RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Fat storage influences fasting endurance more than body size in an ungulate

L. Monica Trondrud[1] | **Gabriel Pigeon[1,2]** | **Elżbieta Król[3]** | **Steve Albon[4]** | **Alina L. Evans[5]** | **Walter Arnold[6]** | **Catherine Hambly[3]** | **R. Justin Irvine[4,7]** | **Erik Ropstad[8]** | **Audun Stien[9]** | **Vebjørn Veiberg[10]** | **John R. Speakman[3,11,12,13]** | **Leif Egil Loe[1]**

[1]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway; [2]Département de Biologie, Faculté des Sciences, 2500 boul. de l'Université Sherbrooke, Sherbrooke, QC, Canada; [3]School of Biological Sciences, Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, UK; [4]The James Hutton Institute, Aberdeen, UK; [5]Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Elverum, Norway; [6]Department of Interdisciplinary Life Sciences, Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna, Austria; [7]Frankfurt Zoological Society, Addis Ababa, Ethiopia; [8]Faculty of Veterinary Science, Norwegian University of Life Sciences, Oslo, Norway; [9]Department of Arctic and Marine Biology, The Arctic University of Norway, Tromsø, Norway; [10]Norwegian Institute for Nature Research, Trondheim, Norway; [11]Center for Energy Metabolism and Reproduction, Shenzhen Institutes of Advanced Technology, Chinese Academy of Sciences, Shenzhen, China; [12]CAS Center of Excellence in Animal Evolution and Genetics, Kunming, China and [13]State Key Laboratory of Molecular Developmental Biology, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, China

Correspondence
L. Monica Trondrud
Email: monica.trondrud@gmail.com

John R. Speakman
Email: j.speakman@abdn.ac.uk

Funding information
Norges Miljø- og Biovitenskapelige Universitet; Norges Forskningsråd, Grant/Award Number: 267613; Tromsø Research Foundation

Handling Editor: Caroline Isaksson

Abstract

1. The fasting endurance hypothesis (FEH) predicts strong selection for large body size in mammals living in environments where food supply is interrupted over prolonged periods of time. The Arctic is a highly seasonal and food-restricted environment, but contrary to predictions from the FEH, empirical evidence shows that Arctic mammals are often smaller than their temperate conspecifics. Intraspecific studies integrating physiology and behaviour of different-sized individuals may shed light on this paradox.

2. We tested the FEH in free-living Svalbard reindeer *Rangifer tarandus platyrhynchus*. We measured daily energy expenditure (DEE), subcutaneous body temperature (T_{sc}) and activity levels during the late winter in 14 adult females with body masses ranging from 46.3 to 57.8 kg. Winter energy expenditure (WEE) and fasting endurance (FE) were modelled dynamically by combining these data with body composition measurements of culled individuals at the onset of winter (14 years, $n = 140$) and variation in activity level throughout winter (10 years, $n = 70$).

3. Mean DEE was 6.3 ± 0.7 MJ/day. Lean mass, T_{sc} and activity had significantly positive effects on DEE. Across all 140 individuals, mean FE was 85 ± 17 days (range 48–137 days). In contrast to the predictions of the FEH, the dominant factor affecting FE was initial fat mass, while body mass and FE were not correlated. Furthermore, lean mass and fat mass were not correlated. FE was on average 80%

(45 days) longer in fat than lean individuals of the same size. Reducing activity levels by ~16% or T_{sc} by ~5% increased FE by 7% and 4% respectively.

4. Our results fail to support the FEH. Rather, we demonstrate that (a) the size of fat reserves can be independent of lean mass and body size within a species, (b) ecological and environmental variation influence FE via their effects on body composition and (c) physiological and behavioural adjustments can improve FE within individuals. Altogether, our results suggest that there is a selection in Svalbard reindeer to accumulate body fat, rather than to grow structurally large.

KEYWORDS

activity, biologging, daily energy expenditure, doubly labelled water, intraspecific scaling, subcutaneous body temperature, Svalbard reindeer, the Arctic

1 | INTRODUCTION

The effects of the environment on body size and shape of animals (Bergmann, 1847), as well as the relationship between body size and metabolism (Kleiber, 1961), are fundamental principles in ecological and physiological theory. In particular, environmental temperature and resource availability are central drivers of animal energetics, and have subsequently shaped the evolution of body size in animals (Brown et al., 2004; McNab, 2010). The fasting endurance hypothesis (FEH) predicts that animals should be larger in environments where food supply is interrupted over prolonged periods (Lindstedt & Boyce, 1985; Millar & Hickling, 1990), because fat stores increase with body size at a steeper rate than energy expenditure (Calder, 1984). A caveat of this hypothesis is that selection is an intraspecific process, while the scalars used to explain this pattern are derived interspecifically. Although often proposed as a mechanism for observed body size patterns, few studies have tested the FEH at the intraspecific level (Boos et al., 2005; Lundblad & Conway, 2020; Swenson et al., 2007).

There are at least three non-trivial factors that may contribute to the lack of studies properly addressing the role of fasting endurance (FE) as a determinant of body size patterns within a species. First, variation in body size and mass observed within species is typically much smaller than between species (Dunbrack & Ramsay, 1993). Furthermore, intraspecific variation in structural body size may be small, while body mass can vary greatly due to differences in body condition (Dunbrack & Ramsay, 1993; Sheriff et al., 2011). Thus, to evaluate the importance of FE within species, it is necessary to quantify FE across the relevant ranges of both body size and body mass. Second, ecological factors may be more important in influencing the size of internal body stores than structural size. In seasonal environments where food availability varies throughout the year, the amount of resources available largely determines the degree of fattening prior to the food-depleted season (Loe et al., 2021; Pagano et al., 2018). In periods of low resource availability body mass declines, largely driven by the depletion of fat stores (Reimers & Ringberg, 1982). Therefore, body composition may be more relevant

for determining FE than body mass itself. Third, the rate at which internal body stores are depleted depends on the total energy expenditure (Speakman & Westerterp, 2013). Many species inhabiting seasonal environments decrease energy expenditure during the food-depleted seasons (Fletcher et al., 2012; Riek et al., 2019). Reductions in locomotor activity (Arnold et al., 2018), decreased endogenous heat production and an increased tolerance towards low peripheral body temperatures may further facilitate the seasonal drop in energy budgets (Arnold, 2020; Trondrud, Pigeon, Albon, et al., 2021). Individual and temporal variations in energy expenditure may therefore play an additional explanatory role in determining FE within a species (Desforges et al., 2021). Understanding the relative influence of environmental and individual variation on metabolic phenotypes and the capacity of free-living animals to withstand food scarcity can provide potentially novel insights into the role of FE as a driver of natural selection.

The Arctic is one of the most seasonal and temporally food-restricted environments. While the prediction from the FEH would be a selection for large body size in Arctic animals, empirical evidence shows that Bergmann's rule, that is, increasing body size with increasing latitude, does not hold above the Arctic circle (66°N; Huston & Wolverton, 2011). This suggests that Arctic species might have alternative strategies to increase FE rather than having a large body size. To explore this phenomenon, we tested the FEH in a species inhabiting the High Arctic, the Svalbard reindeer *Rangifer tarandus platyrhynchus*. They are among the structurally smallest subspecies of *Rangifer*, yet the relative size of their autumn fat reserves is unprecedentedly large (Pedersen et al., 2019). Variation in body size and mass between cohorts can be up to 20%, as a result of early life conditions (Douhard et al., 2016). Furthermore, individual body mass varies greatly throughout the year with rapid growth and fattening during the short Arctic summer, and a depletion of up to 50% of body mass by the end of winter (Reimers & Ringberg, 1982). Still, Svalbard reindeers' fat reserves are insufficient to cover the energy demands over of the entire winter and must be subsidised by food intake (Tyler, 1987) in a season when snow and ice conditions restrict access to forage. Late winter body mass explains most of

the annual variation in reproduction and survival, and is negatively related to, both early onset of snow in the autumn (Loe et al., 2021) and the severity of rain-on-snow in the subsequent winter (Albon et al., 2017). From the predictions of the FEH, long periods of low food availability, coupled with abrupt food shortage, should have led to a selection for a large body size. Yet, Svalbard reindeer are smaller than contemporary conspecifics in all candidate areas of origin (Yannic et al., 2014), indicating a selection for smaller size and a case of insular dwarfism (Foster, 1964).

