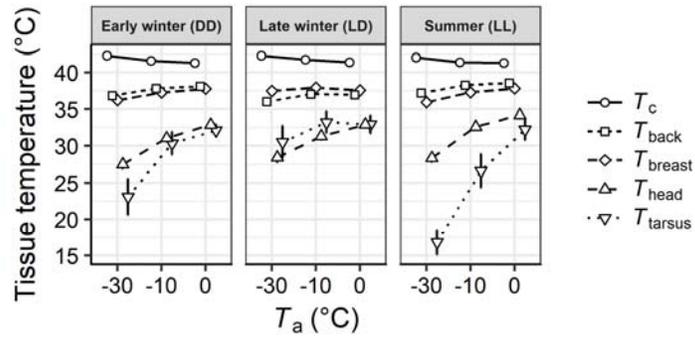
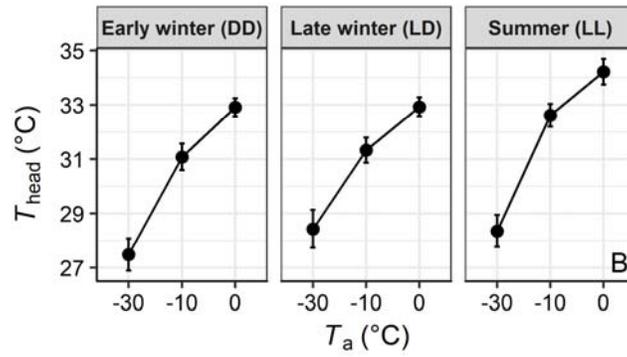


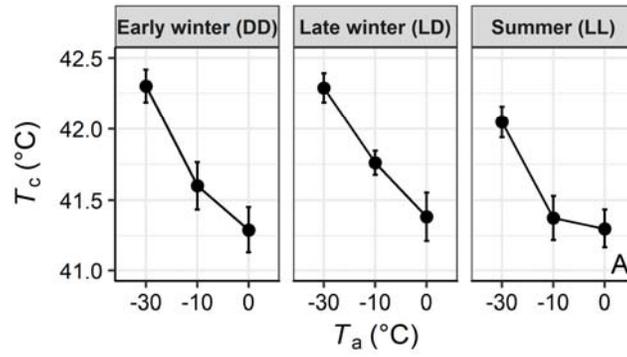
Fig. 2.

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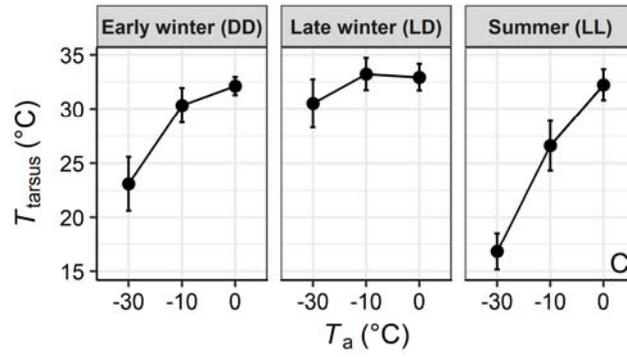
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Fig. 3.

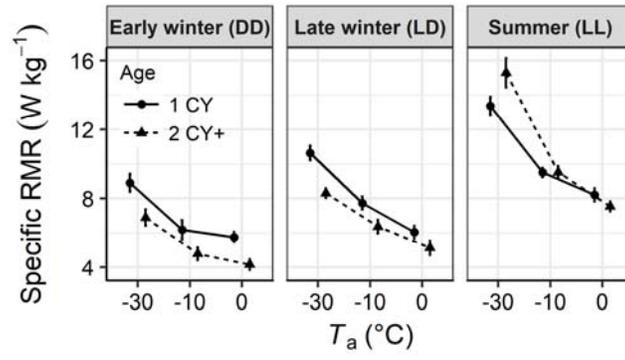


Fig. 4.

