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Flexible use of peripheral heterothermy is associated with fitness-related outcomes in an Arctic ungulate

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Abstract

Lowering core body temperature (T_b) during hibernation or daily torpor can improve energy balance, but heterothermy outside these states is often linked to energetic stress or poor body condition. Whether peripheral cooling can conserve energy and enhance fitness-related outcomes in large non-hibernating mammals remains unknown. We investigated peripheral heterothermy using subcutaneous chest temperature (T_{sc}) in 47 female Svalbard reindeer (Rangifer tarandus platyrhynchus) across three winters. In four females with simultaneous measurements, T_{sc} varied substantially more than rumen temperature. Using a joint mixture model, we identified two thermoregulatory tactics: the less heterothermic tactic was characterised by higher daily median T_{sc} (36.6°C; range: 33.9–38.2°C) and smaller daily T_{sc} amplitudes (2.9°C; 0.2–6.2°C). In contrast, the more heterothermic tactic had lower daily median T_{sc} (35.6°C; 29.8–37.4°C) and greater daily T_{sc} amplitudes (5.0°C; 1.1–18.3°C). The more heterothermic tactic was most prevalent in the harshest winter, and five of 22 females monitored over two winters switched tactics. More heterothermic females were approximately 4 kg heavier in late winter and had higher subsequent reproductive success, mainly through higher body mass. Our results suggest that flexible use of peripheral heterothermy may confer energetic advantages and support fitness-related outcomes during harsh Arctic winters.

KEYWORDS

Svalbard reindeer, biologging, subcutaneous body temperature, peripheral heterothermy, rumen temperature, thermoregulation, body mass, reproductive success, life-history tactic

Introduction

Maintaining homeothermy, a relatively high and stable core body temperature (T_b), is one of the most energetically costly aspects of endothermy[1]. To reduce this cost, many endothermic mammals can employ heterothermy[2], lowering core T_b, particularly when facing energetically challenging conditions[3]. The most extreme examples are hibernation and daily torpor, during which core T_b and metabolic rate are markedly reduced to conserve energy reserves[4]. In hibernation, core T_b may be reduced for days to months, while daily torpor typically lasts for several hours, often during the resting phase [4]. Yet, many species that do not hibernate or enter daily torpor can also lower core T_b by 1–5°C from typical homeothermic levels, often during resting or inactive bouts lasting a few hours[5].

There is increasing evidence that the thermoregulatory tactics used by endotherms fall along a 'heterothermic continuum'[6], reflecting both the propensity of species to employ heterothermy and the magnitude of their thermoregulatory scope, i.e. the range of variation in T_b. Angilletta et al. (2010) proposed that endotherms may range from 'thermal specialists', which maintain a relatively narrow range of T_b under varying environmental conditions, to 'thermal generalists', which display wider variation in T_b[7]. Thus, when limited resources or extreme cold make maintaining a high T_b energetically challenging, thermal generalists are expected to perform better than thermal specialists, whereas the opposite is expected under benign conditions[8].

While the specialist-generalist thermoregulatory framework was initially based on comparisons among species, recent studies have documented similar variation within species, with some individuals being more heterothermic than others. For example, considerable between-individual variation in heterothermy, with high within-individual repeatability, has been documented in laboratory mice[9], yellow-necked mice (*Apodemus flavicollis*)[10], chipmunks (*Tamias striatus*)[11] and rabbits (*Oryctolagus cuniculus*)[12]. Where fitness components have been assessed, however, the use of heterothermy has often been negatively associated with fitness-related outcomes. In chipmunks, greater heterothermy during a food-scarce winter was associated with lower survival and fewer offspring reared the following summer[11], whereas smaller litters were observed after periods of increased heterothermy in yellow-necked mice[13]. In rabbits, larger daily amplitudes in T_b and lower daily minimum T_b were associated with fewer pregnancies[12]. In a study of vervet monkeys (*Chlorocebus pygerythrus*), no link between heterothermy and reproductive success was found[14]. Collectively, these studies indicate that multiple thermoregulatory tactics can exist within a population, but whether a more heterothermic tactic improves fitness-related outcomes remains unclear.

Although many studies have explored heterothermy in terms of changes in core T_b, few have studied the fitness implications of reductions in the temperature of the body periphery, which can effectively insulate the body core by reducing heat loss to the environment[15]. Therefore, peripheral heterothermy should reduce the need for metabolic heat production and confer energy-saving benefits[16]. Such a tactic is likely to be advantageous in extreme cold environments where the gradient between core T_b (~38°C) and the external environment (often below −20°C) can approach or exceed 60°C, imposing high energetic costs for maintaining a high and stable core T_b[17]. Indeed, variation in peripheral temperature, particularly subcutaneous temperature (T_{sc}), has been associated with low ambient temperature[18], low food availability[19], and poor body condition[20,21] in non-hibernating large endotherms inhabiting seasonal and cold environments. This suggests that flexible use of peripheral heterothermy may also be a tactic to conserve energy, potentially enabling the maintenance of high core T_b, under both predictable (i.e. seasonal changes) and unpredictable environmental challenges. Yet, the extent to which this may improve fitness remains unclear, and energy savings from peripheral cooling are generally considered negligible compared with those from reducing core T_b[22].

Here, we investigated variation in peripheral thermoregulatory tactics of Svalbard reindeer (*Rangifer tarandus platyrhynchus*), which are adapted to endure extreme cold and limited food availability during the 8-month Arctic winter. These adaptations include extreme pre-winter fattening [23], thick winter fur insulation[24], peripheral heterothermy of the limbs[25], reduced energy expenditure, heart rate and activity[26,27], and a seasonal reduction in rumen temperature (T_{rumen})[28]. We used biologgers to measure subcutaneous temperature over three winters and simultaneously recorded rumen temperature in a subset of individuals during one winter. First, we compared patterns in T_{rumen} and T_{sc} to explore peripheral versus central body temperature variation during winter. We then assessed whether variation in T_{sc} depended on logger position in the body periphery. To do so, we measured T_{sc} simultaneously at two locations: at the chest, a location that may be influenced by ground surface temperatures while the animal is resting, and on the neck, a location that is not influenced by ground surface temperatures. Second, we employed a joint mixture model[29] to identify possible groups of individuals sharing similar thermoregulatory traits and responses to environmental conditions[30,31]. Using individual daily median T_{sc} and daily T_{sc} amplitude as response variables, we tested whether two distinct thermoregulatory tactics coexisted: a less heterothermic tactic similar to the specialist strategy, and a more heterothermic tactic similar to the generalist strategy proposed by Angilletta et al.[7]. Third, we evaluated whether the different tactics were associated with important fitness-related outcomes: body mass in late winter and subsequent reproductive success[32,33]. Lastly, we assessed whether models using thermoregulatory groups identified from multiple traits were better supported than models using single, continuous

body temperature metrics to explain fitness-related outcomes. These physiological insights may elucidate the extent of flexibility in thermoregulatory tactics and their potential influence on population dynamics.