In this paper, we first quantify the drivers of energy expenditure in free-living Svalbard reindeer. Specifically, we measured daily energy expenditure (DEE) in females during the late Arctic winter (March/April) using the doubly labelled water (DLW) method (Butler et al., 2004), in relation to body composition, activity and subcutaneous body temperature (T_{sc}). Second, we constructed and parameterised a dynamic model of energy use (Speakman & Westerterp, 2013) using the measurements of DEE and body composition data collected from autumn culls of 140 Svalbard reindeer females over 14 years (Albon et al., 2017) to quantify winter energy expenditures (WEE) and FE. This enabled us to test the central prediction of the FEH that larger individuals, both skeletally and by mass, have greater FE than smaller individuals. Furthermore, we evaluated the relative importance of adjustments in activity levels and T_{sc} for FE. Investigating individual variation in energetics provides a potential advance in understanding environment–body size relationships and their implications for survival.

2 | MATERIALS AND METHODS

2.1 | Animals and study system

The study was conducted in Nordenskiöld Land, Svalbard (77°50′–78°20′N, 15°00′–15°60′E) during the late winter (March–April) 2017 and 2018. We used a total of 21 adult Svalbard reindeer females in their prime age (3–7 years old, body mass [M_b] range 46.3–57.8 kg), which had been marked as calves as part of a long-term capture–mark–recapture study (Albon et al., 2017). Males have not been followed in detail. In the study area, the plant growing season typically lasts from snow melt (early June) until late August, when temperatures and day length decline (Van Der Wal & Stien, 2014). Reindeer mate in October and gestation lasts for about 7.5 months, with calving occurring in early June (Albon et al., 2017).

2.2 | Capture and handling

Animals were caught using snowmobiles (Omsjø et al., 2009), and blood samples were collected from the jugular vein. Animals were weighed (±0.5 kg), length of hind leg (±1 mm, hereafter 'leg length') was measured as an indicator of body size and pregnancy status was checked using ultrasound (Kaixin Electronic Instrument Co.; Table S2). All animals were fitted with GPS collars containing activity

sensors (Vectronic Aerospace GmbH), and in 2018, also fitted with a biologger to record T_{sc} (details in 2.4).

2.3 | Daily energy expenditure by doubly labelled water technique

All 21 animals were caught and dosed with DLW to measure DEE. The estimates of DEE were obtained in 2017 ($n = 6$) and 2018 ($n = 17$), with two animals studied in both years (Table S2). This technique has been validated by indirect calorimetry in a wide range of mammals, providing an accurate measure of DEE over periods of several days (Butler et al., 2004). Animals were first blood sampled for background levels of ^{18}O and ^2H (Method A: Speakman & Racey, 1987) and then dosed with ~0.3 ml of DLW (65 atom% ^{18}O, 35 atom% ^2H) per kg of M_b. The DLW was injected into the jugular vein, on the opposite side from the blood sampling. The animals were recaptured 2 days later to obtain initial (equilibrated) blood samples, and then 7–10 (2017) or 14–20 (2018) days later to collect final blood samples. The differences in timing between the 2 years reflected a lack of knowledge of reindeer metabolism in the first year, resulting in large excess of isotopes in the final 2017 samples. Therefore, the time span between initial and final sampling was extended in 2018 to improve the protocol. Blood samples were stored in flame-sealed glass capillaries at room temperature for further processing. Details on the isotope analyses and calculations are provided in Appendix A1; the results are presented in Table S3. Total body water (TBW) was calculated from the deuterium dilution space (N_d) assuming that N_d corresponds to 104% of TBW (Schoeller et al., 1986). The conversion of TBW ($N_d/1.04$) to lean mass assumed that lean tissue contains on average 73% water (Marken Lichtenbelt et al., 1994). This calculation does not account for water content in the digestive tract, which may lead to a bias in estimating lean mass (Andrew et al., 1995). We therefore assumed that the gut fill accounts for 22% of the reindeer's body mass, and that the water content of the gut is 85%, as reported for Svalbard reindeer, previously (Sørmo et al., 1999; Staaland et al., 1979). The estimated gut water content was subtracted from the lean mass. Hereafter, these values are referred to as isotope-derived lean mass corrected for gut water ($M_{lean(I)}$).

2.4 | Biologging of subcutaneous body temperature (T_{sc})

In 2018, the measurements of DEE were coupled with the recordings of T_{sc} using a small biologger (Star-Oddi DST-CentiHRT, Star-Oddi). Loggers were implanted subcutaneously on the chest, left sternum or caudal to the left elbow, under anaesthesia with intranasal medetomidine (details in Appendix A2). T_{sc} was recorded with an accuracy of 0.1°C every 15 min by a calibrated thermistor in the biologger (details in Appendix A3). Out of the 17 biologgers deployed in 2018, only 14 were successfully retrieved the following year and only seven had successfully stored data for the period October–April

(Table S2). For the model of T_{sc} over winter, we also included data from three individuals with biologger but without DEE measurements. To investigate the effect of T_{sc} on DEE, we used the mean T_{sc} recorded in the DLW measurement period.

2.5 | Locomotor activity and environmental data

The GPS collars contain an activity sensor that recorded gravitational acceleration along two axes, X and Y, which represented back–forward and right–left movements respectively. Activity was recorded as the difference in acceleration between two consecutive measurements, characterising the mean acceleration in each axis over a 5-min period within a relative range between 0 and 255 (Krop-Benesch et al., 2011). When exploring the effect of daily activity on DEE, we used the sum of X and Y over the DLW measurement period, divided by the duration of this period (in days). Daily activity values ranged from 12,809 to 23,651 across individuals. To parameterise our model of FE, we used activity data derived from 70 individuals between 2009 and 2019 (267 individual-year combinations) for the 7-month winter period (October 20–May 20, 212 days, defined by Tyler, 1987). Here, activity was calculated as the daily sum of acceleration of X and Y (range 0–64428, $n = 38,646$). Activity data were downloaded directly from the collar during the capture event in 2019. The GPS collars also recorded temperature (hereafter T_{ac}), which is a reliable source of fine-scale temperature for wildlife ecological studies (Ericsson et al., 2015). Because the temperature logger was situated on top of the collar, it absorbed solar radiation and to some extent reflected the microclimate the animal was experiencing.

2.6 | Autumn body composition

To estimate the body composition of reindeer in autumn, we used data from adult female Svalbard reindeer (3–9 years old, $n = 140$) from the same population as the current study, which were culled in late October (19–27) from 1994 to 2007 (Albon et al., 2017). To derive representative body size (leg length, mm) and body composition phenotypes, we selected the mean, the 10th and 90th quantiles of lean mass derived from regressions of body composition ($M_{lean(R)}$). On these, we added the fat stores, hereafter 'fat mass' (M_{fat}), derived from the mean, the 10th and 90th quantiles of M_{fat} as % of $M_{lean(R)}$ (20, 13 and 27% respectively). This resulted in five representative body size and composition phenotypes: (a) 'average', (b) 'small and lean', (c) 'small and fat', (d) 'large and lean' and (e) 'large and fat' (Table 1; Figure S1). We set 40% loss of muscle and organ mass as the threshold before an animal dies from starvation (Tyler, 1987). Body composition details are provided in Table 1. The calculations of body composition for selection of phenotypes are described in detail in Appendix A4.

