

A Summer Heat Wave Reduced Activity, Heart Rate, and Autumn Body Mass in a Cold-Adapted Ungulate

L. Monica Trondrud^{1,*}

Gabriel Pigeon^{1,2}

Elżbieta Król³

Steve Albon⁴

Erik Ropstad⁵

Jouko Kumpula⁶

Alina L. Evans⁷

John R. Speakman^{3,8}

Leif Egil Loe¹

¹Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway; ²Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Quebec, Canada; ³School of Biological Sciences, Institute of Biological and Environmental Sciences, University of Aberdeen, Aberdeen, United Kingdom; ⁴James Hutton Institute, Craigiebuckler, Aberdeen, United Kingdom; ⁵Faculty of Veterinary Science, Norwegian University of Life Sciences, Ås, Norway; ⁶Wildlife Ecology Group, Natural Resources Institute Finland, Inari, Finland; ⁷Department of Forestry and Wildlife Management, Inland Norway University of Applied Sciences, Campus Evenstad, Elverum, Norway; ⁸Shenzhen Key Laboratory of Metabolic Health, Center for Energy Metabolism and Reproduction, Institute of Biology and Biotechnology, Shenzhen Institute of Advanced Technology, Chinese Academy of Sciences, Shenzhen, China; Center of Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China; and State Key Laboratory of Molecular Developmental Biology, Institute of Genetics and Developmental Biology, Chinese Academy of Sciences, Beijing, China

Accepted 3/31/2023; Electronically Published 6/5/2023

Online enhancements: appendixes.

ABSTRACT

Heat waves are becoming more frequent across the globe and may impose severe thermoregulatory challenges for endotherms. Heat

stress can induce both behavioral and physiological responses, which may result in energy deficits with potential fitness consequences. We studied the responses of reindeer (*Rangifer tarandus tarandus*), a cold-adapted ungulate, to a record-breaking heat wave in northern Finland. Activity, heart rate, subcutaneous body temperature, and body mass data were collected for 14 adult females. The post-heat wave autumn body masses were then analyzed against longitudinal body mass records for the herd from 1990 to 2021. With increasing air temperature during the day, reindeer became less active and had reduced heart rate and increased body temperature, reflecting both behavioral and physiological responses to heat stress. Although they increased activity in the late afternoon, they failed to compensate for lost foraging time on the hottest days (daily mean temperature $\geq 20^{\circ}\text{C}$), and total time active was reduced by 9%. After the heat wave, the mean September body mass of herd females (69.7 ± 6.6 kg, $n = 52$) was on average $16.4\% \pm 4.8\%$ lower than predicted (83.4 ± 6.0 kg). Among focal females, individuals with the lowest levels of activity during the heat wave had the greatest mass loss during summer. We show how heat waves impose a thermoregulatory challenge on endotherms, resulting in mass loss, potentially as a result of the loss of foraging time. While it is well known that environmental conditions affect large herbivore fitness indirectly through decreased forage quality and limited water supply, direct effects of heat may be increasingly common in a warming climate.

Keywords: climate change, biologging, reproduction, thermoregulation, heat dissipation, ruminants, behavioral plasticity.

Introduction

Climate change is happening at an unprecedented rate and is particularly pronounced in the polar regions (Pörtner et al. 2019; Rantanen et al. 2022). There is also evidence of an increase in the occurrence of heat waves in the terrestrial Arctic (Dobricic et al. 2020). Extreme high-temperature events may pose a thermoregulatory challenge for endotherms, since dissipation of body heat becomes more difficult (Schmidt-Nielsen 1997; Speakman and Król 2010), especially for cold-adapted species (Brivio et al. 2019) and lactating females (Zhao et al.

*Corresponding author; email: monica.trondrud@nmbu.com, monica.trondrud@gmail.com.

2020). To reduce the risk of hyperthermia under hot environmental conditions, endotherms employ thermoregulatory responses that can be energetically costly (McNab 2002), and/or they reduce activity, which impacts energy acquisition and allocation (Speakman and Król 2010; van Beest and Milner 2013). How cold-adapted animals cope under high environmental temperatures, and the consequences of their responses, may affect their growth, development, and ultimately fitness in a rapidly warming climate (Stillman 2019).

Avoiding, or reducing, the risk of hyperthermia may involve several behavioral and physiological adjustments. For example, animals may seek cooler microclimates to reduce radiant heat loads and increase convective heat loss (Mitchell et al. 2018), modify peripheral blood flow to elevate skin/surface temperatures (Irving and Krog 1955), or employ evaporative cooling via increased panting or sweating (Parker and Robbins 1984). Among ungulates, the use of thermal refugia (such as forest canopies providing shade [van Beest et al. 2012], cool ground [Williamsen et al. 2019], or snow patches [Sarmiento et al. 2019]) can be an effective buffer against heat stress. Other responses include lowering food intake (Shively et al. 2019) and reducing exercise intensity or movement rates (Brivio et al. 2019; Zhou et al. 2022). Also, spending less time foraging during the hottest part of the day and increasing foraging activity at dawn and/or dusk (as documented in temperate, alpine, and desert ungulates; Aublet et al. 2009; Shrestha et al. 2014; Ditmer et al. 2018) can reduce heat load without compromising overall foraging time (Semenzato et al. 2021). However, if temperatures remain high for long periods or if animals are unable to adopt alternative foraging patterns, behavioral buffering of heat stress may be insufficient and could potentially lead to lowered energetic investment in somatic growth (van Beest and Milner 2013) and to depressed reproductive output (Igono et al. 1992; Dash et al. 2016). Indeed, it has been suggested that in mammals, the ability to dissipate body heat is a key factor limiting energy expenditure (Speakman and Król 2010).