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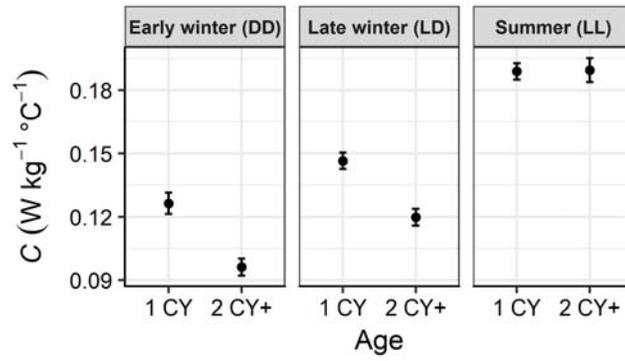
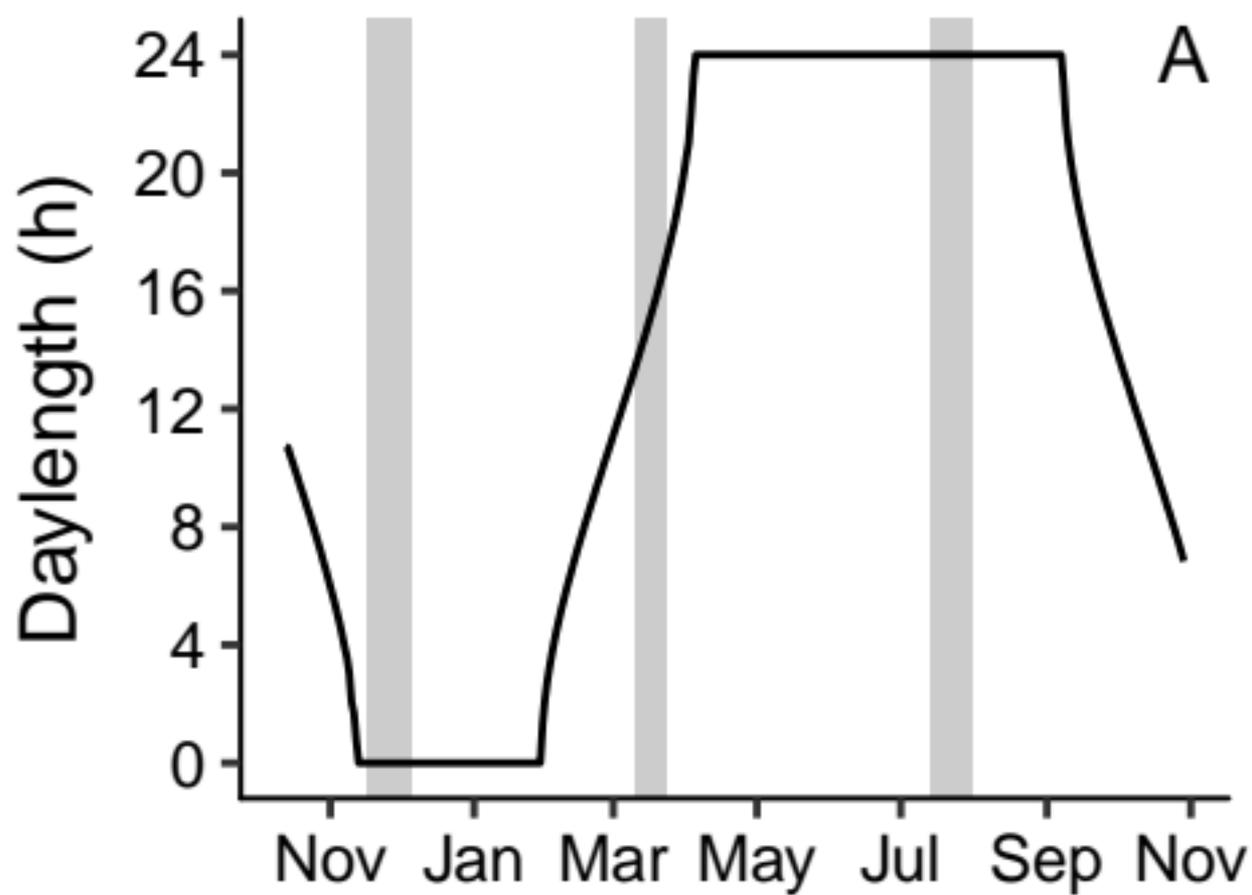


Fig. 5.