2.7 | Statistical analyses

All statistical analyses were conducted using R version 4.0.0 (The R Core Team, 2020). DEE was modelled using linear regression based on 14 individuals with complete data, with the following candidate variables: mean M_b (kg) between initial and final blood sample points, pregnancy status, age (as a continuous variable), mean daily T_{sc}, mean daily activity and $M_{lean(I)}$. Because $M_{lean(I)}$ and M_b were correlated, we compared models containing either $M_{lean(I)}$ or M_b using Akaike's information criteria for small sample size (AICc; Burnham & Anderson, 2002). The inclusion of $M_{lean(I)}$ yielded a more parsimonious model (ΔAICc = −1.9) and therefore $M_{lean(I)}$ was selected as the candidate variable to represent mass. The full model was simplified using a backward stepwise deletion approach, presented in Appendix B (Crawley, 2015).

Daily activity between October 20 and May 20 was modelled in relation to T_{ac} and body size (leg length). We used a generalised additive mixed-effects model (gamm), using the *bam* function for very large datasets (MGCV package; Wood, 2017). We fitted time (days) as a thin plate regression spline, with year and individual as random effects for both slope and intercept (separately). An autoregressive

TABLE 1 Characterisation of five body size and composition phenotypes of Svalbard reindeer females based on the data from the adult females culled in October 1994–2007 ($n = 140$, Albon et al., 2017). Selection of phenotypes is described in Appendix A4. WEE was based on average activity levels, and fasting endurance (FE) assumes an activity level at zero to infer metabolism at rest. Details on these calculations are described in Appendix C1

Phenotype	M_b	$M_{lean(R)}$	M_{fat} %	LL	M_{fat}	E_{tot}	% E_{fat}	WEE	% E_{food}	FE	% M_b loss
Average	68	52.8	20	281	10.6	492	84	1728	74	79 ± 1	38
Small–lean	57	46.1	13	276	6.0	315	78	1936	66	101 ± 2	42
Small–fat	63	46.1	27	276	12.4	547	87	1874	80	56 ± 1	33
Large–lean	73	60.3	13	284	7.9	408	79	1572	68	101 ± 2	41
Large–fat	80	60.3	27	284	16.3	711	88	1548	83	56 ± 1	33

Abbreviations and units: M_b, body mass (kg); $M_{lean(R)}$, regression-derived lean mass (kg); M_{fat} %, fat mass as percent of $M_{lean(R)}$; LL, length of hind leg (mm); M_{fat} fat mass (kg); E_{tot}, total energy reserve (MJ); % E_{fat}, percentage of E_{tot} derived from fat (lipids), remaining percent is derived from proteins; WEE, winter energy expenditure (MJ); % E_{food}, percentage of WEE contributed by food intake; FE, mean ± SD of fasting endurance (days); % M_b loss, percent loss of M_b at end of fasting period (death).

function was used to account for within-individual temporal auto-correlation. In addition, T_{sc} data were available for nine individuals. We fitted a gamm modelling daily mean T_{sc} (3,228 records) against activity and T_{ac} (fixed effects), with the same structure as the activity model, except that year was excluded as random effect because the data were from a single winter.

To estimate FE, we used predictions based on the best fitting model of DEE, which included $M_{lean(I)}$, mean daily T_{sc} and mean daily activity as explanatory variables (Table S4). For each winter day, DEE was predicted using $M_{lean(R)}$, predicted activity and T_{sc} from the models described above, for all 140 individuals and the five body size and composition phenotypes. At each time step t (one day), the mass of each body compartment was recalculated based on the depletion of energy reserves from fat and protein (Speakman & Westerterp, 2013; Figure S4), and DEE was predicted from the recalculated $M_{lean(I)}$. A graphical presentation of the model input and steps is presented in Figure 1 and further details are provided in Appendix C. In the simulations of fasting, metabolisable energy from food was set to zero, and thus all energy expended was derived from internal stores. FE was modelled for all individuals assuming resting conditions (zero activity) or with predicted activity levels (see below). The model was iterated 100 times per individual and 1000 times per phenotype. Details on how uncertainty was included, and sensitivity analyses are provided in Appendix C.

To estimate the influence of adjustments in activity and/or T_{sc} levels, we extracted the theoretical 10th and 90th quantiles based on random effect variance of the individual random intercepts in activity (−3,982, +3,982) and T_{sc} (−1.9, +1.9) models. These values were then added to the mean predictions to generate high and low levels of activity and/or T_{sc}, resulting in a mean difference of ±16% in activity and ±5% in T_{sc}. We modelled FE at all nine combinations (low, mean and high level of both activity and T_{sc}) for the five body size and composition phenotypes, resulting in 45 combinations of body phenotype, activity level and T_{sc} level. Using the FE model, we calculated the minimum amount of metabolisable energy obtained from food required to survive the winter to derive an estimate of WEE. For simplicity, this was fixed at a constant value throughout the winter. We selected the lowest value that would allow survival for 212 days, while sustaining normal activity and T_{sc}, for each of the 140 individuals. Model uncertainties were not included in these analyses.

3 | RESULTS

3.1 | Drivers of daily energy expenditure

Daily energy expenditure in late winter ranged between 5.5 and 8.1 MJ/day, with a mean ± standard deviation (SD) of 6.3 ± 0.7 MJ/day. DEE was higher in animals with higher lean mass, higher mean T_{sc} and higher activity levels (Figure 2). Together, $M_{lean(I)}$, T_{sc} and activity explained 52% of the individual variation in DEE ($p = 0.02$).

Singularly, $M_{lean(I)}$, T_{sc} and activity explained 39%, 20% and 10% of the variance in (they sum to >52% due to colinearity between T_{sc} and activity; more details in Figure S2).
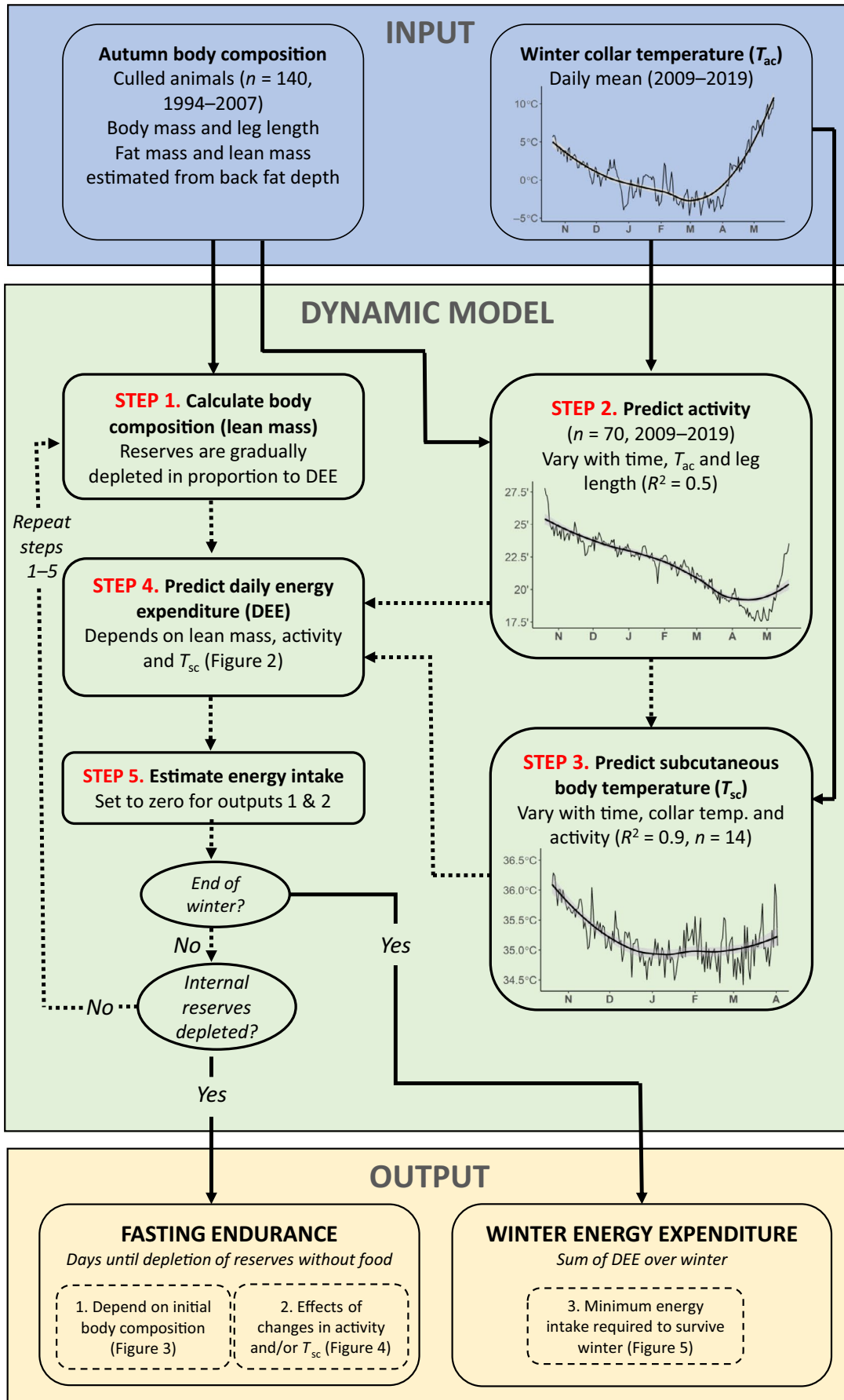
3.2 | Estimates of fasting endurance