Reindeer (*Rangifer tarandus*) are large ungulates with a circumpolar distribution in the Northern Hemisphere. They are the only cervids with a long history of domestication and are an important livestock in local communities and indigenous traditions in Fennoscandia and Siberia (Røed et al. 2008). With their relatively large body size and highly insulating pelage, reindeer are well adapted to the cold Arctic climate. Their thermoregulatory adaptations are efficient at saving water and retaining body heat in the cold and maximizing heat dissipation when hot (Folkow and Mercer 1986; Johnsen et al. 1990). In captivity, resting reindeer in their summer coats begin to show signs of heat stress (thermal tachypnea) at air temperatures (T_a 's) exceeding 25°C (Blix and Johnsen 1983). Furthermore, reindeer fed ad lib. reduce their dry matter intake as T_a 's increase in summer (Thompson and Barboza 2014). Although this suggests that reindeer may be susceptible to heat stress during summer, little is known about the ability of reindeer to cope with sporadic extreme heat events under natural conditions.

In summer 2018, northern Europe experienced a record-breaking heat wave that caused droughts and wildfires (Peters

et al. 2020). The heat wave in Scandinavia lasted 21 d (Kueh and Lin 2020), during which several areas above the Arctic circle (66°N) recorded the highest temperature anomalies since 1961. In northern Finland (Inari region), the monthly mean temperature in July was 19.2°C, which was 5.1°C higher than the climatological mean for this region, with anomalously high air pressure and little precipitation (Sinclair et al. 2019). Here, we investigated the behavioral and physiological responses of semidomesticated reindeer (*R. t. tarandus*) during the 2018 heat wave. In response to higher T_a 's, we expected that adult female reindeer would reduce activity levels (prediction 1), particularly in the hottest part of the day, and then compensate this reduction by increasing activity in the cooler parts of the day (Semenzato et al. 2021). In addition, we expected that females with calves would spend more time being active (i.e., foraging) than females without calves because of the energetic demands of lactation (Denryter et al. 2020). We also anticipated that reindeer would exhibit increased resting heart rate (HR) and subcutaneous body temperature (T_{sc} ; prediction 2) to facilitate heat dissipation via peripheral vasodilation and hence via thermal conduction through the skin. Furthermore, we expected that females with calves would display more pronounced thermoregulatory responses to alleviate heat stress at lower T_a thresholds, in accordance with the heat dissipation limitation theory (Speakman and Król 2010). Last, we predicted that females unable to compensate their energy needs as a result of reduced (or lost) foraging time in summer would have lower body mass (BM) in autumn (prediction 3; van Beest and Milner 2013), and we expected that variation in mean annual BM over three decades would correlate with prevailing summer temperatures.

Methods

Animals and Study Area

Reindeer at the Kutuharju Reindeer Research Facility (Kaamanen, northern Finland, 69°8'N, 26°59'E; fig. A1-1) consist of a herd of ~100 animals that belong to the Reindeer Herders' Association. The herding management includes keeping reindeer in two large enclosures (~13.8 and ~15 km², respectively) after calving until the rut, after which animals are moved to a winter enclosure (~15 km²) and then to a calving paddock (~0.3 km²) in spring to give birth (for further details on the study area, see appendix 1). The herd graze freely on natural pastures from May to November, after which they are provided with silage and pellets as a supplementary feed in winter. During the period from September to April, animals are weighed monthly by being gathered from the large enclosures and moved into the calving paddock. From here, they are corralled and guided individually to an indoor handling facility containing a caged floor scale, which the reindeer walk onto to be weighed.

The study involved biologging 14 female reindeer from the Kutuharju herd (focal animals are shown in table A1-1) in summer 2018. Before the present study, 10 of these individuals had been confined to the calving paddock and handled repeatedly from May 31 to June 16, 2018, as part of an energetics study using the doubly labeled water technique (Trondrud 2021). During this

period, they received supplemental feeding. They were let out on natural pastures with the rest of the herd on June 17. For the analyses of activity, HR, and body temperature, we used data collected in the period from June 20 to August 20, 2018, to exclude the period when 10 of the 14 individuals were repeatedly handled while still capturing the heat wave period (fig. 1). There were negligible differences between the two groups in all aspects of the analyses described below (details in appendix 2).

Heart Rate and Subcutaneous Body Temperature Data

In February 2018, the focal females were instrumented with an HR and temperature logger (DST centi-HRT, Star-Oddi, Gardabaer, Iceland). The surgical protocol is described in appendix 1. The DST centi-HRT sensors recorded HR and T_{sc} every 15 min. HR was automatically calculated from a 4-s electrocardiogram at a 150-Hz measurement frequency alongside an index for signal quality. Additional data processing is described in appendix 1.

Activity Data

Animals were fitted with collar-mounted triaxial accelerometers (VERTEX Plus activity sensor, Vectronic Aerospace, Berlin) to monitor their activity levels. These sensors recorded acceleration (g) in three directions representing back-forward,

lateral, and dorsal-ventral movements at an 8-Hz resolution. For each axis, partial dynamic body acceleration (PDBA) was calculated by subtracting the static acceleration and using a 4-s running average from the raw acceleration (Shepard et al. 2008). We estimated vectorial dynamic body acceleration (VeDBA) by calculating the square root of the sum of squared PDBAs (Wilson et al. 2020). We aggregated VeDBA data into 15-min sums (hereafter referred to as sum VeDBA) to match the HR and T_{sc} records. Corrections for time offsets are described in section 1.3 of appendix 1. Because of battery failure in four of the DST centi-HRTs, only 10 of the 14 individuals had complete data from both types of loggers (activity and HR).

Weather and Climate Data

We set up a local HOBO weather station (Onset, Bourne, MA) mounted on a 2-m-tall tripod in May 2018 that measured T_a ($^{\circ}\text{C}$) at 15-min intervals. The placement of the station was between the two summer paddocks. These measurements were matched to the nearest time stamps for VeDBA, HR, and T_{sc} recordings. Also, we obtained weather records from the nearest public weather stations for the years 1990–2021 (table A1-2). Weather station IDs and locations relative to the study area are shown in figure A1-1.