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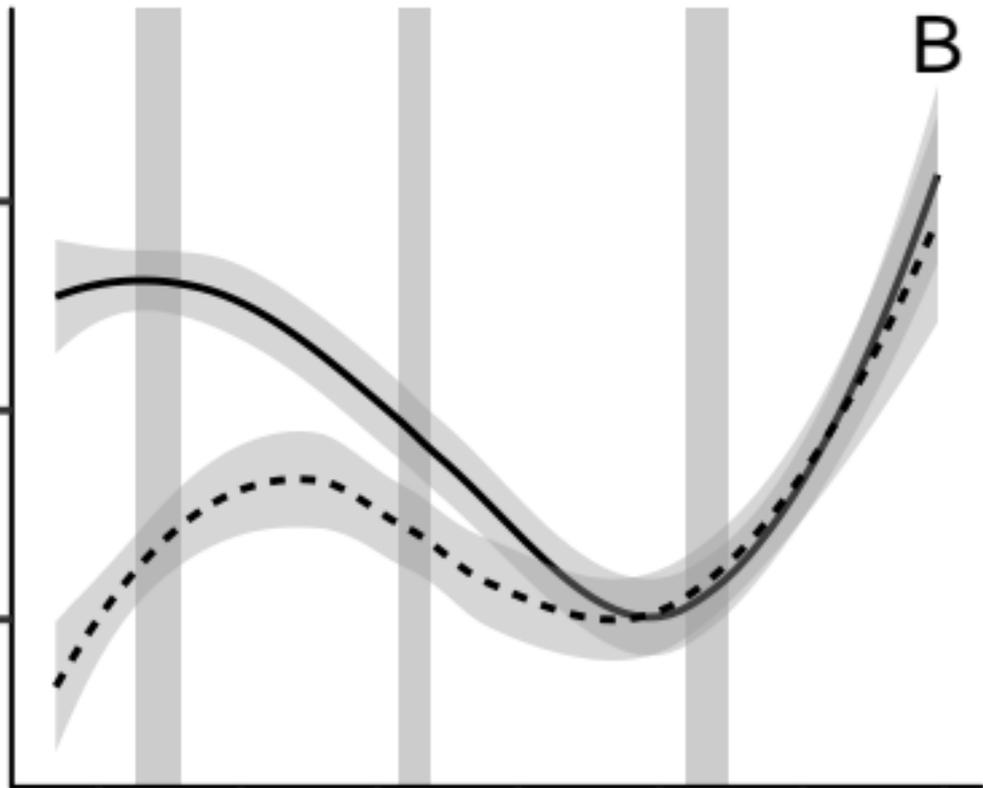
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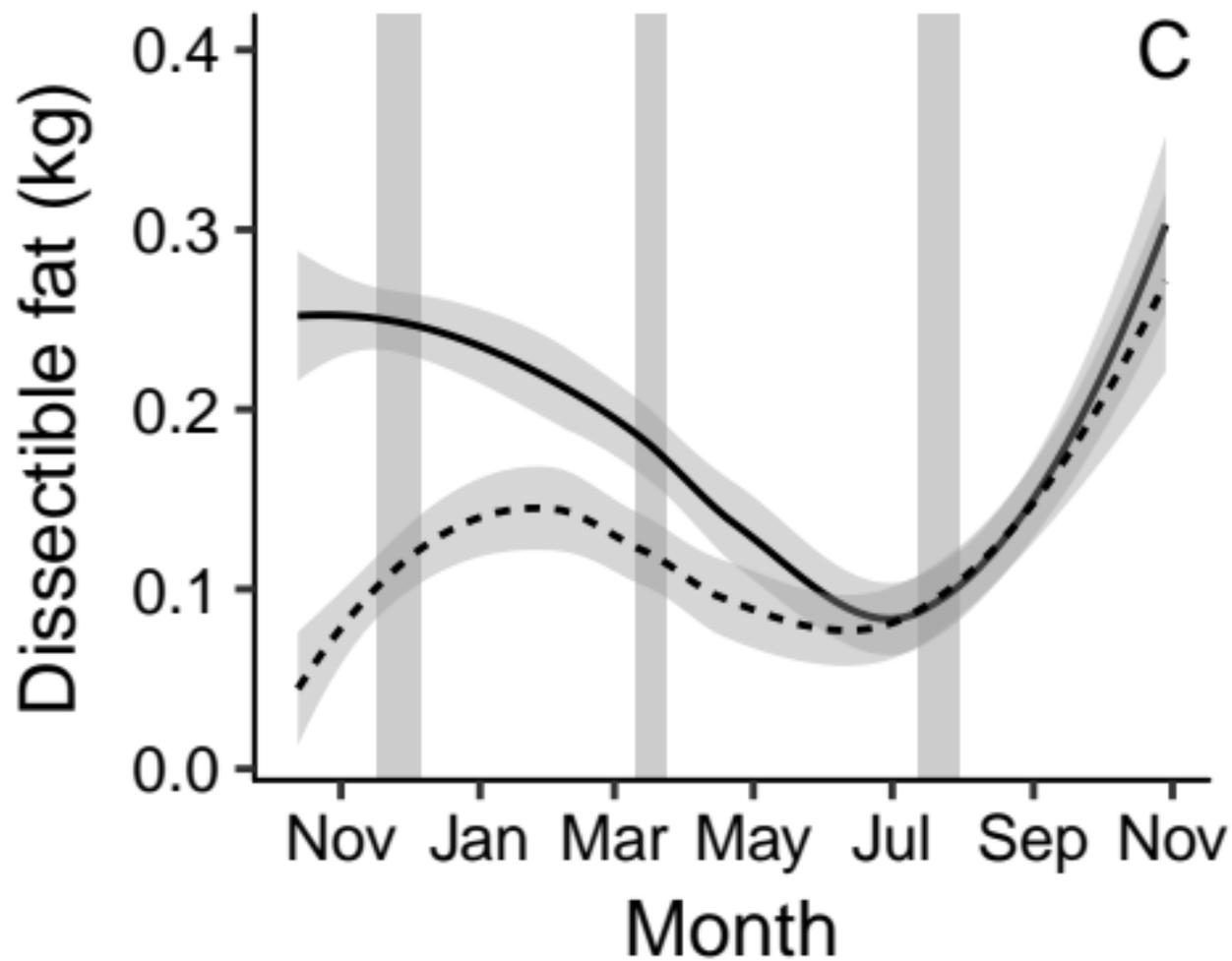
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0.7