Fasting endurance was mostly determined by fat reserves rather than body size or mass, in contrast to the prediction from the FEH. Across all 140 individuals, mean ± SD of FE was 85 ± 17 days (range 48–137 days) under the theoretical assumption that individuals are continuously resting (Figure 3). The most important determinant of FE was initial fat mass (M_{fat}, Adj. $R^2 = 0.74$, $p < 0.001$), followed by lean mass ($M_{lean(R)}$; Adj. $R^2 = 0.18$, $p < 0.001$). M_{fat} and $M_{lean(R)}$ were not correlated ($r = 0.07$, $p = 0.4$) and had opposite effects on FE: greater M_{fat} increased FE (Figure 3a), while greater $M_{lean(R)}$ caused a decrease in FE (Figure 3b). In contrast, M_{fat} and M_b were positively correlated ($r = 0.5$, $p < 0.001$), but M_b was not a significant determinant of FE (Adj. $R^2 = −0.01$, $p = 0.8$, Figure 3c). Finally, while FE decreased with increasing body size (leg length: Figure 3d), leg length explained relatively little of the variation in FE (Adj. $R^2 = 0.04$, $p < 0.01$).

Variation between the five body size and composition phenotypes reinforces this pattern. The 'average' individual would survive 79 ± 1 days without food (with assumed continuous rest). The two fat phenotypes (both small and large size) would survive 101 ± 2 days, and the two lean phenotypes (both small and large size) were predicted to survive 56 ± 1 days. Thus, FE was 45 days (~80%) longer in fat than in lean individuals of the same size (Table 1). FE did not differ between small and large size, within fat and lean phenotypes (Table 1).

3.3 | Effects of activity and subcutaneous body temperature (T_{sc}) on fasting endurance

Reductions in both activity levels and T_{sc} increased FE (Figure 4). Daily activity decreased with time over winter, reaching a minimum around April 27, before increasing again in May (Figure S3). Furthermore, daily activity decreased with ambient temperature (T_{ac}) and was higher in individuals with larger skeletal size, with the fixed and random effects explaining 49% of the variation in activity (Table S5). T_{sc} increased with daily activity and T_{ac}, which together with the random effects explained 89% of the variation in T_{sc} (Table S6). Sustaining lower activity levels (~16% reduction) could prolong FE by 7% on average, whereas increasing activity levels (~16% increase) would shorten FE by 6%. While lowering T_{sc} (~5% reduction) would only improve FE by on average 4%, sustaining increased T_{sc} (~5% increase) would shorten FE by as much as 22%, on average. In the simulations, the greatest FE (81 days) was predicted for the large and fat phenotype sustaining low activity and low T_{sc}, whereas the shortest FE (28 days) was predicted for the small and lean phenotype sustaining high activity and high T_{sc}.

INPUT

Autumn body composition
Culled animals (*n* = 140, 1994–2007)
Body mass and leg length
Fat mass and lean mass
estimated from back fat depth

Winter collar temperature (T_{ac})
Daily mean (2009–2019)

DYNAMIC MODEL

STEP 1. Calculate body composition (lean mass)
Reserves are gradually depleted in proportion to DEE

STEP 2. Predict activity
(*n* = 70, 2009–2019)
Vary with time, T_{ac} and leg length (R^2 = 0.5)

Repeat steps 1–5

STEP 4. Predict daily energy expenditure (DEE)
Depends on lean mass, activity and T_{sc} (Figure 2)

STEP 5. Estimate energy intake
Set to zero for outputs 1 & 2

STEP 3. Predict subcutaneous body temperature (T_{sc})
Vary with time, collar temp. and activity (R^2 = 0.9, *n* = 14)

End of winter?

No

Yes

Internal reserves depleted?

No

Yes

OUTPUT

FASTING ENDURANCE
Days until depletion of reserves without food

1. Depend on initial body composition (Figure 3)

2. Effects of changes in activity and/or T_{sc} (Figure 4)

WINTER ENERGY EXPENDITURE
Sum of DEE over winter

3. Minimum energy intake required to survive winter (Figure 5)

FIGURE 1 Schematic diagram of calculations steps to derive fasting endurance (FE) and winter energy expenditure (WEE) in Svalbard reindeer. The model calculates each step for 1 day at a time, making a loop that is broken when energy reserves are depleted, or when reaching end of winter (day 212). Solid arrows represent data fed into the model prior to the loop, while dashed lines represent steps that are repeated each day consecutively. For the WEE calculation, a fixed value of energy from food (in MJ) is fed into the loop (step 5) and is increased by increments of 0.5 MJ until the loop reaches the end of winter before energy reserves are depleted. To estimate FE, energy from food is set to zero