Results

(a) Patterns of variation in rumen (T_{rumen}) and subcutaneous (T_{sc}) temperatures

We successfully retrieved simultaneous subcutaneous chest temperature (T_{sc}) and rumen temperature (T_{rumen}) data from four individuals during the winter of 2018/19. Median T_{rumen} across winter was approximately 3°C higher than median chest T_{sc} (Table 1). T_{rumen} also exhibited considerably less variation across the 24 h period, whereas T_{sc} declined during inactive bouts, which typically lasted around 3 h (mean of 168 ± 79 min) (Figure 1a). Similar temporal patterns are illustrated for additional individuals and time periods in Figure S2, indicating that temperature variation was most pronounced in the body periphery. In the winter of 2022/23, we obtained simultaneous chest and neck T_{sc} data from seven individuals. Chest and neck measurements showed similar daily median T_{sc} and daily T_{sc} amplitudes across winter (Table 1).

Table 1. Descriptive statistics of body temperatures of adult female Svalbard reindeer measured over three winter periods (December–March). Values are presented separately for each winter period and measurement location. Shown are the medians of all individuals' daily median temperature and daily temperature amplitude, with the ranges of daily values in parentheses. N indicates the number of ID-years with available data for each measurement location and winter period.

Winter	**Measurement location**	**Daily median temperature (°C)**	**Daily temperature amplitude (°C)**	**N**
		Median (range) of daily values	*Median (range) of daily values*	
2018/19	Rumen	38.3 (37.9–38.7)	0.94 (0.4–1.8)	**8[a]**
	Subcutaneous - chest	35.4 (29.8–37.4)	4.4 (1.3–18.3)	**15**
2021/22	Subcutaneous - chest	36.5 (34–37.5)	3.2 (0.8–15.1)	**38**
2022/23	Subcutaneous - chest	36.4 (32.3–38.2)	3.3 (0.2–12.1)	**16**
	Subcutaneous - neck	36.7 (34.7–38.1)	3.5 (0.8–12.0)	**13[b]**

([a]) four and ([b]) seven of these had simultaneous chest T_{sc} data.

Across the 24 h period, fluctuations in T_{sc} measured at the chest reflected similar fluctuations in temperatures recorded subcutaneously at the neck, but with some apparent temporal offsets, likely due to differential clock drift at the fine temporal scale (Figure 1b). Bland–Altman plots indicated that the temperatures showed good agreement at the daily level (Figure S3), but that neck temperatures tended to be slightly higher than those recorded on the chest (median difference of 0.7°C; range −1.0 to 2.3°C). Thus, the similar patterns in temperatures recorded at the neck (not in contact with the ground while resting) and chest (potentially in contact with snow while resting) suggest that snow contact was not a major driver of variation in chest T_{sc}. Hereafter, all analyses of T_{sc} were based on chest measurements as these were the only measurements available across all three winters (Figure S4, Tables S1 and S2).

Collar-recorded temperatures were lowest in 2018/19 (mean ± SD [range] = −4.5 ± 5.5°C [−19.9; 8.8]), indicating colder microclimatic conditions experienced by the animals compared to the other two winters (−3.2 ± 5.0°C [−22.9; 8.1] and −0.9 ± 4.4°C [−13.6; 13.0] in 2021/22 and 2022/23, respectively). Late-winter body mass was lowest in 2018/19 (49.5 ± 6.0 kg) and highest in 2022/23 (54.4 ± 5.1 kg) (Table S3).

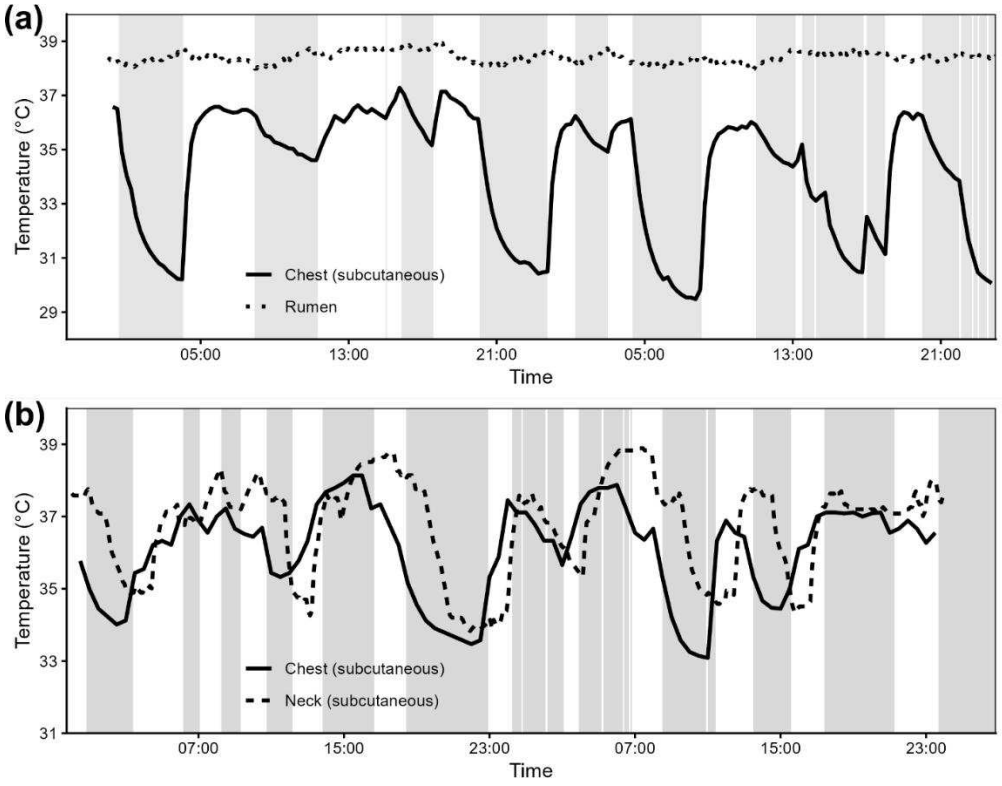


Figure 1. Representative examples of fluctuations over 48 h in (a) subcutaneous chest temperature (solid line) and rumen temperature (dotted line) and (b) subcutaneous chest temperature (solid line) and neck temperature (dashed line) in female Svalbard reindeer in December 2018 (a) and December 2022 (b). Grey shaded regions indicate inactive bouts, while white regions indicate active bouts. Temporal mismatches between chest and neck temperature records in (b) are likely due to clock drift.