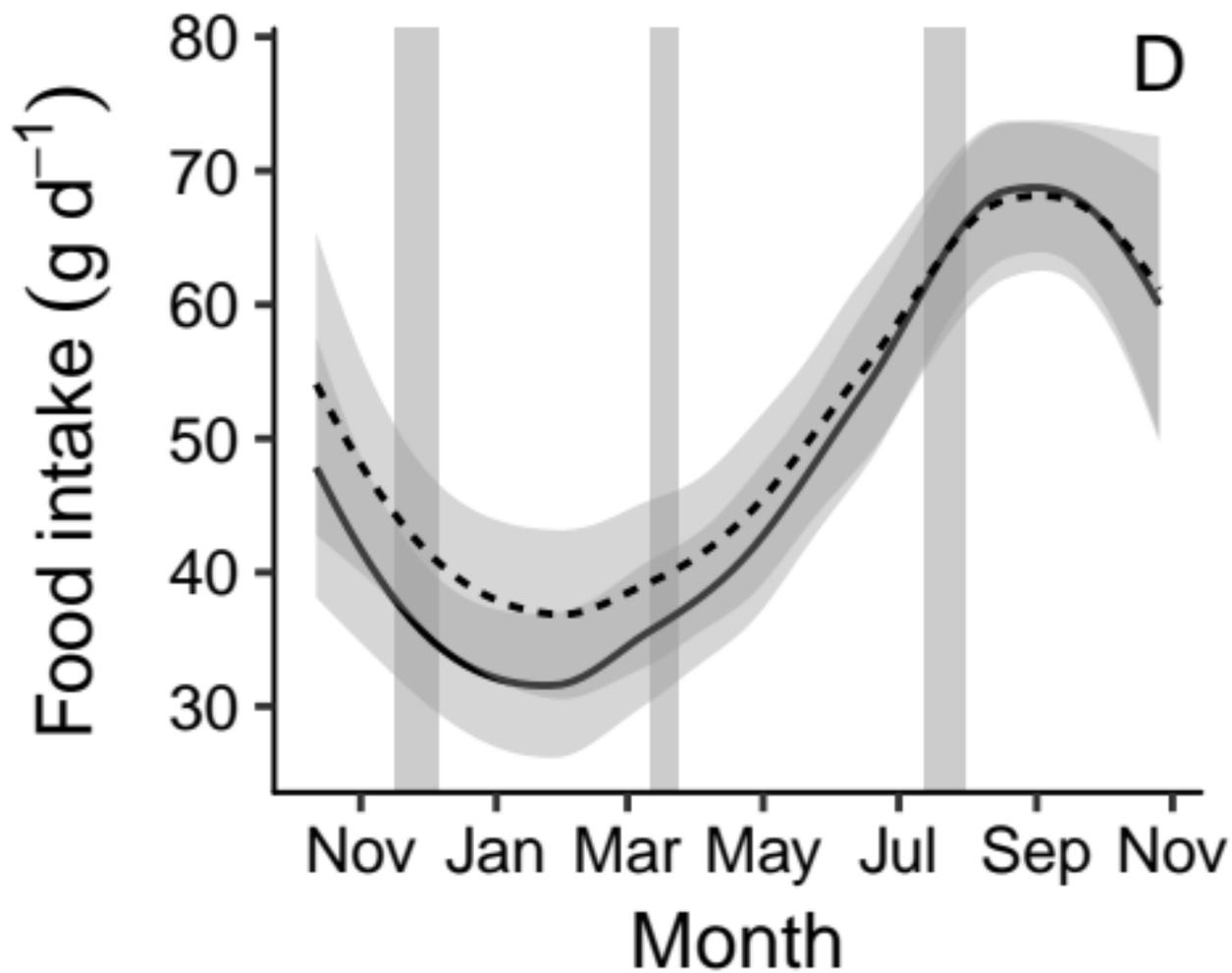
Nov Jan Mar May Jul Sep Nov