FIGURE 2 Daily energy expenditure (DEE) of Svalbard reindeer females ($n = 14$) as a function of (a) isotope-derived lean mass corrected for gut water ($M_{lean(l)}$, kg), (b) subcutaneous body temperature (T_{sc}; °C) and (c) mean daily activity level. In each regression, the points are adjusted for the other variables. The straight lines represent the predicted relationship, and the shaded areas are the 95% confidence intervals of the fitted model
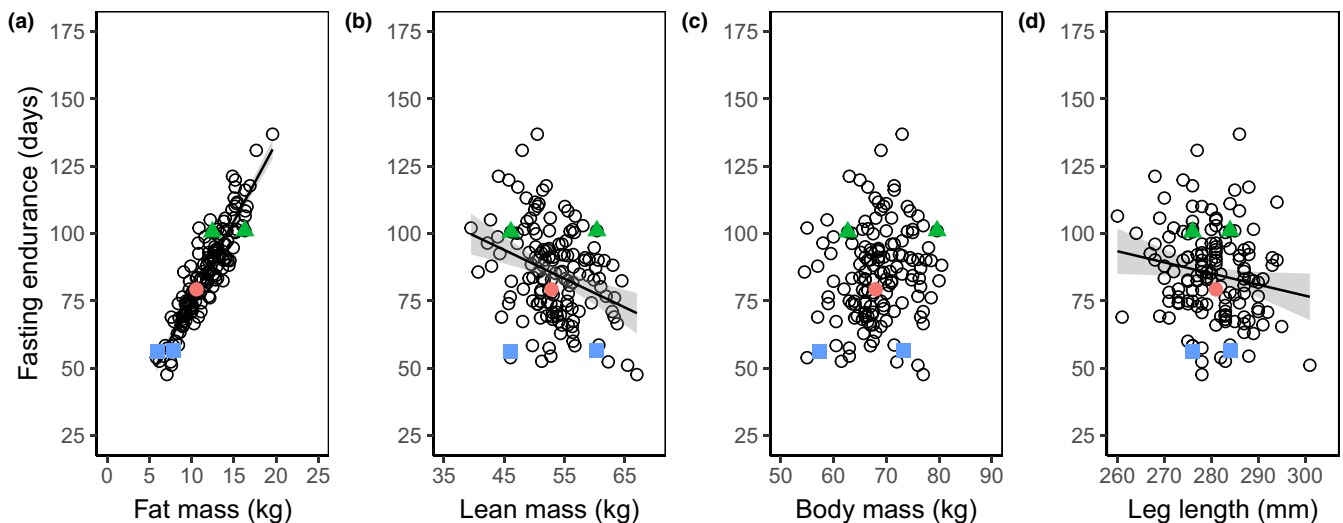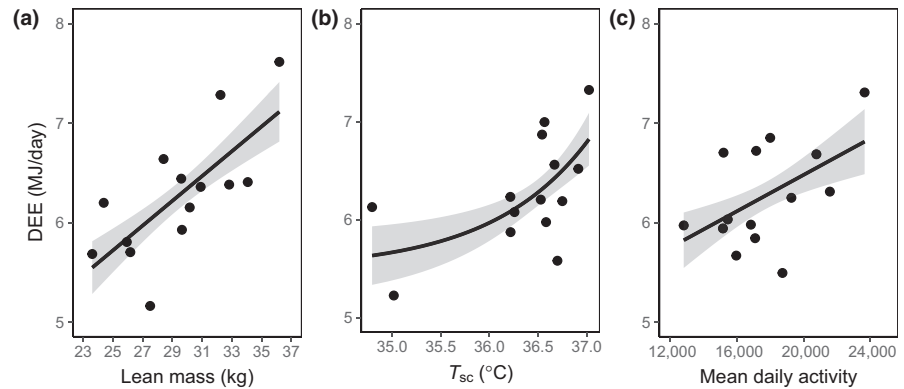
FIGURE 3 Fasting endurance (FE) estimated for Svalbard reindeer females ($n = 140$, open circles) and five body size and composition phenotypes ($n = 5$, filled shapes) under the assumption of continuous rest and zero food intake, against (a) initial body mass ($p = 0.8$), (b) initial fat mass (Adj. $R^2 = 0.74$, $p < 0.001$), (c) initial lean mass (Adj. $R^2 = 0.18$, $p < 0.001$) and (d) leg length (Adj. $R^2 = 0.02$, $p = 0.04$). Pink circles, green triangles and blue squares represent average, fat and lean individuals respectively (see Table 1 for details)

3.4 | Contribution of food intake to winter energy expenditure

Individuals with fat mass greater than that predicted for their body mass would survive with a lower food intake compared with individuals that fall below the fitted regression line of fat mass to body mass (Figure 5). The mean estimated WEE was $1,742 \pm 129$ MJ (range 1,404–2,055 MJ) over 212 winter days. The average phenotype would have to obtain a minimum of $1,248 \pm 146$ MJ (range 958–1,704 MJ) as metabolisable energy from food to survive the winter. Thus, internal fat stores contributed on average to $28 \pm 6\%$ (range 16%–44%) of WEE at mean activity and T_{sc} levels (Figure 5; Table 1).

The difference in WEE between lean and fat individuals of similar size was small (Table 1).

4 | DISCUSSION

The FEH has been criticised for lacking ecological context (McNab, 2010), but many of the tools to investigate this idea in large mammals have only recently become available. The FEH, as originally proposed by Millar and Hickling (1990) was based on the interspecific scaling exponents of fat and body mass (Calder, 1984). As a result, the FEH assumes that the only way to store additional
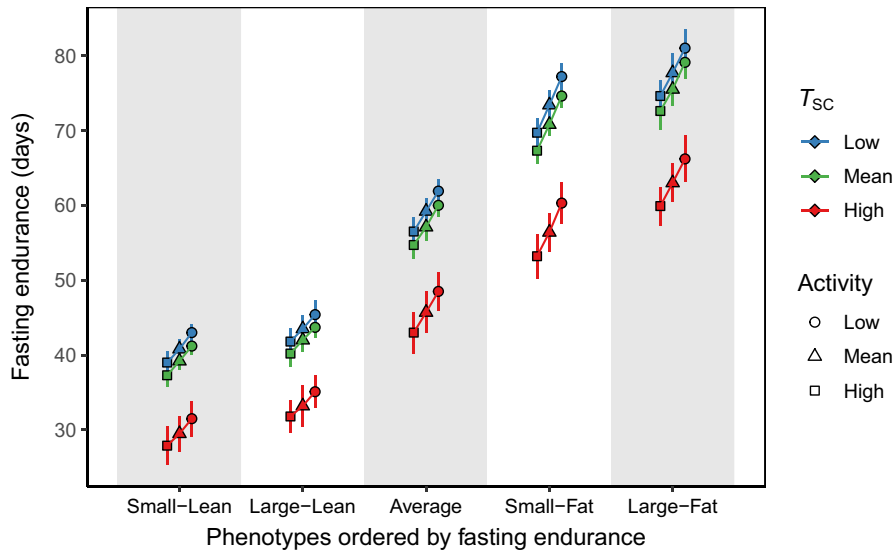
FIGURE 4 Fasting endurance (FE) estimated for five body size and composition phenotypes of Svalbard reindeer females, sustaining low (circles), mean (triangles) and high (squares) activity levels, and maintaining low (blue), mean (green) and high (red) subcutaneous body temperature (T_{sc}) during winter. The result is a constantly lowered or increased activity (±16%) and/or T_{sc} (±5%) sustained until energy reserves are depleted (death occurs). The vertical lines represent the 95% confidence interval for each prediction, drawn from 100 simulations
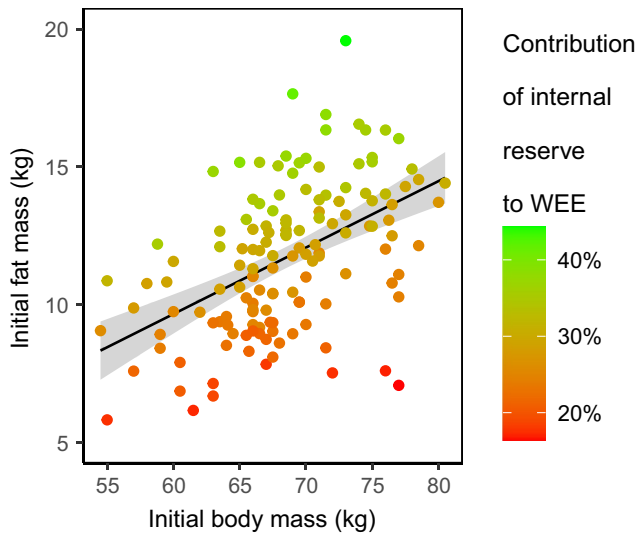
FIGURE 5 Relationship between initial fat mass and initial body mass in Svalbard reindeer females ($n = 140$). Data were collected at the beginning of winter (late October). The colour gradient represents the contribution of internal body reserves to the winter energy expenditure (WEE) over 212 days. The straight line shows the regression of initial fat mass to initial body mass, and the shaded area represents the 95% confidence intervals of the regression

fat is to become larger. We found no correlation between FE and body size and only a small correlation with mass, suggesting that animals of any size can increase the size of their fat stores to increase FE. Consistent with our findings, there is likely a strong selection in Svalbard reindeer to accumulate body fat ahead of the long winter rather than investing in structural growth from an early age. This may explain the paradox of their relatively small size in an environment strongly favouring enhanced FE.