(b) Identification of thermoregulatory tactics

Both daily median T_{sc} and daily T_{sc} amplitudes were highly repeatable within the individual-years: adjusted R = 0.85 [95% CI: 0.84, 0.86] and unadjusted R = 0.64 [0.63, 0.65] for daily median T_{sc} and adjusted R = 0.70 [95% CI: 0.61,0.76] and unadjusted R = 0.64 [0.52, 0.73] for daily T_{sc} amplitude, demonstrating that both traits are relevant for the identification of thermoregulatory tactics. The joint mixture model provided greater support for a two-group model than for a model without grouping, indicating that ID-years did not belong to a single homogeneous thermoregulatory group (ΔAIC = 6867, ΔBIC = 6757). One group was characterised by lower daily median T_{sc} and greater daily T_{sc} amplitude, consistent with a more heterothermic tactic (green, n = 26 ID-years, Figure 2). The other group was characterised by higher daily median T_{sc} and lower daily T_{sc} amplitude, consistent with a less heterothermic tactic (blue, n = 43 ID-years, Figure 2). The proportion of ID-years assigned to the more heterothermic group varied among winters (Table S4): 8 of 15 ID-years in 2018/19 (53%), 14 of 38 ID-years in 2021/22 (37%) and 4 of 16 ID-years in 2022/23 (25%). Overall, five of 22 individuals recorded in two winters changed tactic, and four of these were initially classified as more heterothermic and adopted a less heterothermic tactic in the second monitoring year.

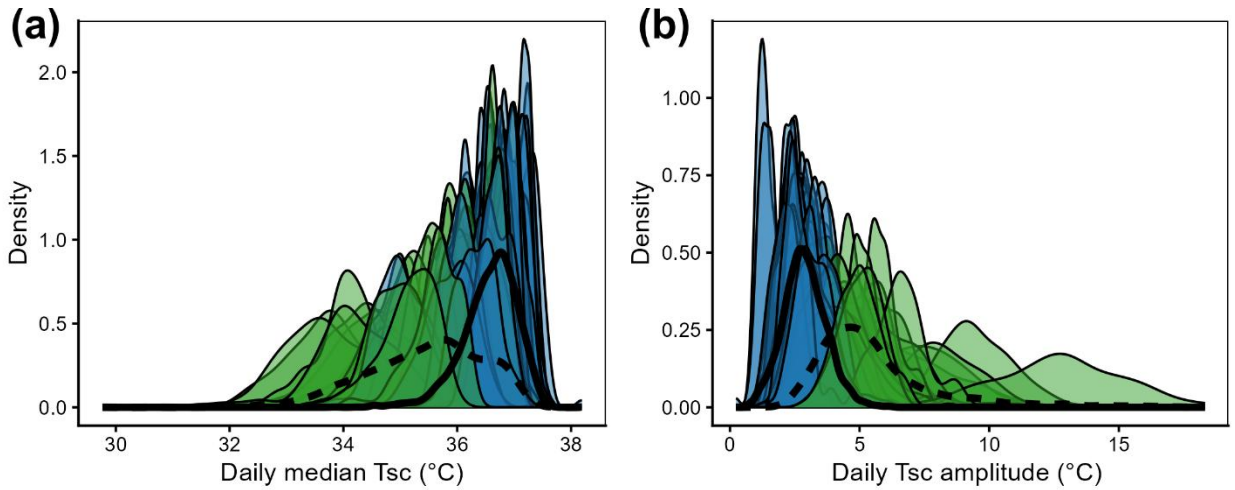


Figure 2. Density curves of (a) daily median T_{sc} and (b) daily T_{sc} amplitude in female Svalbard reindeer across three winters. Individual density curves, shown for each ID-year, are colour-coded according to the group assigned by the joint mixture model: green indicates the more heterothermic group and blue indicates the less heterothermic group. Thick lines represent the average density curves for each group, with dashed and solid lines representing the more and less heterothermic groups, respectively.

There was between-year variation in daily median T_{sc} (Figure 3a) and daily T_{sc} amplitude (Figure 3d, Table S5) in the more heterothermic group, but not in the less heterothermic group. Daily median T_{sc} increased with both higher collar-recorded temperatures (Figure 3b, range –23°C to 13°C) and a greater proportion of time active (Figure 3c, 20–75% active). In both cases, the predicted increase across the entire range of collar-recorded temperatures and proportion of time active was greater (i.e. non-overlapping CI of slopes; Table S5) for the more heterothermic tactic (1.5°C and 1.3°C, respectively) than for the less heterothermic tactic (1.0°C and 0.1°C, respectively). Daily T_{sc} amplitude showed weaker associations with collar-recorded temperature (Figure 3e) and proportion of time active (Figure 3f) than daily median T_{sc}, with less clear differences between the two tactics. In the more heterothermic group, daily T_{sc} amplitude was nearly unchanged across the range of collar-recorded temperatures, whereas it decreased in the less heterothermic group (Figure 3e, predicted changes of 0.1°C and –0.8°C, respectively). In both groups, daily T_{sc} amplitude decreased with increasing proportion of time active (Figure 3f, predicted changes of −1.0°C and −0.4°C for the more and less heterothermic group, respectively), and these slopes did not differ between the groups (Table S5). Lastly, while daily median T_{sc} increased over the course of winter with similar slopes in both groups, daily T_{sc} amplitude decreased, with only a marginal change in the more heterothermic group (Table S5).