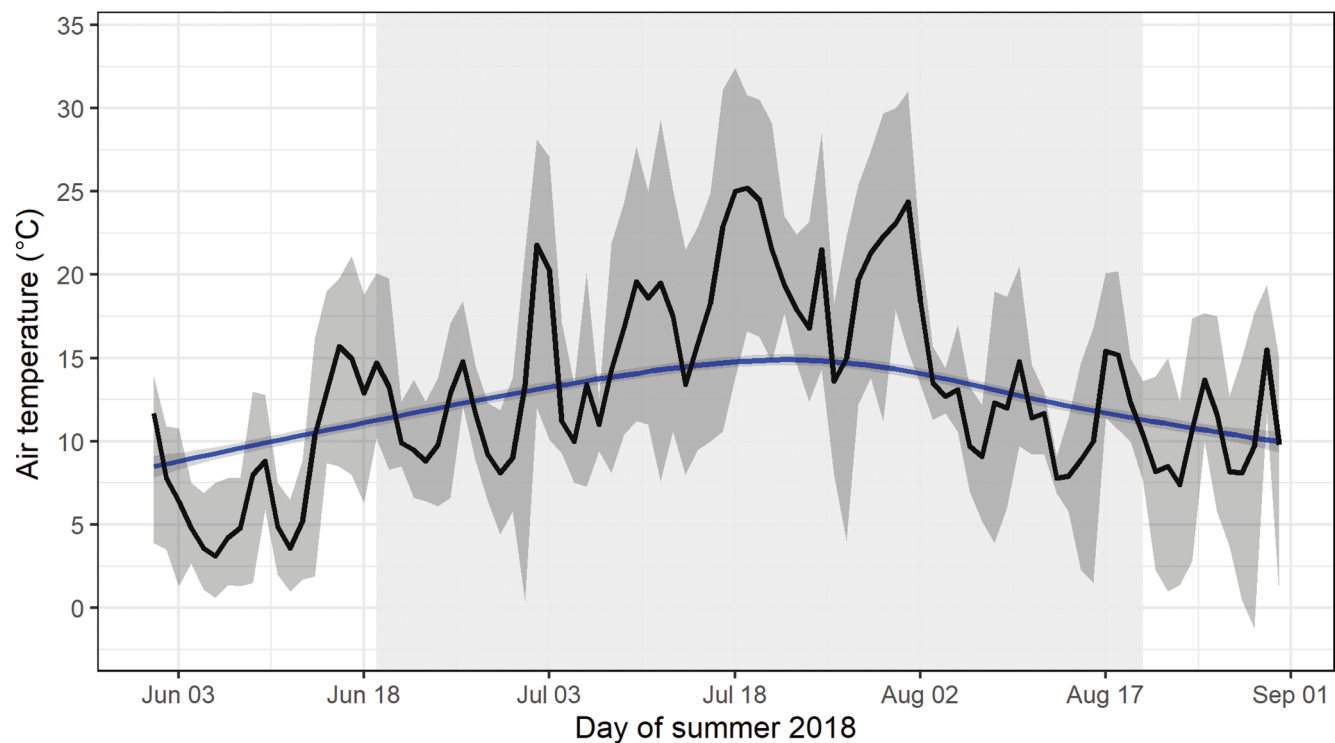


Figure 1. Daily mean air temperatures (black line) recorded from a local weather station during summer 2018 in Kaamanen, northern Finland. The dark gray shading indicates the temperature amplitude for each day (daily maxima and minima). The light gray shading denotes the period during which activity, heart rate, and subcutaneous body temperature were used in the analysis of reindeer responses to environmental conditions (June 20–August 20, 2018). The blue line indicates the daily mean air temperatures recorded between 1990 and 2021 by a weather station ~60 km from the study site (station ID 102033).

Body Mass of Reindeer

We used the April and September BMs of adult females (3–15 yr old) and their calves in the Kutuharju herd that were collected between 1990 and 2021 (tables A1-3, A1-4). Because this is a research herd, some individuals had been part of experimental feeding programs in the past; therefore, they were not included in BM analyses. Since 1990, a total of 1,519 September BMs from 344 unique individuals were used. The median number of records (i.e., years weighed) per individual was 5 (range: 1–13 records).

Statistical Analyses

All statistical analyses were conducted in R version 4.1.1 (R Core Team 2021). Mean values are presented with standard deviation, and parameter estimates are presented with standard error. We fitted hidden Markov models (HMMs) to 15-min sum VeDBA using the package *momentuHMM* (McClintock and Michelot 2018). HMMs assume that the observed pattern is driven by an underlying latent state sequence (a finite Markov chain). These states can then be used as proxies to interpret an animal's unobserved behavior (Langrock et al. 2012). We assumed only two underlying states thought to represent time spent inactive (i.e., resting) and active (fig. A1-3). The active state thus contains multiple forms of movement (e.g., foraging, walking, and running), but reindeer spend more than 50% of the time foraging in summer (Skogland 1980). We fitted several HMMs to evaluate both external-level (temperature and time of day [ToD]) and individual-level (calf status) effects on the probability of occupying each state (stationary state probabilities). The combination of the explanatory variables in each HMM is listed in table A1-5. T_a was fitted as a continuous variable with a piecewise polynomial spline with eight knots, which was asserted from visual inspection of the model outputs. We included sine and cosine terms for ToD to account for cyclicity. In addition, to assess the impact of T_a on activity patterns, we fitted five temperature-day categories, together with an interaction with ToD. These categories were based on quintiles (20% intervals) of the distribution of temperature data from our local weather station during the period from June 20 to August 20, 2018, with ranges of <10°C (cold), 10°C–13°C (cool), 13°C–16°C (intermediate), 16°C–20°C (warm), and $\geq 20^\circ\text{C}$ (hot). We evaluated the significance of each variable on the stationary state probabilities from the confidence intervals of each estimate, and we evaluated the goodness of fit of each model using Akaike information criteria (AIC; Burnham and Anderson 2002), retaining models within $\Delta\text{AIC} < 5$. We extracted the most likely state occupied by an individual using the Viterbi function, resulting in the optimal state pathway (i.e., a two-level categorical variable indicating whether the individual was most likely resting or active). We used this output to calculate daily activity budgets (percentage of time spent active).