Month

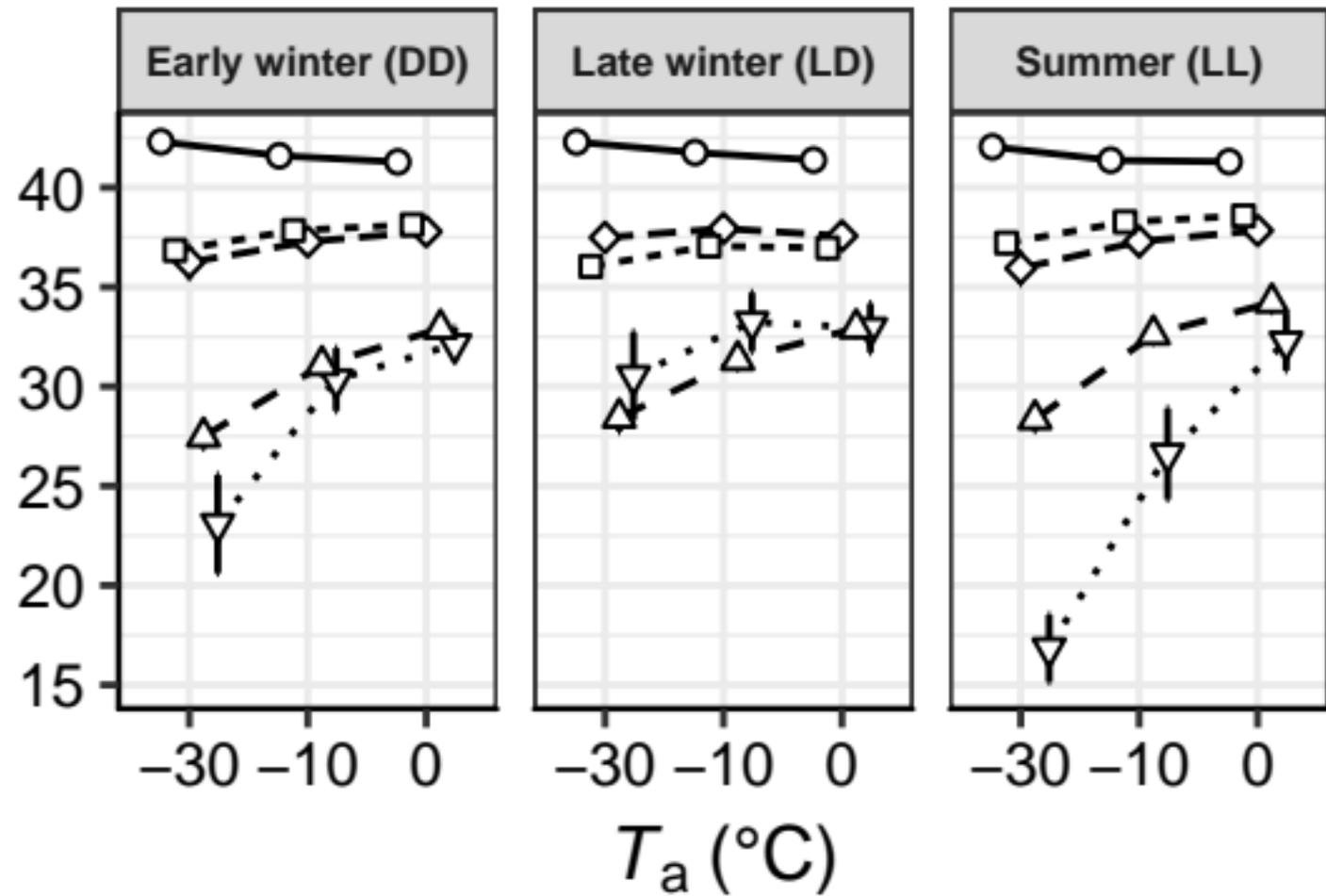
B