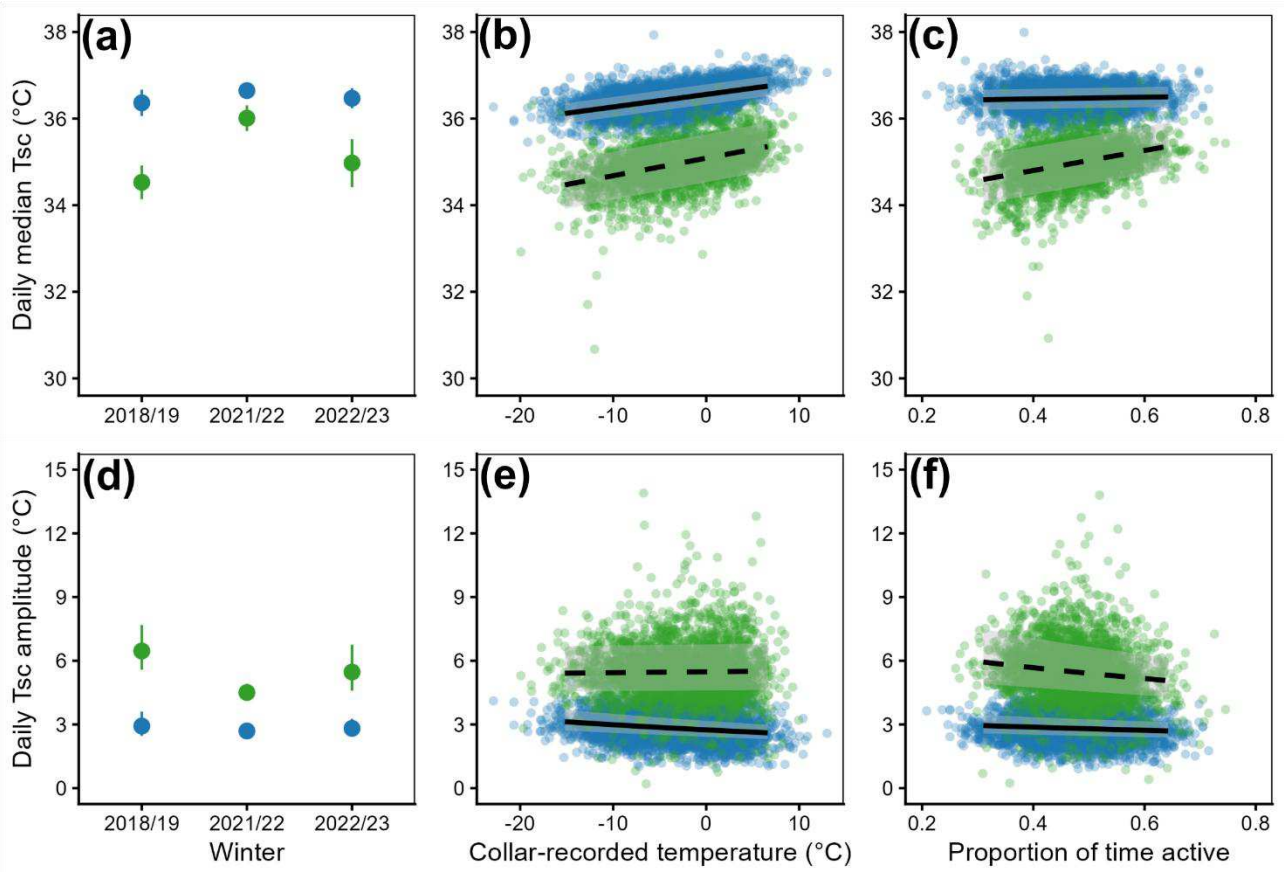


Figure 3. Predicted responses in daily median T_{sc} (panels a–c) and daily T_{sc} amplitude (panels d–f) in female Svalbard reindeer in relation to winter (a, d), collar-recorded temperature (b, e) and proportion of time active (c, f). Colours and line types distinguish the assigned groups displaying different tactics: green points and dashed lines represent responses associated with the more heterothermic tactic, while blue points and solid lines represent responses associated with the less heterothermic tactic. Model predictions were drawn from refitted models based on group assignment and initial parameters from the joint mixture model. In each panel, the other variables were fixed at group-level means. In panels b, c, e and f, predictions were also fixed to winter 2022/23. Lighter pastel bands and error bars indicate the 95% confidence intervals for each prediction, and lightly shaded points are partial residuals.

(c) Thermoregulatory tactics and fitness-related outcomes

The relationships among thermoregulatory tactic, late-winter body mass and subsequent reproductive success were assessed using a confirmatory path analysis. No missing paths were detected ($\chi^2 = 0.219$, p = 0.639, df = 1; Fisher's C = 0.89, p = 0.641, df = 2). The model supported an indirect pathway linking thermoregulatory tactic to reproductive success through late-winter body mass (Figure 4a). On average, individuals adopting the more heterothermic tactic were 2.4 kg heavier than the year-specific mean (95% CI 0.47; 4.42), while individuals adopting the less heterothermic tactic were 1.5 kg lighter than the year-specific mean (95% CI −3.09; 0.02) (Figure 4b), corresponding to a difference of about 4 kg between groups. This higher body mass translated

into an increased probability of having a calf at heel in August, from 0.41 (95% CI 0.19; 0.66) for an individual 1.5 kg lighter than the year-specific mean, to 0.83 (95% CI 0.56; 0.95) for an individual 2.5 kg heavier than the year-specific mean (Figure 4c). The large uncertainty around the estimated direct effect of thermoregulatory tactic on reproductive success indicates that this was imprecisely estimated (Figure 4a). Nevertheless, the global effect of thermoregulatory tactic was large, owing mainly to the magnitude of the indirect pathway through body mass (Figure 4d). As a result, the probability of having a calf at heel in August was 0.35 (95% CI 0.18; 0.56) for the less heterothermic group, compared with 0.79 (95% CI 0.51; 0.93) for the more heterothermic group. Overall, the model including thermoregulatory tactic as a predictor was better supported than the "null" model (ΔAICc = 8.3), as well as similar models with either winter median T_{sc} or winter median daily T_{sc} amplitude (ΔAICc = 3.7 for both models).