We matched the activity states derived from HMMs to the HR and T_{sc} data. We opted to investigate the drivers of variation in HR and T_{sc} only within the inactive state to simplify analyses. HR and T_{sc} were fitted as response variables in separate generalized additive mixed effects models (GAMMs), which in-

cluded the following smooth terms: calendar day as a thin-plate regression spline, ToD (h, knots = 10) as a cubic regression spline, and individual as a random intercept. All models were fitted using a restricted maximum likelihood, a penalization value (λ) of 1.4 (Wood 2017), and an autoregressive structure to account for temporal autocorrelation. We used the *gam.check* function from the *mgcv* package to select knots. The sum VeDBA from the previous 15 min was included as a predictor in all models. All models were fitted with the same following set of explanatory variables: sum VeDBA, age, BM, calf status (yes/no), T_a , and interactions between calf status and T_a as well as between BM and T_a . The models were initially fitted with the same explanatory variables using maximum likelihood and simplified through a stepwise backward model selection approach, with a likelihood ratio test performed at each removal step. In both models, age was the only variable that fell out, and it was removed from the final models (table A1-6).

To investigate whether the heat wave in summer 2018 affected subsequent BM change, we fitted a GAMM using September BM as the response variable and calf status (yes/no), April BM, and age (range: 3–15 yr; as a thin-plate regression spline) as predictor variables. Individual ID and year were included as random intercepts. This model was fitted using data for all years (1990–2021). We included the following environmental variables in separate models: mean T_a in July, sum of days with daily mean $T_a \geq 20^\circ\text{C}$, cumulative degree days $\geq 20^\circ\text{C}$ (i.e., sum of daily mean temperatures $\geq 20^\circ\text{C}$) from June 1 to August 31, total precipitation (mm) from June 1 to August 31, and interactions between precipitation and temperature variables. All models were run twice, excluding the BMs in 2018 in the second run. We compared models including environmental variables against the base model, following the same approach as that used for adult BMs. We repeated the analysis for calf BMs in September, and the model was fitted with the following explanatory variables in the base: calf sex (female/male), calf birth weight, weight of mother in April, and age of mother as a thin-plate regression spline, including mother ID and year as random intercepts. Model selection was performed using AIC (tables A1-11–A1-13).

Finally, we compared the change in BM from April to September 2018 against the activity patterns recorded in summer 2018 for 13 individuals with available BM data from both periods. We fitted linear regressions with the average daily time spent in activity, the time spent active on the hottest days, and the difference in activity levels between the hottest days and the intermediate days as the explanatory variables, including an additive effect of having a calf. We evaluated the models using AIC (table A1-14).

Results

Air Temperature Characteristics of the Summer 2018 Heat Wave in Northern Finland

Summer 2018 was exceptionally warm. During the sampling period (June 20–August 20, 2018), T_a ranged from 4.4°C to 30.5°C, with the highest daily mean T_a of 25.1°C recorded on

July 18 and 19. All but 5 d in July 2018 had a daily mean T_a above the 30-yr (1991–2020) climate normal (14.0°C; fig. 1), and 15 of these days were at least 5°C higher than the climate normal. In summer 2018, the sum of daily mean temperatures $\geq 20^\circ\text{C}$ was 48.1°C, compared to a median of 2.7°C across all other years (range: 0°C–23.7°C; table A1-2), and there was a total of 16 d when the mean T_a exceeded 20°C (hot days), compared to a median of 2 d across all other years. From the local weather station, instantaneous (15-min) temperatures peaked between 1100 and 1600 hours for all daily temperature categories (fig. 2A).

Prediction 1: Changes in Activity Levels in Response to Rising Air Temperature

Two of the HMMs explained similar amounts of the variation in state probabilities in reindeer (table A1-5). The first HMM contained ToD, ID, and calf status interactions with T_a (AIC weight = 0.74). The probability of being active was stable between 5°C and 20°C and decreased curvilinearly as T_a continued to increase beyond 20°C (fig. 3A). Overall, females with calves had a higher probability of being active at temperatures between 5°C and 20°C than females without calves, but this difference disappeared when T_a exceeded 20°C.

The second HMM contained a ToD interaction with T_a categories (AIC weight = 0.26, $\Delta\text{AIC} = 2$). This model showed that reindeer displayed a diel activity pattern that shifted with increasing temperatures, with no differences between females with and without calves. Overall, the probability of being active was highest during midday on the coldest days (daily mean T_a : $<10^\circ\text{C}$, 10°C – 30°C) but with a relatively weak diel pattern (fig. 2B). The diel pattern became more pronounced on days with higher mean daily T_a , with a reduced probability of being active during the hottest part of the day, followed by the increased probability of being active during the cooler parts of the evening (fig. 2B). As predicted, this compensation resulted in similar daily activity budgets, with animals being, on average, active for 63.4% ($<10^\circ\text{C}$), 63.7% (10°C – 13°C), 64.4% (13°C – 16°C), and 63.9% (16°C – 20°C) of the day (fig. 2C). However, on the hottest days (daily mean T_a : $>20^\circ\text{C}$), activity levels were strongly reduced in the morning, and evening activity peaks were attenuated (fig. 2C), resulting in a reduction in daily activity budgets to 58.0% (9% change).

Prediction 2: Changes in Subcutaneous Body Temperature and Heart Rate

As expected, reindeer T_{sc} increased linearly as T_a rose (fig. 3B). While the slopes were significantly different between females with and without calves, the difference was small (table A1-7). Across the whole range of observed T_a 's (4.4°C–30.5°C), T_{sc} varied by 2.1°C and 1.6°C for females with and without calves, respectively. In contrast to our prediction, resting HR declined as T_a rose (fig. 3C; table A1-8), and this response was significantly steeper in females with calves—for every 1°C increase in T_a , HR declined by 0.5 bpm for females with calves and by 0.3 bpm for females without calves. Across the observed T_a range,

predicted resting HR declined from 77 to 63 bpm in females with calves and from 66 to 59 bpm in females without calves. The difference between females with and without calves was therefore greatest at low T_a (mean difference of 11 bpm at a T_a of 4°C) but differed by only 4 bpm at the highest T_a . For both T_{sc} and HR, we found significant interactions between T_a and BM (tables A1-7, A1-8), where heavier females tended to have a higher T_{sc} at low T_a but a lower T_{sc} at high T_a (compared to lighter females). However, the effect size of the interaction was small, with large overlapping confidence intervals for the predictions (fig. A1-9a). For HR, heavier females tended to have a slightly lower HR at low T_a , but this difference disappeared as T_a increased (fig. A1-9b).