Our estimated mean DEE (6.3 MJ/day) was similar to previously measured resting metabolic rate of captive Svalbard reindeer (6.5 MJ/day; Nilssen et al., 1984). Since DEE includes energy expended both

during activity and rest, this result suggests that Svalbard reindeer in the wild have a greater ability to reduce energy expenditure during winter than previously assumed. More than half of the variation in DEE was explained by $M_{lean(l)}$, T_{sc} and activity. The fact that lean mass explains more variation in metabolic rate than body mass is comparable to results in humans and apes (Pontzer et al., 2016). Lean mass comprises the 'metabolically active' tissue, while fat is relatively 'metabolically inert' (Elia, 1992), although fat tissue may play an important role in metabolic regulation (Kaiyala et al., 2010). Positive relationships between DEE by the DLW technique and activity or displacement (movement) have been shown in other larger mammals (Pagano et al., 2018; Riek et al., 2019; Scantlebury et al., 2014). Although T_{sc} increases with activity, we also show a positive relationship between T_{sc} and DEE, independent of activity. T_{sc} varies more than core body temperature, particularly in large mammals (Irving & Krog, 1955). In our study, mean T_{sc} ranged from 34.8 to 37.0°C, whereas the rumen temperature of Svalbard reindeer in winter is typically between 38 and 38.5°C (Arnold et al., 2018). The positive relationship between T_{sc} and DEE suggests that peripheral cooling (heterothermy) is a potential mechanism to conserve energy during winter (Arnold et al., 2004; Trondrud, Pigeon, Albon, et al., 2021).

In contrast to the predictions of the FEH, we found that FE did not increase with body size or mass, but rather decreased with body size (measured as both lean mass and leg length) and increased with fat mass. Because larger bodies also have greater lean mass, which is expensive to maintain, a larger body alone does not appear to be advantageous when food is depleted in the winter. The FEH predicts that it is better to be larger because the relative scaling exponents across species suggest that the only way to store more fat is to have a bigger body with a larger lean mass. In fact, animals within a species can add fat without the need to be structurally larger. As adipose tissue is the main energy reserve in Svalbard reindeer, high fat mass is crucial for enhanced FE. The disparity between expected scaling of body reserves to body size and FE is also evident for polar bears (Dunbrack & Ramsay, 1993); survival through prolonged seasonal fasting in polar bears is mainly determined by body condition

(fatness) and not size (Mathewson & Porter, 2013). Although FE has been found to increase with body mass in muskoxen *Ovibos moschatus*, Desforges et al. (2019) did not investigate variation in body reserves within a given body mass. In many species, the ratio of fat to body mass is constrained by physiological and/or ecological factors (Dunbrack & Ramsay, 1993; Jacobs et al., 2011). Body fatness is not constrained by predation risk in Svalbard reindeer because polar bears rarely attempt to kill them (Derocher et al., 2000). However, there is a substantial variation in fatness relative to body mass, indicating that some individuals are not able to maximise energy storage before the onset of winter. For example, non-lactating females in October were ~5% heavier than lactating females, suggesting that lactation hinders greater accumulation of body fat (Albon et al., 2017). Furthermore, later onset of snow in autumn has been shown to positively influence late winter body mass (Loe et al., 2021). Consequently, the high seasonality in energy supply and stochasticity during winter likely contributes to shaping a selection for fat and small phenotypes in Svalbard reindeer.

Many ungulates display pronounced seasonal adjustments in locomotor activity, body temperature and energy expenditure (reviewed in Arnold, 2020), which is also evident for Svalbard reindeer (Trondrud, Pigeon, Albon, et al., 2021). We found that adjustments in T_{sc} and activity levels can alter the FE of Svalbard reindeer by up to 20% if both parameters are reduced at the same time. A caveat of the effect of activity is the assumption made by our model that animals are fasting even during high activity, although increased activity could reflect greater foraging efforts. The greatest change to FE was induced by having a high T_{sc}, which is likely an effect of the exponential relationship between T_{sc} and DEE. Similar results have been demonstrated for musk oxen, using a process-based modelling approach, in that lower body temperatures led to reductions in the rate of body reserve depletion and to increased fitness (Desforges et al., 2021). Furthermore, Desforges et al. (2021) found that initial body condition was important for determining the benefit of reducing body temperature—the greater initial body condition, the lower the benefit of reduced body temperature for overwinter survival. Although we did not find any major differences in the effect of adjusting activity or T_{sc} between individuals of different body conditions, our results do demonstrate a general benefit of combined behavioural and physiological adjustments to conserve energy in response to food scarcity.

5 | CONCLUSIONS

The FEH is one of several central hypotheses that aim to explain the evolution of mammalian body size, in which the main premise is that the only way to get fatter is to get bigger. We demonstrate that this reasoning does not necessarily hold true within a species. Instead, we show that FE was primarily dependent on the amount of fat that individuals were able to accrue before winter. Consequently, individuals have comparatively limited scope to reduce their energy

expenditure by lowering their T_{sc} and/or activity levels. Nonetheless, we emphasise that extending FE even by a few days through behavioural and physiological adjustments could prevent death, as most mortalities occur at the very end of the winter (Reimers, 1983). Our study is a demonstration that the theoretical premises of the FEH may not hold empirically, due to the large impact of environmental factors on intraspecific variation in body composition.

AUTHORS' CONTRIBUTIONS

L.E.L., S.A., J.R.S., E.K. and L.M.T. conceived the ideas and planned the study; R.J.I. and V.V. collected the body composition harvest data; S.A., R.J.I., L.E.L., E.R., A.S. and V.V. collected activity data; A.L.E. and E.R. performed surgery; E.K., E.R., L.E.L., S.A., R.J.I., A.S., W.A., A.L.E., V.V. and L.M.T. performed the DLW field study; C.H. analysed DLW results; L.M.T. and G.P. did the statistical analyses, in interactions with E.K., J.R.S. and W.A.; L.M.T. led the writing of the manuscript. All the authors contributed to editing and approved the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.83bk3j9qv (Trondrud, Pigeon, Król, et al., 2021).

ORCID

L. Monica Trondrud (iD) https://orcid.org/0000-0002-1846-6656
Gabriel Pigeon (iD) https://orcid.org/0000-0002-9166-8633
Elżbieta Król (iD) https://orcid.org/0000-0002-5637-9334
Steve Albon (iD) https://orcid.org/0000-0002-0811-1333
Alina L. Evans (iD) https://orcid.org/0000-0003-0513-4887
Walter Arnold (iD) https://orcid.org/0000-0001-6785-5685
Catherine Hambly (iD) https://orcid.org/0000-0002-2947-4539
R. Justin Irvine (iD) https://orcid.org/0000-0002-0411-6217
Audun Stien (iD) https://orcid.org/0000-0001-8046-7337
John R. Speakman (iD) https://orcid.org/0000-0002-2457-1823
Leif Egil Loe (iD) https://orcid.org/0000-0003-4804-2253

REFERENCES

Albon, S. D., Irvine, R. J., Halvorsen, O., Langvatn, R., Loe, L. E., Ropstad, E., Veiberg, V., Wal, R., Bjørkvoll, E. M., Duff, E. I., Hansen, B. B., Lee, A. M., Tveraa, T., & Stien, A. (2017). Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Global Change Biology*, 23(4), 1374–1389. https://doi.org/10.1111/gcb.13435

Andrew, S. M., Erdman, R. A., & Waldo, D. R. (1995). Prediction of body composition of dairy cows at three physiological stages from deuterium oxide and urea dilution. *Journal of Dairy Science*, 78(5), 1083–1095. https://doi.org/10.3168/jds.S0022-0302(95)76725-X

Arnold, W. (2020). Review: Seasonal differences in the physiology of wild northern ruminants. *Animal*, 14(S1), S124–S132. https://doi.org/10.1017/S1751731119003240

Arnold, W., Ruf, T., Loe, L. E., Irvine, R. J., Ropstad, E., Veiberg, V., & Albon, S. D. (2018). Circadian rhythmicity persists through the Polar night and midnight sun in Svalbard reindeer. *Scientific Reports*, 8(1), 14466. https://doi.org/10.1038/s41598-018-32778-4

Arnold, W., Ruf, T., Reimoser, S., Tataruch, F., Onderscheka, K., & Schober, F. (2004). Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology*, 286(1), R174–R1811. https://doi.org/10.1152/ajpregu.00593.2002

Bergmann, C. (1847). Uber die Verhaltnisse der warmeokonomie der Thiere zu uber Grosso. *Gottinger Studien*, 3, 595–709.