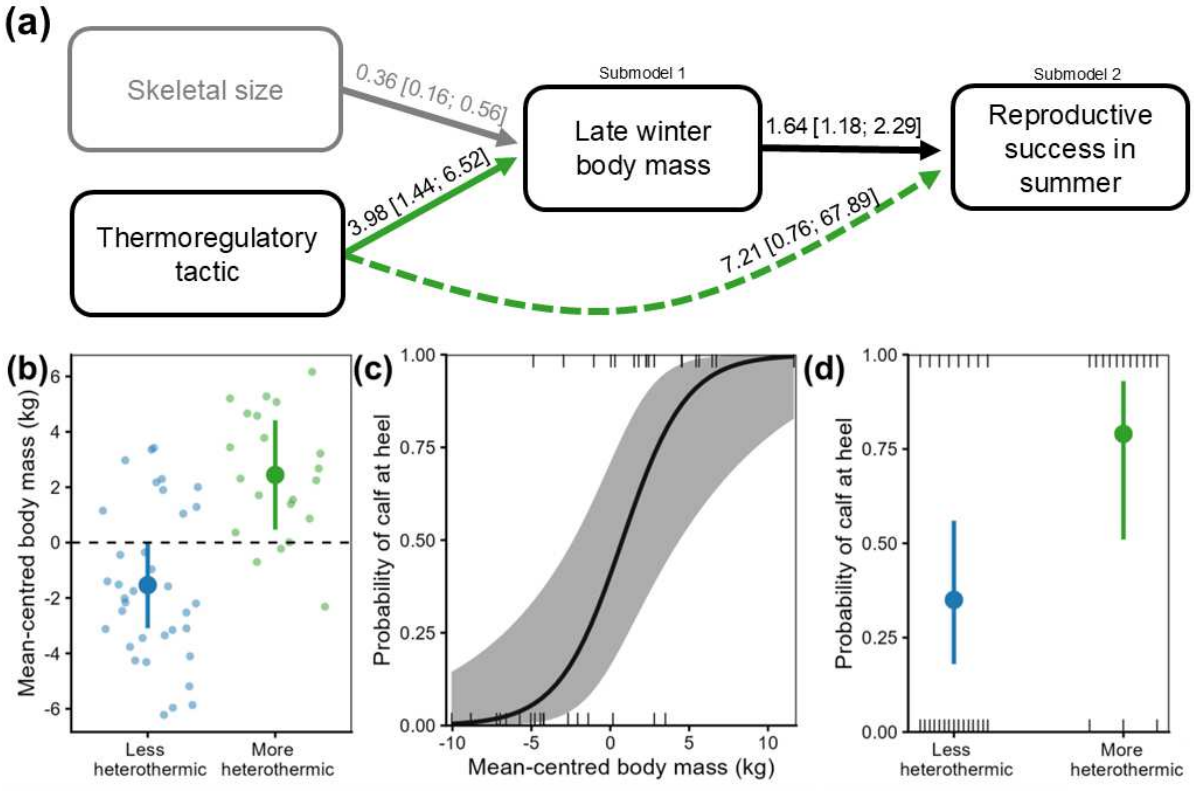


Figure 4. Relationships between thermoregulatory tactics and fitness-related outcomes in adult female Svalbard reindeer. Panel (a) illustrates the fitted piecewise structural equation model with unstandardised effects and their 95% confidence intervals, with solid arrows representing supported effects and dashed arrows representing unsupported effects. Estimates for reproductive success (probability of having a calf at heel in August) were calculated from odds ratios. For thermoregulatory tactic, the contrast is between the more heterothermic tactic and the less heterothermic tactic, indicated in green. Panel (b) shows the direct effect of thermoregulatory tactics on mean-centred late-winter body mass, after controlling for skeletal size. Panel (c) shows the direct effect of mean-centred body mass (BM) on the probability of having a calf at heel

in August. Panel (d) shows the global effect of thermoregulatory tactics on the probability of having a calf at heel in August. In panels (b) and (d), the large, coloured points are group-level predictions with 95% CIs; the smaller individual points in panel (b) represent partial residuals. The vertical lines at the top and bottom of panels (c) and (d) represent observed reproductive outcomes.

Discussion

Non-torpid heterothermy has been documented in a large range of endotherm taxa[5,34–36], yet a significant knowledge gap exists regarding the flexibility of thermoregulatory tactics within species. In Svalbard reindeer, a non-hibernating large mammal living in an extreme environment, we identified two thermoregulatory tactics differing in T_{sc} variation during winter. We show that adult females vary in their peripheral heterothermy use, and that the more heterothermic tactic was i) more common in the harshest winter, ii) displayed stronger responses to environmental and individual conditions, and iii) was positively associated with higher body mass in late-winter, and subsequent reproductive success. In contrast to studies showing that core-temperature heterothermy reduces fitness-related outcomes in non-hibernating small mammals[11–13], or is only expressed in individuals under poor conditions in larger mammals[35,37], our study provides evidence for a positive association between peripheral heterothermy and fitness-related outcomes in a non-hibernating large mammal. Peripheral heterothermy in Svalbard reindeer may therefore help preserve body reserves during the Arctic winter, when food resources are limited. We suggest that flexible use of peripheral heterothermy may prove to be an important tactic for coping with energetically challenging conditions, particularly in cold and stochastic environments.

(a) Subcutaneous temperature fluctuations are consistent with peripheral vasoconstriction

As documented in a wide range of endotherms (ungulates[38,39], emperor penguins[36], rabbits[40]), temperature fluctuations in reindeer were more pronounced at peripheral sites (chest and neck) than in the rumen, used here as a proxy for central body temperature. Variation in peripheral temperature closely followed the activity pattern of the individual, declining gradually during inactive bouts, and increasing rapidly with the onset of activity. This relationship is consistent with activity-related muscular heat production[41], likely contributing to the positive association between the daily proportion of time active and daily median T_{sc}, although this association was less marked in less heterothermic individuals than in more heterothermic individuals. Our main analyses were based on chest T_{sc}, but a similar temporal pattern was observed in temperatures recorded subcutaneously in the neck.

Despite a span in collar-recorded temperature of over 30°C, the response in daily median T_{sc} was relatively small (~1.5°C) and even smaller for daily T_{sc} amplitude. The highly insulating properties of Svalbard reindeer fur[24] may partly explain why we observed only this relatively weak effect of collar-recorded temperature on T_{sc}. Nonetheless, the decline in T_{sc} during inactive bouts is consistent with reduced peripheral blood flow due to vasoconstriction. Temperature records alone cannot establish vasoconstriction as the primary cause, however, because passive cooling and reduced activity-related heat production may also contribute to this pattern[41]. Similar patterns in neck and chest T_{sc} suggest that direct contact with snow was not the principal driver of these fluctuations. A plausible energy-saving mechanism is that peripheral vasoconstriction reduces heat transfer from the core to peripheral tissues, lowering peripheral temperature and heat loss to the environment, thereby enabling the maintenance of core T_b at a lower metabolic cost[18,25,41].

(b) The more heterothermic tactic was associated with higher late-winter body mass

The proportion of individuals using the more heterothermic tactic was highest during the harshest of the three winters, characterised by extensive rain-on-snow and icing that likely restricted access to forage, which coincided with the lowest mean late-winter body mass of the animals[32]. This supports the idea that maintaining high daily median T_{sc}, together with a low daily T_{sc} amplitude, is energetically costly and largely unaffordable under food limitation[42,43], and when exposed to cold. Indeed, individuals employing a more heterothermic tactic were heavier than individuals using the less heterothermic tactic, suggesting a potential fitness-related benefit of peripheral heterothermy. Although studies of other ungulates have documented marked seasonal differences in core T_b (lower in winter[34,44–46]), only one has studied between-year differences of the same season in relation to contrasting environmental conditions and their association with body mass[37]. This study of Cape buffalo [37] found lower mean T_b and greater core-temperature heterothermy in a winter drought than in a subsequent normal winter. In the drought, when green forage was scarce, animals were in poorer condition and significantly lighter. However, to our knowledge, no previous study has examined the association between individual variation in peripheral heterothermy and subsequent fitness-related outcomes in a large non-hibernating mammal.

A limitation of our study is the lack of data on body mass prior to winter. Even though thermoregulatory tactic was assigned from T_{sc} data collected over the four months prior to weighing, we cannot rule out the possibility that the body mass differences found in late winter were present already at the onset of winter, before the individuals exhibited different thermoregulatory tactics. However, a causal contribution of thermoregulatory tactic to late-winter body mass remains plausible, based on two premises. Firstly, daily energy expenditure (DEE) in

311 Svalbard reindeer during winter is positively correlated with T_{sc}, after accounting for variation in
312 daily activity levels[47], consistent with energetic costs associated with maintaining higher peripheral
313 temperatures. Indeed, a difference in daily mean T_{sc} of 1°C, from 37°C (mean DEE of ~6.8 MJ/day)
314 to 36°C (mean DEE of ~6.0 MJ/day), corresponded to approximately 12% lower DEE. Secondly,
315 theoretical models predict that small reductions in body temperature can significantly improve
316 winter energy budgets, as shown using T_{sc} in Svalbard reindeer[47] and vaginal temperature in
317 muskox (*Ovibos moschatus;*[48]). In female muskox, a model of winter heterothermy showed that a
318 0.8°C drop in vaginal temperature could result in a 10–30% increase in spring energy reserves and a
319 potential 20–30% increase in winter survival.
320
321 **(c) Individuals using the more heterothermic tactic had higher subsequent reproductive**
322 **success**