Prediction 3: Effects of the Summer 2018 Heat Wave on Autumn Body Mass

The mean adult female BM of the herd in September 2018 (69.7 ± 6.6 kg, $n = 52$) was the lowest recorded over the years 1990–2021 (fig. 4A; table A1-3). Calf status, age, and April BM together with random effects for ID and year explained 87.5% of the variation in September BM over the 32 yr (table A1-9). On average, having a calf reduced September BM by ~ 3.9 kg. Using this model to calculate the expected BMs for individuals in September 2018, we found that these were, on average, $16.4\% \pm 4.8\%$ lower than expected (expected mean = 83.4 ± 6.0 kg). Furthermore, we found a significant negative association between cumulative degree days and September BM of herd females across the years 1990–2021 (tables A1-10, A1-11). However, when excluding data from 2018, the models containing any summer weather variables were indistinguishable from the null model, emphasizing that 2018 was an exceptional year in terms of BM patterns and weather extremes (fig. 4B). Also in 2018, calves were on average 6.5 ± 3.0 kg ($15\% \pm 6.6\%$) lighter than expected (43.7 ± 2.9 kg; table A1-12), while none of the models containing environmental variables outperformed the null model (table A1-13).

Among the 14 focal animals for which we had activity data, we had BMs from both April and September for 13 individuals. Here, we found a positive association between absolute mass change (difference between April BM and September BM) in 2018 and average activity levels in summer (slope = 1.0, SE = 0.4, $P = 0.02$), with the intercept being 6.3 kg lower for females with a calf than for those without a calf (fitted as an additive effect; SE = 2.6, $P = 0.04$; fig. 4C). Although the effect was statistically significant, the model could not be distinguished from the null model (table A1-14). In partial support of prediction 3, individuals who were less active in summer tended to have the greatest negative mass change from April to September 2018 (fig. 4C) when accounting for the effect of having a calf.

Discussion

Our data provide evidence of heat stress in semidomesticated reindeer in northern Finland during the unprecedented summer heat wave of 2018. When reindeer were inactive at higher T_a 's, their T_{sc} 's increased, and their HRs declined, a combination

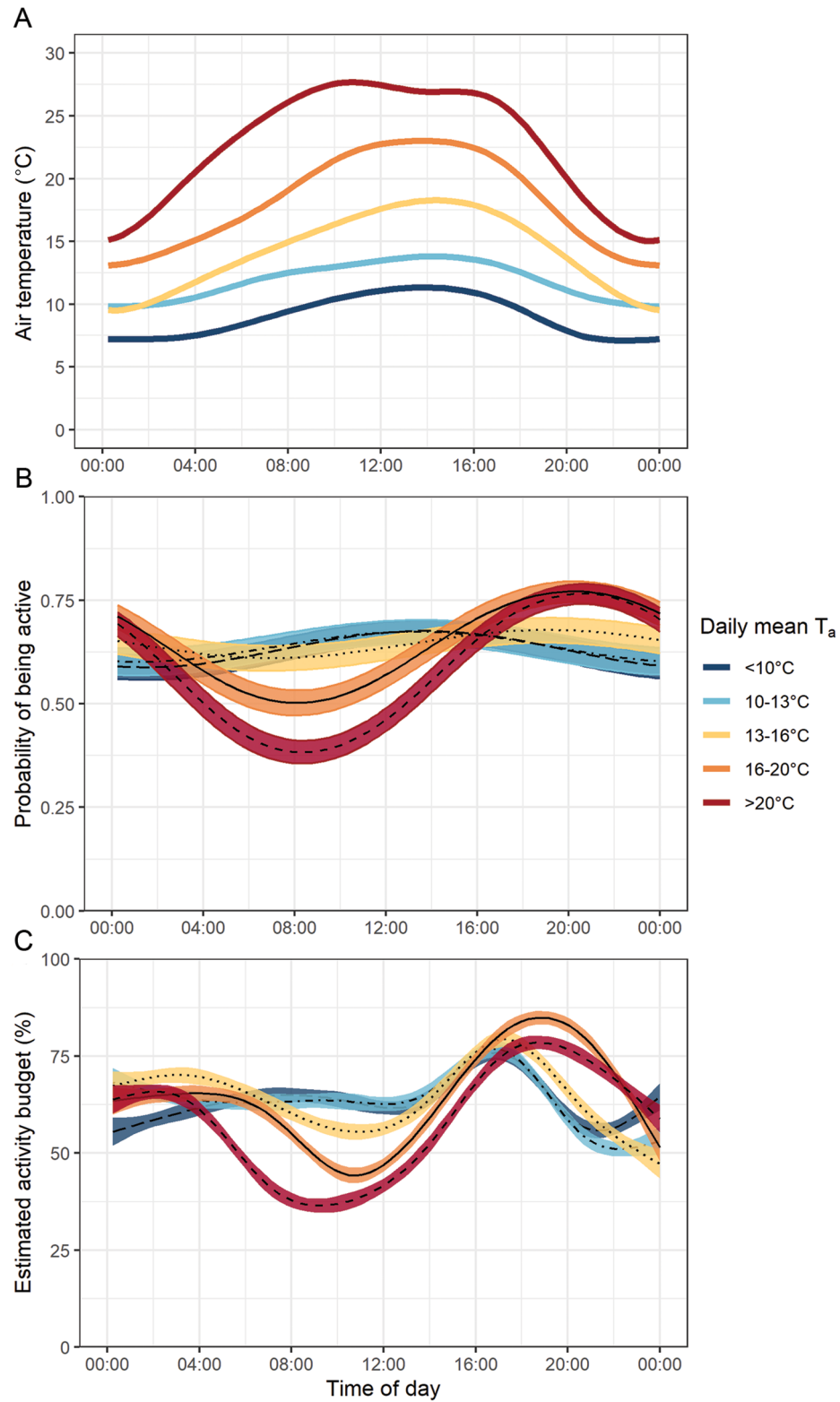


Figure 2. Air temperatures (T_a 's) and mean activity levels of 14 adult female reindeer from June 20 to August 20, 2018, in Kaamanen, northern Finland. A, Smoothed average T_a 's plotted over 24 h for different daily mean T_a categories. B, Probability of being active plotted over 24 h for different daily mean T_a categories estimated from a hidden Markov model. The lines show the predicted mean probability, and the shaded regions represent the 95% credible interval for each prediction. C, Estimated daily activity budgets (percentage of time active) plotted over 24 h, derived from the probability estimates of a hidden Markov model, grouped by different daily mean T_a categories, and shown as smoothed averages across all individuals.