Boos, M., Thouzeau, C., Delacour, G., Artois, M., Marchandeurs, S., Jean-Claude, P., & Robin, J. P. (2005). Body condition assessment and prediction of fasting endurance in wild rabbits (*Oryctolagus cuniculus*). *Wildlife Research*, 32(1), 75–83. https://doi.org/10.1071/WR03112

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789. https://doi.org/10.1890/03-9000

Burnham, K. P., & Anderson, D. R. (2002). Model selection and multimodel inference: A practical information-theoretic approach. In *Ecological modelling* (2nd ed., Vol. 172). https://doi.org/10.1016/j.ecolmodel.2003.11.004

Butler, P. J., Green, J. A., Boyd, I. L., & Speakman, J. R. (2004). Measuring metabolic rate in the field: The pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology*, 18(2), 168–183. https://doi.org/10.1111/j.0269-8463.2004.00821.x

Calder, W. A. I. (1984). *Size, function and life history*. Harvard University Press.

Crawley, M. J. (2015). *Statistics: An introduction using R* (2nd ed.). John Wiley & Sons Ltd.

Derocher, A. E., Wiig, Ø., & Bangjord, G. (2000). Predation of Svalbard reindeer by polar bears. *Polar Biology*, 23(10), 675–678. https://doi.org/10.1007/s003000000138

Desforges, J., Beest, F. M., Marques, G. M., Pedersen, S. H., Beumer, L. T., Chimienti, M., & Schmidt, N. M. (2021). Quantifying energetic and fitness consequences of seasonal heterothermy in an Arctic ungulate. *Ecology and Evolution*, 11(1), 338–351. https://doi.org/10.1002/ece3.7049

Desforges, J.-P., Marques, G. M., Beumer, L. T., Chimienti, M., Blake, J., Rowell, J. E., Adamczewski, J., Schmidt, N. M., & van Beest, F. M. (2019). Quantification of the full lifecycle bioenergetics of a large mammal in the high Arctic. *Ecological Modelling*, 401, 27–39. https://doi.org/10.1016/j.ecolmodel.2019.03.013

Douhard, M., Loe, L. E., Stien, A., Bonenfant, C., Irvine, R. J., Veiberg, V., Ropstad, E., & Albon, S. (2016). The influence of weather conditions during gestation on life histories in a wild Arctic ungulate. *Proceedings of the Royal Society B: Biological Sciences*, 283(1841), https://doi.org/10.1098/rspb.2016.1760

Dunbrack, R. L., & Ramsay, M. A. (1993). The allometry of mammalian adaptations to seasonal environments: A critique of the fasting endurance hypothesis. *Oikos*, 66(2), 336. https://doi.org/10.2307/3544822

Elia, M. (1992). Organ and tissue contribution to metabolic rate. In J. M. Kinney & H. N. Tucker (Eds.), *Energy metabolism: Tissue determinants and cellular corollaries* (pp. 61–79). Tucker Raven Press Ltd.

Ericsson, G., Dettki, H., Neumann, W., Arnemo, J. M., & Singh, N. J. (2015). Offset between GPS collar-recorded temperature in moose and ambient weather station data. *European Journal of Wildlife Research*, 61(6), 919–922. https://doi.org/10.1007/s10344-015-0968-7

Fletcher, Q. E., Speakman, J. R., Boutin, S., Mcadam, A. G., Woods, S. B., & Humphries, M. M. (2012). Seasonal stage differences overwhelm environmental and individual factors as determinants of energy expenditure in free-ranging red squirrels. *Functional Ecology*, 26(3), 677–687. https://doi.org/10.1111/j.1365-2435.2012.01975.x

Foster, J. B. (1964). Evolution of mammals on Islands. *Nature*, 202(4929), 234–235. https://doi.org/10.1038/202234a0

Huston, M. A., & Wolverton, S. (2011, August 1). Regulation of animal size by eNPP, Bergmann's rule, and related phenomena. *Ecological Monographs*, 81, 349–405. https://doi.org/10.1890/10-1523.1

Irving, L., & Krog, J. (1955). Temperature of skin in the arctic as a regulator of heat. *Journal of Applied Physiology*, 7(4), 355–364. https://doi.org/10.1152/jappl.1955.7.4.355

Jacobs, S. R., Edwards, D. B., Ringrose, J., Elliott, K. H., Weber, J. M., & Gaston, A. J. (2011). Changes in body composition during breeding: Reproductive strategies of three species of seabirds under poor environmental conditions. *Comparative Biochemistry and Physiology - B Biochemistry and Molecular Biology*, 158(1), 77–82. https://doi.org/10.1016/j.cbpb.2010.09.011

Kaiyala, K. J., Morton, G. J., Leroux, B. G., Ogimoto, K., Wisse, B., & Schwartz, M. W. (2010). Identification of body fat mass as a major determinant of metabolic rate in mice. *Diabetes*, 59(7), 1657–1666. https://doi.org/10.2337/db09-1582

Kleiber, M. (1961). *The fire of life: An introduction to animal energetics*. Wiley.

Krop-Benesch, A., Berger, A., Streich, J., & Scheibe, K. (2011). *Activity pattern. User's manual*. Vectronic Aerospace GmbH.

Lindstedt, S. L., & Boyce, M. S. (1985). Seasonality, fasting endurance, and body size in mammals. *American Naturalist*, 125(6), 873–878. https://doi.org/10.1086/284385

Loe, L. E., Liston, G. E., Pigeon, G., Barker, K., Horvitz, N., Stien, A., Forchhammer, M., Getz, W. M., Irvine, R. J., Lee, A., Movik, L. K., Mysterud, A., Pedersen, Å. Ø., Reinking, A. K., Ropstad, E., Trondrud, L. M., Tveraa, T., Veiberg, V., Hansen, B. B., & Albon, S. D. (2021). The neglected season: Warmer autumns counteract harsher winters and promote population growth in Arctic reindeer. *Global Change Biology*, 27(5), 993–1002. https://doi.org/10.1111/gcb.15458

Lundblad, C. G., & Conway, C. J. (2020). Testing four hypotheses to explain partial migration: Balancing reproductive benefits with limits to fasting endurance. *Behavioral Ecology and Sociobiology*, 74(2), 1–16. https://doi.org/10.1007/s00265-019-2796-3

Mathewson, P. D., & Porter, W. P. (2013). Simulating polar bear energetics during a seasonal fast using a mechanistic model. *PLoS ONE*, 8(9), e72863. https://doi.org/10.1371/journal.pone.0072863

McNab, B. K. (2010, April 3). Geographic and temporal correlations of mammalian size reconsidered: A resource rule. *Oecologia*, 164, 13–23. https://doi.org/10.1007/s00442-010-1621-5

Millar, J. S., & Hickling, G. J. (1990). Fasting endurance and the evolution of mammalian body size. *Functional Ecology*, 4(1), 5. https://doi.org/10.2307/2389646