323 Since late-winter body mass is the main determinant of reproductive success in Svalbard reindeer[33],
324 it is unsurprising that the apparent reproductive advantage of the more heterothermic tactic was
325 mediated by higher late-winter body mass. Svalbard reindeer are capital breeders that rely on
326 internal reserves during late gestation and the first weeks of lactation, before high-quality forage
327 becomes abundant. If peripheral heterothermy attenuates the depletion of body reserves over winter,
328 females are expected to have a lower probability of pregnancy loss[49] and more energy available for
329 subsequent lactation. We could not determine whether reproductive failure occurred before or after
330 parturition because of the limited sample of females with both confirmed pregnancy in late winter
331 and calf status recorded in August. However, low late-winter maternal body mass has previously
332 been shown to strongly predict pregnancy loss in a larger dataset[32].
333 Studies on the link between reproductive success and individual variation in heterothermy
334 are scarce. Hetem et al.[35] suggested that for larger mammals, individuals with greater daily
335 amplitudes in core T_b could be expected to experience reduced reproductive success and fitness, as
336 these responses have generally been employed by animals already in poor condition. Indeed,
337 reduced reproductive output has been associated with increased heterothermy use in some small
338 mammals[11,13]. This may occur because low core T_b can impede foetal development[50], or because a
339 low energetic state triggers several responses that favour survival, including both heterothermy and
340 reduced reproductive investment[12]. Conversely, Desforges et al.[48] argued that reducing core T_b in
341 muskox could mitigate the negative effects of poor pre-winter body condition or reduced winter
342 food accessibility, leading to higher spring energy reserves and thereby enhancing the probability of
343 future reproductive success. Although rumen temperature, used as a proxy for central body
344 temperature, showed relatively little variation in our small sample of Svalbard reindeer, the

association between the more heterothermic tactic in peripheral T_b and higher late-winter body mass is consistent with this broader prediction. Individuals adopting the more heterothermic tactic did so from early winter, suggesting that this tactic was not solely a response to critically depleted body reserves but an anticipatory reaction to the upcoming challenges of the long Arctic winter.

(d) Quantifying within-population variation in thermoregulatory tactics

While mixture regression models have been successfully applied in ecological studies, such as identifying groups of individuals within a population with contrasting life-history tactics[30,51], applying this approach to individual physiological data remains rare (but see[31]). An advantage of using the joint mixture model framework in our study was that it allowed us to combine two complementary thermoregulatory traits (median and amplitude in T_{sc}) to detect different tactics within the population. This approach allowed us to reveal that not only did individuals vary in their T_{sc} patterns, but the two tactics also responded differently to environmental variation and activity levels. In line with the specialist-generalist framework[7,8], the more heterothermic tactic employed by Svalbard reindeer resembled the "generalist" strategy: greater variation in peripheral temperature across a wide range of environmental conditions, was associated with better fitness-related outcomes. Consistent with this framework, the greatest proportion of individuals employed the more heterothermic tactic during the harshest winter, 2018/19. However, the predicted advantage of the less heterothermic tactic under more benign conditions[8] was not evident in our data from the two milder winters. While we describe the two groups identified as distinct thermoregulatory tactics, we recognise that heterothermy is expressed along a continuum, as reflected in the specialist-generalist framework[5,9,10]. Thus, the two tactics we identified should not be interpreted as strictly fixed categories, but as dominant combinations of daily median T_{sc} and daily T_{sc} amplitude within continuous thermoregulatory variation. Our study emphasises the potential insights gained from combining two complementary thermoregulatory traits within a joint mixture-model framework, particularly in cases where distinct tactics can be categorised into a limited number of broader groups.

(e) Why is the more heterothermic tactic not used by all individuals every winter?

The apparent fitness-related advantages associated with the more heterothermic tactic in Svalbard reindeer raise the intriguing question of why this thermoregulatory tactic is not used by all individuals across all winters. One possible explanation is that greater peripheral heterothermy incurs costs or trade-offs under some conditions. Although our study was not long enough to directly assess the impact of peripheral heterothermy on survival, the following plausible trade-offs

might influence this relationship. First, cooling of peripheral tissues could potentially impair locomotor performance until tissues rewarm, which might be costly where rapid responses to predators are required. However, this cost is likely to be limited in Svalbard reindeer because they experience very low levels of natural predation[52,53]. Second, rewarming cooled peripheral tissues may itself carry energetic costs. Opportunities to offset these costs through basking, as employed for instance by Alpine ibex[54], are absent during the polar night. Third, heterothermy may impair immune function[55], although evidence for this effect largely concerns reductions in core T_b rather than peripheral cooling. While our study did not assess immunocompetence directly, a comparative analysis across Norwegian reindeer populations suggests that Svalbard reindeer have relatively low diversity at the major histocompatibility locus[56], which may influence their capacity to respond to pathogens[57]. Whether cooling of the body periphery further affects susceptibility to infection remains unknown[58].

Conclusions

In the context of global climate change, where extreme weather events and resource scarcity are becoming more frequent, flexible and rapid physiological and behavioural responses are potentially key mechanisms that enable individuals to cope and populations to persist[59]. Our findings support the emerging view that heterothermy in free-living mammals should be interpreted as a flexible physiological response to energetic constraint rather than simply a breakdown of homeothermy[22]. For Svalbard reindeer, peripheral heterothermy may reduce overwinter energy expenditure under resource-limited conditions. As climate change progresses at unprecedented rates in the Arctic[60], and particularly in Svalbard[61], weather stochasticity and unpredictability in the availability of resources in winter are also increasing, making peripheral heterothermy a potentially important tactic for this species. More broadly, these results align with recent climate-change physiology frameworks proposing that mammalian thermoregulation reflects interacting pressures from environmental conditions and energy availability, rather than being simply governed by ambient temperature[22] (but see[44]). Our study extends that framework to an Arctic ungulate and highlights peripheral heterothermy as a potentially important tactic for resilience in increasingly variable winter environments.

Methods

(a) Study system

The study was conducted in Nordenskiöld Land, Svalbard (77°50'–78°20' N, 15°00'–15°59' E) on adult female Svalbard reindeer individually marked as part of a long-term capture-mark-recapture study[32]. We focused on females because winter thermoregulation could then be linked to late-winter body mass and subsequent reproductive success. We collected data during two study periods: from captures in March/April 2018 to recaptures in 2019 and from captures in April 2021 to recaptures in 2022 and/or 2023. While the second period spanned two consecutive winters, each winter was analysed independently due to differing environmental conditions (e.g., temperature and precipitation patterns) and their distinct impacts on the reindeer population. Our analyses focused on winter periods, when energetic consequences of heterothermy were likely most relevant[47]. The analysed winter periods spanned from 1 December to 27 March 2019, 23 March 2022 and 14 March 2023, respectively, ending before each capture season to exclude effects of capture disturbance on body temperature and activity levels[62].