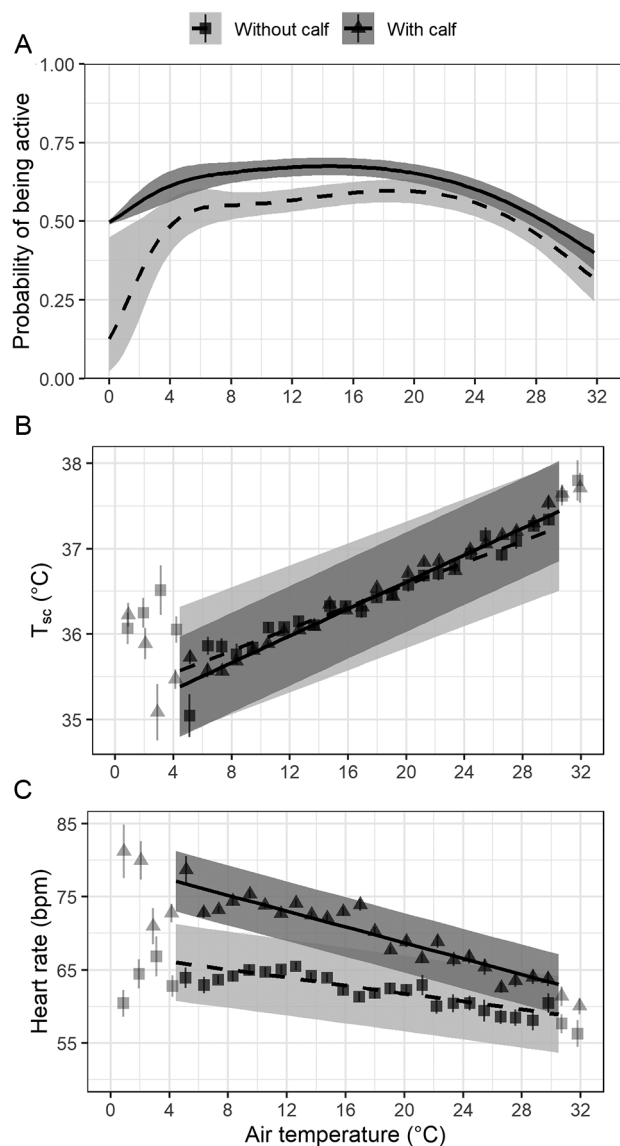


Figure 3. Responses of 10 adult female reindeer with calves (dark gray, triangles) and without calves (light gray, squares) to instantaneous air temperatures from June 20 to August 20, 2018, in Kaamanen, northern Finland. A, Probability of being active predicted from a hidden Markov model. B, Subcutaneous body temperatures (T_{sc} 's) predicted from a generalized additive mixed effects model. Points show adjusted mean \pm SEM. C, Resting heart rates predicted from a generalized additive mixed effects model. Points show adjusted mean \pm SEM. In B and C, the shaded areas show the 95% confidence interval for each prediction, and faint points outside the predictions represent the lower 1% and upper 99% of the data. All predictions and adjusted points are corrected for other explanatory variables in each model.

that may indicate a heat-related decline in food intake (Shively et al. 2019). Reindeer adjusted behaviorally to warm daytime temperatures by reducing their midday activity levels. They compensated for this reduction by being more active later in the day when it was cooler. However, above 20°C, this compensation was incomplete, resulting in a potential loss of daily

feeding time. Consequently, individuals that were less active during summer had depressed weight gain in September. While some of this depressed BM could be due to lower food quality in a warm and dry summer, we suggest that high heat loads may have contributed to this mass loss, operating through depressed activity level, reduced HR, and increased body temperature. Since BM influences reproduction and survival, we anticipate that more intense heat waves may increasingly impact fitness in mammals.

Because behavioral responses to environmental change are considered less costly than physiological responses (Hetem et al. 2014), animals are expected to first display thermoregulatory behavior when faced with conditions outside their thermoneutral zone (Mitchell et al. 2018). Here, we demonstrate that reindeer reduced their activity levels when T_a 's exceeded 20°C to likely (1) minimize heat production from being active and seek thermal refugia, such as shade and cool ground (Mitchell et al. 2018), and/or (2) reduce food intake to reduce heat load from rumination (Thompson and Barboza 2014; Shively et al. 2019), although this may be confounded by decreased food quality coinciding with heat (Turbill et al. 2011). On days when T_a exceeded 20°C only briefly around midday, reindeer compensated for lost foraging time by increasing activity in the cooler parts of the day, a response also seen in other temperate (van Beest and Milner 2013), alpine (Semenzato et al. 2021; Zhou et al. 2022), and desert (Hetem et al. 2012) ungulates. However, reindeer failed to compensate for the reduced midday activity on the very hottest days during the heat wave, resulting in an overall reduction of daily activity. Similar results have been found in male alpine ibex (*Capra ibex*), where the need to thermoregulate on warm days resulted in individuals foraging in areas with poorer vegetation without subsequent behavioral compensation to make up for low-quality forage (Mason et al. 2017). When animals are not able to compensate for lost feeding time, reduced daily activity and subsequently lower daily food intake may have detrimental consequences for fitness when facing long-lasting and chronically high heat loads (van Beest and Milner 2013; Fuller et al. 2021).