Nilssen, K. J., Sundsfjord, J. A., & Blix, A. S. (1984). Regulation of metabolic rate in Svalbard and Norwegian reindeer. *The American Journal of Physiology*, 247(5 Pt 2), R837–R841. https://doi.org/10.1152/ajpregu.1984.247.5.R837

Omsjoe, E. H., Stien, A., Irvine, J., Albon, S. D., Dahl, E., Thoresen, S. I., Rustad, E., & Ropstad, E. (2009). Evaluating capture stress and its effects on reproductive success in Svalbard reindeer. *Canadian Journal of Zoology*, 87(1), 73–85. https://doi.org/10.1139/Z08-139

Pagano, A. M., Durner, G. M., Rode, K. D., Atwood, T. C., Atkinson, S. N., Peacock, E., Costa, D. P., Owen, M. A., & Williams, T. M. (2018). High-energy, high-fat lifestyle challenges an Arctic apex predator, the polar bear. *Science (New York, NY)*, *359*(6375), 568–572. https://doi.org/10.1126/science.aan8677

Pedersen, Å. Ø., Paulsen, I. M. G., Albon, S., Arntsen, G. B., Hansen, B. B., Langvatn, R., Loe, L. E., Le Moullec, M., Overrein, Ø., Peeters, B., Ravolainen, V., Ropstad, E., Stien, A., Tyler, N. J. C., Veiberg, V., van der Wal, R., Andersen, R., Beumer, L. T., & Eischeid, I., … Trondrud, L. M. (2019). Svalbard reindeer (*Rangifer tarandus platyrhynchus*) A status report. In *Report Series 151*. Norwegian Polar Institute.

Pontzer, H., Brown, M. H., Raichlen, D. A., Dunsworth, H., Hare, B., Walker, K., Luke, A., Dugas, L. R., Durazo-Arvizu, R., Schoeller, D., Plange-Rhule, J., Bovet, P., Forrester, T. E., Lambert, E. V., Thompson, M. E., Shumaker, R. W., & Ross, S. R. (2016). Metabolic acceleration and the evolution of human brain size and life history. *Nature*, *533*(7603), 390–392. https://doi.org/10.1038/nature17654

Reimers, E. (1983). Mortality in Svalbard Reindeer. *Holarctic Ecology*, *6*(2), 141–149. https://doi.org/10.1111/j.1600-0587.1983.tb01075.x

Reimers, E., & Ringberg, T. (1982). Body composition, mortality and population regulation of Svalbard reindeer. *Canadian Journal of Zoology*, *60*, 1812–1821. https://doi.org/10.7557/2.2.2.417

Riek, A., Stölzl, A., Marquina Bernedo, R., Ruf, T., Arnold, W., Hambly, C., Speakman, J. R., & Gerken, M. (2019). Energy expenditure and body temperature variations in llamas living in the High Andes of Peru. *Scientific Reports*, *9*(1), 4037. https://doi.org/10.1038/s41598-019-40576-9

Scantlebury, D. M., Mills, M. G. L., Wilson, R. P., Wilson, J. W., Mills, M. E. J., Durant, S. M., Bennett, N. C., Bradford, P., Marks, N. J., & Speakman, J. R. (2014). Flexible energetics of cheetah hunting strategies provide resistance against kleptoparasitism. *Science*, *346*(6205), 79–81. https://doi.org/10.1126/science.1256424

Schoeller, D. A., Ravussin, E., Schutz, Y., Acheson, K. J., Baertschi, P., & Jequier, E. (1986). Energy expenditure by doubly labeled water: Validation in humans and proposed calculation. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *250*(5), R823–R830. https://doi.org/10.1152/ajpregu.1986.250.5.R823

Sheriff, M. J., Kenagy, G. J., Richter, M., Lee, T., Tøien, Ø., Kohl, F., Buck, C. L., & Barnes, B. M. (2011). Phenological variation in annual timing of hibernation and breeding in nearby populations of arctic ground squirrels. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1716), 2369–2375. https://doi.org/10.1098/rspb.2010.2482

Sørmo, W., Haga, O. E., Gaare, E., Langvatn, R., & Mathiesen, S. D. (1999). Forage chemistry and fermentation chambers in Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Journal of Zoology*, *247*(2), 247–256. https://doi.org/10.1111/j.1469-7998.1999.tb00988.x

Speakman, J. R., & Racey, P. A. (1987). The equilibrium concentration of oxygen-18 in body water: Implications for the accuracy of the doubly-labelled water technique and a potential new method of measuring RQ in free-living animals. *Journal of Theoretical Biology*, *127*(1), 79–95. https://doi.org/10.1016/S0022-5193(87)80162-5

Speakman, J. R., & Westerterp, K. R. (2013). A mathematical model of weight loss under total starvation: Evidence against the thrifty-gene hypothesis. *Disease Models & Mechanisms*, *6*(1), 236–251. https://doi.org/10.1242/dmm.010009

Staaland, H., Jacobsen, E., & White, R. G. (1979). Comparison of the digestive tract in Svalbard and Norwegian reindeer. *Arctic and Alpine Research*, *11*(4), 457–466. https://doi.org/10.2307/1550563

Swenson, J. E., Adamič, M., Huber, D., & Stokke, S. (2007). Brown bear body mass and growth in northern and southern Europe. *Oecologia*, *153*(1), 37–47. https://doi.org/10.1007/s00442-007-0715-1

The R Core Team. (2020). *R: A language and environment for statistical computing*. Retrieved from https://www.r-project.org/

Trondrud, L. M., Pigeon, G., Albon, S., Arnold, W., Evans, A. L., Irvine, R. J., Krol, E., Ropstad, E., Stien, A., Veiberg, V., Speakman, J. R., & Loe, L. E. (2021). Determinants of heart rate in Svalbard reindeer reveal mechanisms of seasonal energy management. *Philosophical Transactions of the Royal Society B: Biological Sciences*. In press. https://doi.org/10.1098/rstb.2020.0215

Trondrud, L. M., Pigeon, G., Król, E., Albon, S., Evans, A. L., Arnold, W., & Loe, L. E. (2021). Data from: Fat storage influences fasting endurance more than body size in an ungulate. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.83bk3j9qv

Tyler, N. J. C. (1987). *Natural limitation of the abundance of the high arctic svalbard reindeer*. University of Cambridge. https://doi.org/10.17863/CAM.20267

Van Der Wal, R., & Stien, A. (2014). High-arctic plants like it hot: A long-term investigation of between-year variability in plant biomass. *Ecology*, *95*(12), 3414–3427. https://doi.org/10.1890/14-0533.1

Van Marken Lichtenbelt, W. D., Westerterp, K. R., & Wouters, L. (1994). Deuterium dilution as a method for determining total body water: Effect of test protocol and sampling time. *British Journal of Nutrition*, *72*(4), 491. https://doi.org/10.1079/BJN19940053

Wood, S. N. (2017). *Generalized additive models: An Introduction with R* (2nd ed.). Chapman and Hall/CRC.

Yannic, G., Pellissier, L., Ortego, J., Lecomte, N., Couturier, S., Cuyler, C., Dussault, C., Hundertmark, K. J., Irvine, R. J., Jenkins, D. A., Kolpashikov, L., Mager, K., Musiani, M., Parker, K. L., Røed, K. H., Sipko, T., Þórisson, S. G., Weckworth, B. V., Guisan, A., … Côté, S. D. (2014). Genetic diversity in caribou linked to past and future climate change. *Nature Climate Change*, *4*(2), 132–137. https://doi.org/10.1038/nclimate2074

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

> **How to cite this article:** Trondrud LM, Pigeon G, Król E, et al. Fat storage influences fasting endurance more than body size in an ungulate. *Funct Ecol*. 2021;00:1–11. https://doi.org/10.1111/1365-2435.13816