The mean air temperatures (December–March) during the three winters were −9.9°C (range −20.6 – 3.8), −9.2°C (range −22.9 – 5.6) and −8.3°C (range −17.3 – 6.7), respectively (Svalbard Airport, SN99840, ~30 km from the study area). The cumulative December–March amount of precipitation falling as rain, a measure of the degree of icing restricting access to forage[63], was 36.4, 5.8, and 26.6 mm, respectively. The study population increased from an estimated 2760 [95% confidence interval, CI 2479−2783] individuals in 2018 to 3490 [95% CI 3190−3598] in 2022 (Pigeon et al., unpublished data, using the method in[64]), extending a long-term trend[65]. In the study area, the plant growing season typically lasts from snowmelt in early June until late August, when day length and air temperature begin to decline[66], after which plant senescence is rapid[67]. Reindeer mate in October, gestation lasts for about 7.5 months and females give birth to a single calf in early June[23]. We determined the reproductive success of individual females by observing the presence of a calf in August.

(b) Animal handling and instrumentation

Reindeer were caught using a net between two snowmobiles[62]. Immediately after capture, animals were weighed using a hanging scale (± 0.5 kg), hind-leg length was measured as an indicator of skeletal size and pregnancy was determined using ultrasound (Vscan Extend, GE HealthCare, Chicago, United States). Females were fitted with GPS collars containing activity and temperature sensors that recorded data every 5 min (Vectronic Aerospace GmbH, Berlin, Germany, ~0.75 kg).

While collar temperature may be influenced by the body temperature of the animal, it also captures effects of solar radiation [68]. Because it was recorded on each animal, collar temperature provided a more representative proxy for the thermal microclimate experienced by the individual than air temperature recorded at a weather station further from the study site.

In 2018, 34 animals were instrumented with a biologging device (details in Electronic Supplementary Material, ESM) that recorded temperature (accuracy ± 0.1°C) (DST Centi-HRT, Star-Oddi, Garðabær, Iceland; Figure S1), placed subcutaneously to the left side of the sternum towards the axilla. Of these, 30 units were retrieved with useful data. Eleven of these animals were also instrumented with a rumen bolus that recorded heart rate and temperature (Ruminal Implant Transmitter, RIT, Vectronic Aerospace; Figure S1) with an accuracy of ± 0.1°C[28]. The RITs were introduced into the pharynx with an applicator and then swallowed by the reindeer into the rumen-reticulum. These units transmitted data to the collar, and the data were downloaded after collar retrieval. In 2021, 60 animals were instrumented with Centi-HRT loggers implanted in the same location as in 2018. In 2022, we implanted an additional temperature logger in 20 of these individuals (MCP9802; Microchip Technology Inc., Chandler, AZ, USA, Figure S1), laterally and subcutaneously on the neck. Details on the surgical implantation are found in the supplementary material. The MCP9802 loggers consisted of a digital temperature sensor coated with inert surgical wax. These loggers were flat (34 × 20 × 6 mm, 5 g). Measurements were calibrated using a water bath and a TESTO 950 thermometer (accuracy ± 0.1°C). Because the animals do not rest with their upper neck against the ground (i.e. "flat out"), the loggers placed in the neck were used to verify that resting on a cold surface was not the major source of variation in the T_{sc} recorded by the chest loggers. In some cases, animals were not recaptured, loggers were not recovered from animals that died, or loggers malfunctioned. The final data set therefore consisted of 47 individuals with complete data for the analyses of peripheral heterothermy (activity and temperature from the collar, T_{sc} from the chest and biometric data from captures), of which 22 were recorded over two winters, resulting in 69 ID-years. A complete overview of implanted loggers and data availability is provided in Table S1 and detailed sample sizes for all individuals in Table S2. All methods were performed in accordance with the relevant guidelines and regulations and are reported following ARRIVE guidelines.

(c) Biologger programming, data retrieval and processing

The chest loggers deployed in 2018 were programmed to record at 15 min intervals, whereas in 2021 the loggers recorded every 30 min, with no post-filtering of these data. To ensure that the

logging intervals did not influence the data, we compared daily values estimated from 15-min data and subsampled at 30 minutes for the same data set. Pearson's correlations ranged from 0.98 to 0.99 and within-individual linear regression slopes ranged from 0.95 to 1.02. The RITs recorded temperatures every 3 min. We used filtered T_{rumen} as a proxy for central body temperature. Because drinking and feeding affect the temperature of the rumen, the temperature records of the rumen loggers were manually filtered to remove feeding events, which were determined as a drop of more than 0.25°C between two consecutive 3 min measurements[28]. The MCP9802 loggers deployed subcutaneously on the neck in 2022 were programmed to record temperatures every 6 min, and no post-filtering of these data was performed. For the analyses of variation in T_{sc} and identification of thermoregulatory tactics, we used data from the chest loggers, because these were the only temperature data available across all three winters. We focused on two metrics: daily median T_{sc} and daily T_{sc} amplitude (the difference between the daily maximum and minimum T_{sc}). Daily median T_{sc} was used to represent central tendency, while daily T_{sc} amplitude represented daily variability in peripheral temperature and hence the extent of peripheral heterothermy.

The GPS collars contained a sensor that recorded gravitational acceleration along three axes: back-forward (X), right-left (Y) and up-down (Z). For our analysis, we used only the X and Y axes to calculate activity levels, as some older collars only recorded data in these two axes. Activity values were recorded on a relative scale between 0 and 255, characterising the mean acceleration in each axis over a 5 min period[69]. Activity values showed a bimodal pattern with a clearly identifiable threshold at 25, which we used to define active and inactive periods (see details in ESM). We used this bimodal classification to calculate the daily proportion of time active by dividing the number of active 5 min periods by the total number of periods recorded per day. Some times the activity sensors had missing data (i.e. NA's). We retained only days for which at least 50% of the 5 min periods contained non-missing values, resulting in the removal of 17 ID-dates in total (0.25% of all ID-dates available).

(d) Statistical analyses

All statistical analyses were conducted with R version 4.5.0[70]. Summary statistics are presented as mean ± standard deviation (SD), median and range, or proportions as appropriate. Model parameter estimates are presented with 95% confidence intervals (CIs). In all modelling steps, we assessed model performance and collinearity between variables using the packages 'DHARMa' [71] and 'performance'[72].