In addition, we found a negative association between HR and increasing T_a 's in summer, but we did not observe a breakpoint similar to that seen in activity patterns or that shown for reindeer in captivity at around 25°C (Blix and Johnsen 1983). A decline in HR with increasing ambient temperature has also been documented in free-ranging moose (*Alces alces*; Thompson et al. 2020) and Svalbard reindeer (*Rangifer tarandus platyrhynchus*; Trondrud et al. 2021) as well as in cattle (*Bos spp.*) in metabolic chambers (Beatty et al. 2006; de Andrade Ferrazza et al. 2017). Reductions in HR could be explained by an increased water intake, which would subsequently increase blood volume and result in a higher stroke volume (Beatty et al. 2006; Thompson et al. 2020). Although the reindeer in our study had free access to drinking water via streams and small lakes, we did not have the means to quantify water consumption. However, in captive reindeer, dry matter intake has been found to decline linearly with increasing T_a (Thompson and Barboza 2014), and both HR and activity patterns are associated with dry matter intake in reindeer

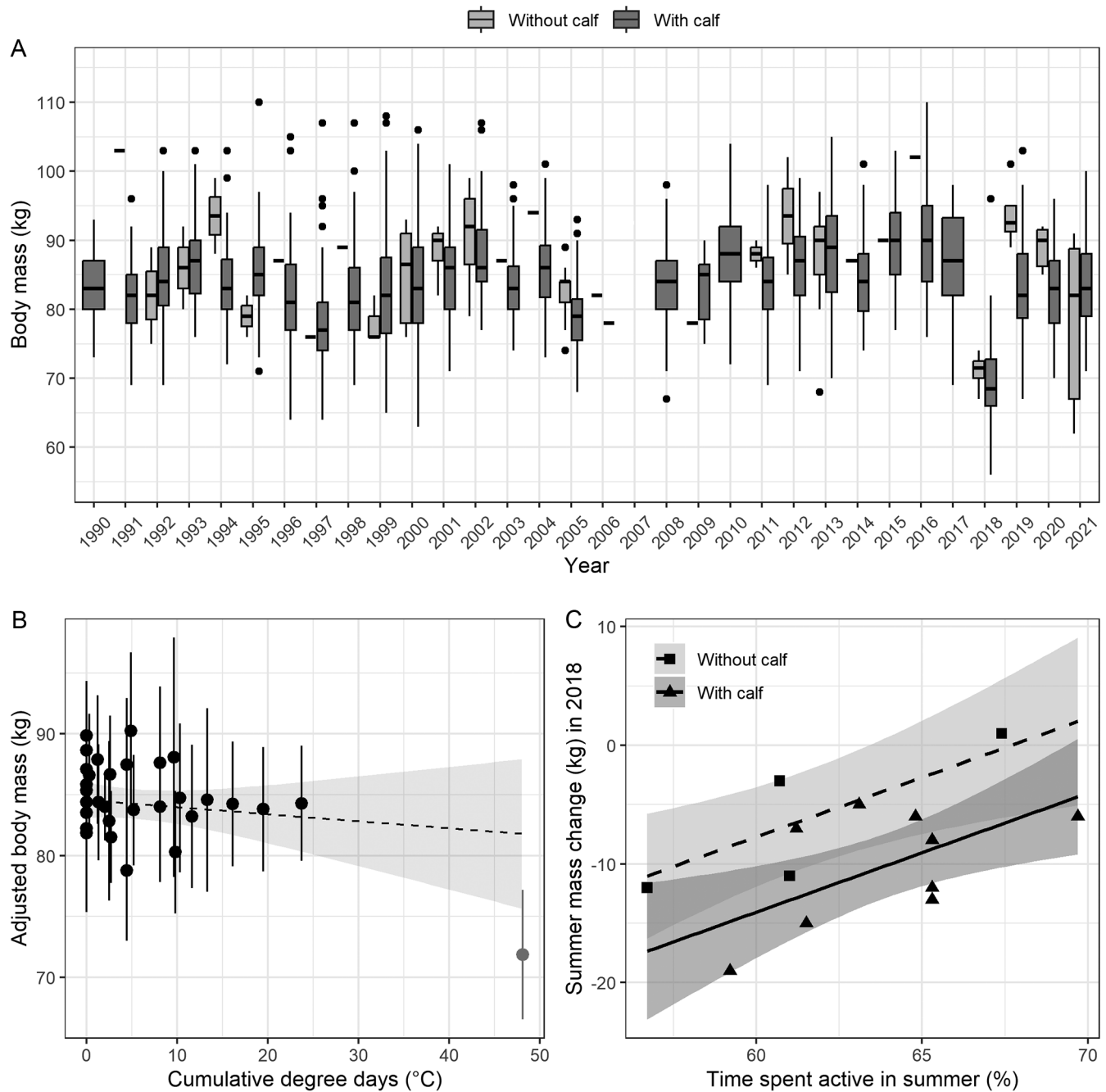


Figure 4. *A*, Median September body mass of adult female reindeer with calves (dark gray) and without calves (light gray) in each year from 1990 to 2021 ($n = 1,519$ September body masses, 344 individuals). We excluded 2007 because of insufficient data in unmanipulated individuals. Horizontal lines show the median, lower and upper ends of the boxes correspond to the first and third quartiles, and whiskers extend to up to 1.5 times the interquartile range. Points are outliers outside 1.5 times the interquartile range. Horizontal lines outside of the boxplots represent single values for when there were not enough data points to create a boxplot for the group-year combination. *B*, September body mass across all years of available data (1990–2021, except 2007) as a function of cumulative degree days (sum of daily mean temperatures $\geq 20^{\circ}\text{C}$). The points are adjusted for each female's age, April body mass, and calf status. The dashed line represents the predicted relationship between body mass and cumulative degree days in summer when excluding the year 2018 (gray point). *C*, Summer mass change (difference between April body mass and September body mass) in 2018 against the mean activity level (%) during summer in 13 adult female reindeer that were either with a calf (triangles) or without a calf (squares). The two lines represent the predicted responses for females with a calf (solid line) and without a calf (dashed line) derived from a linear regression with activity level and calf status as the predictors and summer mass change as the response (adjusted $R^2 = 0.41$, $P = 0.03$).

(Mesteig et al. 2000; Nilsson et al. 2006). The reduction in activity levels, coupled with lower resting HR at higher T_a , may suggest that reindeer obtained less food or food of poorer quality on the hottest days during summer.