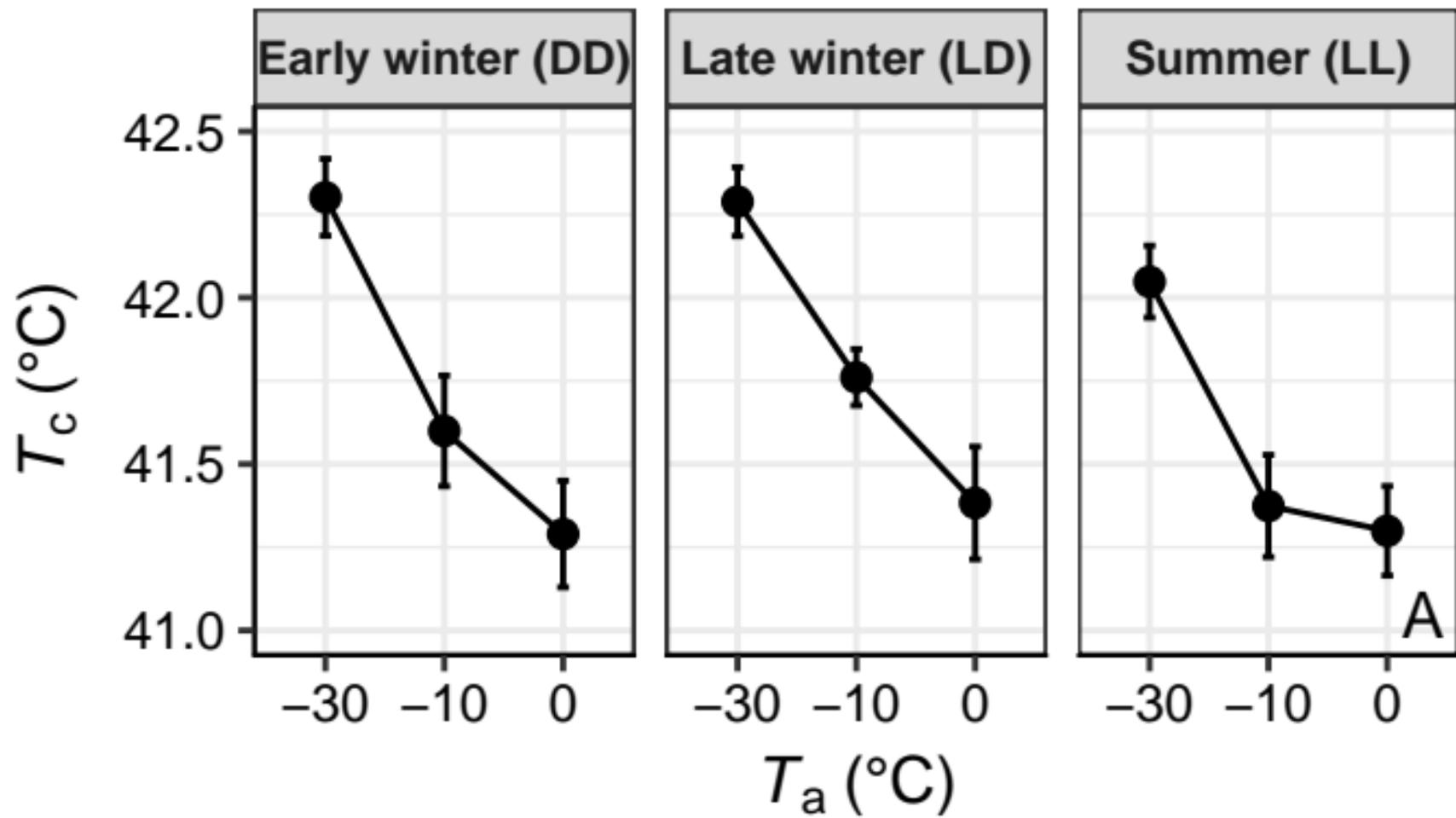