506 ***(i) Patterns of variation in rumen (T_{rumen}) and subcutaneous (T_{sc}) temperatures***

507 We first compared variation in T_{rumen} and T_{sc} visually to assess whether temperature variation was
508 more pronounced in the body periphery than centrally. We then investigated whether variation in T_{sc}
509 was influenced by contact with a cool surface while the animal was lying down. We used Bland–
510 Altman plots [73] to evaluate agreement between temperatures recorded subcutaneously on the chest
511 (potentially in contact with the ground when an animal rested on its left side) and the neck (never in
512 contact with the ground while at rest).
513
514 ***(ii) Drivers of variation in T_{sc}***

515 Next, we explored drivers of variation in daily median T_{sc} and daily T_{sc} amplitude at the population
516 level. We fitted one linear mixed regression and one generalised mixed regression model with a
517 template model builder (glmmTMB package[74]), for daily median T_{sc} and daily T_{sc} amplitude,
518 respectively. The former was fitted with a Gaussian distribution and the latter with a Gamma
519 distribution and inverse link function. Initial models included the following fixed effects after
520 exploration of linearity/non-linearity: calendar day (day since 1 December, continuous), age (in
521 years, fitted as a quadratic term), daily proportion of time active, mean daily collar-recorded
522 temperature (°C, continuous), pregnancy status (0/1, factor) and year (3-level factor). We included
523 the combination of individual identity and year (ID-year) as a random intercept to account for
524 repeated measures on individuals in a specific year. We could not fit year and ID as nested random
525 effects due to the insufficient number of years. Pregnancy status and age contained missing values
526 (pregnancy: n = 12, of which one was also missing age; i.e. age: n = 1 over two ID-years). Using
527 ANOVA, we found that neither age and nor pregnancy status significantly improved the model fit
528 for daily mean T_{sc} (Age: $p = 0.5$; pregnancy: $p = 0.17$), with similar results for the daily T_{sc}
529 amplitude model (age: $p = 0.7$; pregnancy: $p = 0.13$). Therefore, both age and pregnancy were
530 removed from the models to maintain the largest possible sample size.

531 We used the global models to quantify repeatability of each trait. For the median T_{sc} model
532 we extracted the intraclass correlation coefficients for ID-year using the 'icc' function in the
533 package 'performance'. Repeatability of daily T_{sc} amplitude was estimated from the Gamma
534 GLMM with inverse link and a random intercept for ID-year as the among-individual variance
535 divided by the sum of the among-individual variance and the observation-level variance on the link
536 scale. The latter was approximated with the delta method as η^2/ν (η = fixed-effect linear predictor, ν
537 = Gamma shape) and averaged across observations (adjusted repeatability)[75]. We did not use 'icc'
538 for this model, since it applies the log-link residual term and not the inverse-link when using the

delta-method approximation. Running a simulation on the fitted parameters returned similar values with to our manual calculation. For both traits, we bootstrapped the estimations with 500 iterations to extract 95% confidence intervals (CI).

(iii) Identification of thermoregulatory tactics

To assess whether individuals grouped into different thermoregulatory tactics, we fitted a joint mixture regression model using the 'flexmix' package[76]. Briefly, mixture models incorporate a categorical latent variable that segregates individuals into groups sharing similar traits without prior knowledge of the exact variable(s) resulting in this grouping[29]. This allows testing for the presence of groups representing different tactics shared by individuals within a population[30]. Here, we tested specifically for the presence of two groups (two thermoregulatory tactics) by comparing support for a two-group model against support for a model without grouping (a single tactic across the population), based on both Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) as suggested by[30]. The mixture model with the lowest AIC and BIC was considered better supported. We fitted the joint mixture model with two response variables: daily median T_{sc} and daily T_{sc} amplitude. Daily median T_{sc} was fitted with a mixed linear regression driver ('FLXMRlmm'), while daily T_{sc} amplitude was fitted with a generalised linear regression driver ('FLXMRglm') and a Gamma distribution (inverse link function). We used a combined ID-year variable as the grouping level, allowing individuals to be assigned to different groups each winter. In both models, we included the following fixed effects based on the initial model exploration detailed above (continuous covariates were centred to a mean of 0 and scaled to 1 SD): days since 1 December (continuous), daily mean collar-recorded temperature (continuous), daily proportion of time active (continuous) and year (factor with 3 levels). We extracted the grouping assigned to each ID-year from the final mixture model and the posterior probabilities of belonging to a specific group. In order to visualise and compare the parameter effect sizes between the groups and the two response variables, we refitted the mixture models using 'glmmTMB' to extract parameter estimates. We used the posterior probability of belonging to each group as weights within the models, and the parameter coefficients from each response variable and group as starting parameters for the refitted models. This resulted in four refitted models with distinct starting parameters, one for each response variable (daily median T_{sc} and daily T_{sc} amplitude) and each group.

570 ***(iv) Thermoregulatory tactics and fitness-related outcomes***

571 To evaluate fitness-related outcomes associated with each thermoregulatory tactic, we tested
572 whether the two groups differed in body mass measured at the end of each winter (n = 57) and in
573 subsequent reproductive success (calf at heel observed in August [1] or not [0], n = 37). To assess
574 the contribution of direct, indirect and global effects of thermoregulatory tactic and body mass on
575 reproductive success, we performed a confirmatory path analysis[77] using the piecewiseSEM
576 (pSEM) R package[78]. Based on the known impact of mass on reproductive success[32], we built a path
577 model representing the expected causal relationships among the observed variables. The model
578 comprised two sub-models. The first sub-model included body mass as the response variable,
579 thermoregulatory group as the independent variable, hind-leg length as a covariate to control for
580 skeletal size[79], and individual ID as a random intercept using the glmmTMB function with a
581 Gaussian distribution. The second sub-model included reproductive success as a function of body
582 mass and thermoregulatory group, using a generalised linear model (glm) with a binomial
583 distribution and a logit-link function. We could not include individual ID as a random intercept in
584 this sub-model because it led to model singularity, meaning that the sub-model was unable to
585 estimate this effect due to the small sample size and few repeated IDs. Furthermore, with the
586 relatively small sample size for reproductive success (n = 37), we could not include year, a 3-level
587 factor, as this would lead to overfitting. To account for annual variation in body mass and skeletal
588 size, we therefore mean-centred body mass and hind-leg length within each year[80].
589 Lastly, to assess whether a single continuous metric better explained variation in fitness-
590 related outcomes than thermoregulatory group, which was derived from the combination of the two
591 T_{sc} traits, we performed three additional pSEMs. In one pSEM, thermoregulatory group was
592 replaced with winter median T_{sc} (the median of daily median T_{sc} values for each ID-year) and in the
593 other it was replaced with winter median daily T_{sc} amplitude (the median of daily T_{sc} amplitude
594 values for each ID-year). We did not combine the two in one regression due to the high correlation
595 between them (Spearman's rho = −0.71, $p < 0.0001$). We then used AIC corrected for small sample
596 sizes (AICc) to compare the relative support of the three pSEMs, i.e. models including either
597 thermoregulatory group, winter median T_{sc} or winter median daily T_{sc} amplitude as explanatory
598 variables, against a null model with no thermoregulatory predictor. We considered models with
599 $\Delta AICc \leq 2$ to have equivalent support.
600

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Data availability. Public weather data from Longyearbyen Airport can be found online on https://seklima.met.no/. Data and code will be made public along with the publication and can be accessed through a private link for review: https://figshare.com/s/1858eda23e1e14825946

Competing interests. We have no competing interests.

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