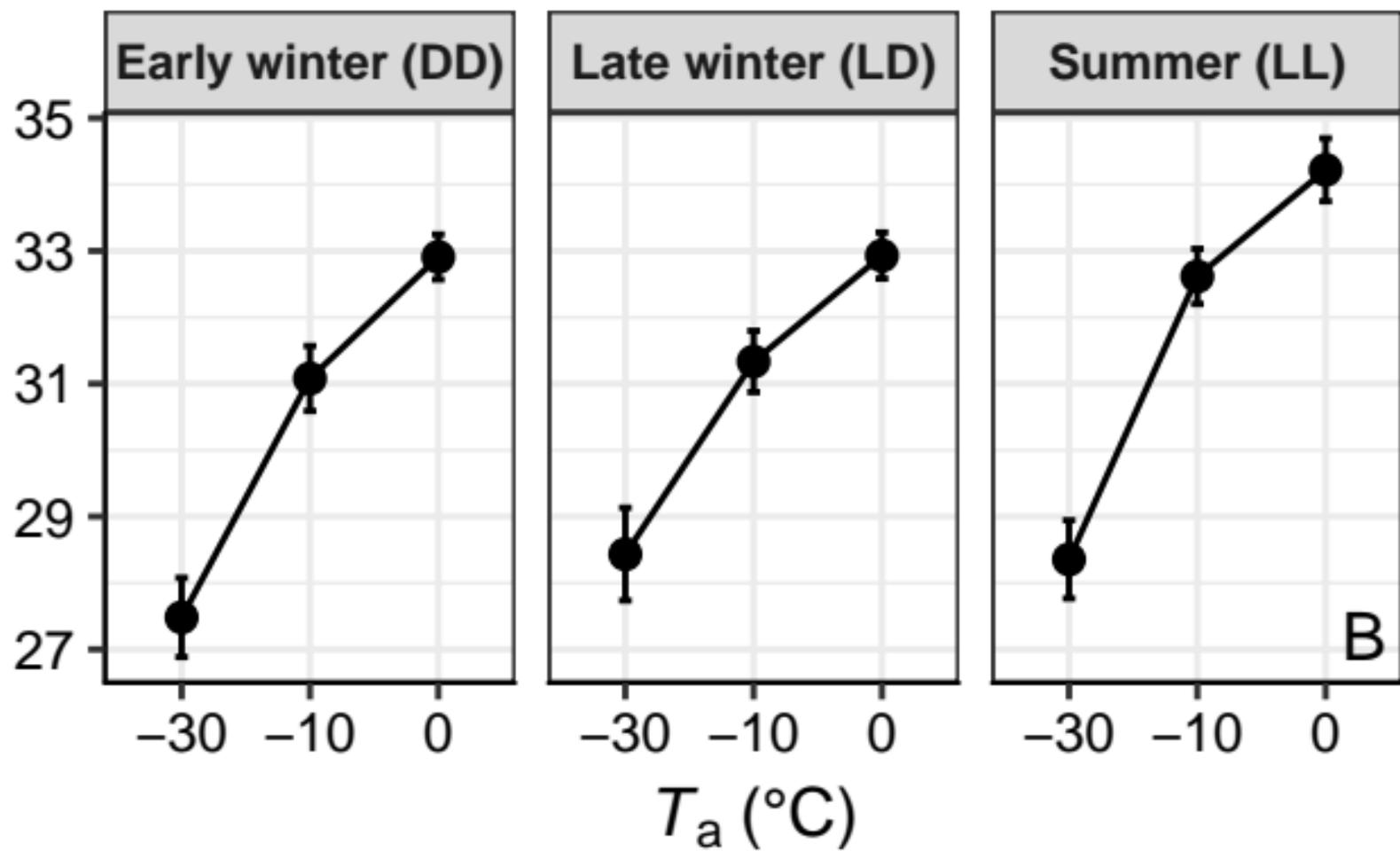
Tissue temperature ($^{\circ}\text{C}$)

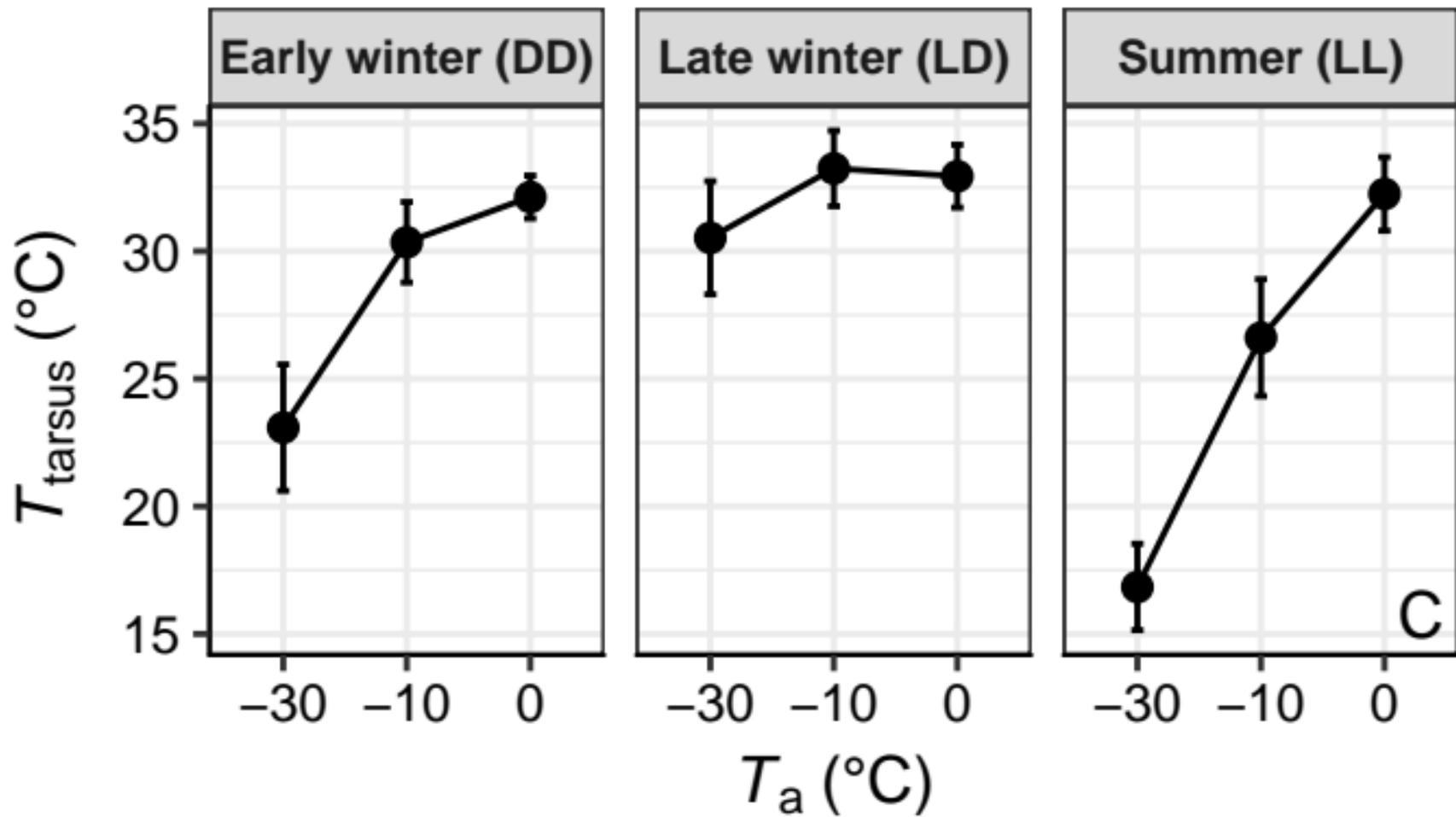


- T_c
- T_{back}
- T_{breast}
- T_{head}
- T_{tarsus}



$T_{\text{head}} (\text{°C})$





Specific RMR (W kg^{-1})