In contrast to the response of HR, we found a positive relationship between T_{sc} and T_a . This is unsurprising as peripherally measured body temperatures, such as temperature of skin, typically display more variation than core body temperature (Schmidt-Nielsen 1997; Lust et al. 2007) and also fluctuate more with variation in T_a (Arnold et al. 2004; Brinkmann et al. 2012). At the highest recorded T_a 's, however, T_{sc} approached values close to core body temperature in reindeer ($\sim 38^\circ\text{C}$; Blix and Johnsen 1983), which may indicate that animals were at risk of developing hyperthermia. However, the main avenues of heat loss in resting reindeer during summer are through convection and radiation, and about 50% of radiant heat loss occurs via the trunk (Folkow and Mercer 1986). Increases in T_{sc} 's may therefore have facilitated heat loss to the environment via vasodilation to defend against increases in core body temperature, a mechanism often employed by desert ungulates (Fuller et al. 2010).

The higher activity levels and resting HRs in females with calves at low and intermediate T_a 's (compared to females without calves) suggests that females with calves had higher energy demands, which is likely because of the high energetic costs of lactation (Bårdsen et al. 2009). Our results are similar to those found in Svalbard reindeer (Trondrud et al. 2021). Although the apparent threshold of T_a at which activity levels began to decline was similar for both groups ($\sim 20^\circ\text{C}$), females with calves reduced HR to a greater extent than females without calves (fig. 3C). Despite similar responses in activity levels and T_{sc} 's, the steeper response in HR could indicate that females with calves were more susceptible to heat stress (Speakman and Król 2010). Indeed, lactating females can be particularly sensitive to heat stress during the late lactational period (Zhao et al. 2020). The energetic demand of lactation can lead to reduced somatic growth in female ungulates that do reproduce that year compared to in female ungulates that do not reproduce that year (Pigeon et al. 2022). In our herd, having a calf reduced September BM by almost 4 kg. Additional constraints on food intake (via environmental heat load) may therefore be of greater consequence for females that reproduce by further constraining the trade-off between investments in reproduction and in maintenance.

In 2018, the September BMs were the lowest recorded in the past 32 yr. Environmental conditions in both spring and summer impact autumn BM in several ungulate species, presumably via changes in forage availability and insect harassment (Aanes et al. 2002; Hurley et al. 2014; Desforges et al. 2021; Johnson et al. 2022). In particular, poor spring conditions and large-scale climatic oscillations may result in lower autumn BMs (Holmes et al. 2021) and reduced population growth (Aanes et al. 2002). However, warmer temperatures in summer can also be associated with increased autumn BM, as shown in Svalbard reindeer (Albon et al. 2017). Insect harassment may also negatively impact body condition, often in interactions with temperature (Mörschel and Klein 1997) and nutritional quality (Johnson et al. 2022). Although the relationship between BM and prevailing weather

during summer was weak when excluding the year 2018, the extreme contrast between this year and the other years was remarkable. Indeed, both recruitment and mass of Swedish moose calves were also reported to be considerably lower in 2018 (Holmes et al. 2021), which was attributed to low forage quality and availability. The exceptionally low BMs of the reindeer in our study in 2018 were likely caused by a combination of multiple environmental factors, including low forage quality due to low precipitation and poor spring conditions, insect harassment, and T_a 's (e.g., see Mörschel and Klein 1997). Based on our findings, we suggest that high environmental heat loads during summer 2018 also contributed to the low BMs via changes in activity patterns and foraging effort to avoid heat stress. This suggestion is corroborated by our subset of females with activity data for which we found a positive association between activity levels and BM change during summer, providing a potential explanation for the lower BMs observed in September 2018. Although there is evidence that female reindeer in captivity can regain fat reserves after weaning their calves (Chan-McLeod et al. 1999), such compensations demand that sufficient food is available. In our study, supplementary feeding in the winter likely alleviated the consequence of reduced mass in 2018, as they had relatively high BMs in the subsequent year (fig. A1-8). The effects of restricted foraging in summer are therefore more likely to have a greater impact for wild ungulates with natural sources of food than for managed herds or domestic livestock that rely on food supplementation.

In recent decades, there have been more frequent and intense heat waves across the globe (Pörtner et al. 2019). Acute heat stress can have detrimental effects on wildlife through mass mortalities, which in large mammals is typically due to dehydration or lack of food (Young 1994; Cheng 2022). However, sublethal, chronic heat stress could lead to alterations in individual behavior, physiology, and therefore fitness, and consequently, it could impact population dynamics (Conradie et al. 2019). We show that reindeer displayed behavioral and physiological signs of heat stress avoidance under environmental temperatures that are predicted to become more common in the Arctic (Pörtner et al. 2019). Although behavioral responses have been documented in a wide array of mammalian species, few studies have investigated the simultaneous response in physiological parameters and the subsequent consequences for BM. Our study emphasizes the importance of a better integration of behavior, physiology, and ecology when investigating animal responses to extreme environmental conditions (Buckley and Huey 2016; Stillman 2019), all of which potentially influence the capacity of individuals to cope with a warming climate (Hetem et al. 2014; Fuller et al. 2021).

Acknowledgments

We are grateful for the feedback from Robyn Hetem and for the constructive inputs from the two anonymous reviewers. We thank Clare Stawski and Murray M. Humphries for commenting on an earlier version of the manuscript. Fieldwork would not be possible without the collaboration with the Reindeer Herders'

Association and the local support from Mika Tervonen, Unto Paadar, Jukka Siitari, and field assistants Elise Tjørnsletten, Kine Øren, and Erlend Søyby. Veterinarians Marja Nourgam and Amanda Høyer Boesen contributed to the anesthesia and surgery of the reindeer. We thank Àsgeir Bjarnason at Star-Oddi for help and guidance with biogger programming and data processing and Larissa Beumer for advice on the hidden Markov model approach. Cassandra Ugland validated the heart rate measurements. The work was supported by the Norwegian Research Council (grants 267613 and 315454). L.E.L., A.L.E., E.R., J.R.S., E.K., and L.M.T. planned the study. J.K. facilitated the fieldwork. E.R., A.L.E., L.M.T., J.K., and L.E.L. conducted the fieldwork, including device deployment, retrieval, and animal handling. L.M.T. curated and analyzed the data together with G.P. L.M.T. drafted the manuscript with input from S.A. All authors contributed to editing and approved the final version of the manuscript. The prior authorization for all procedures carried out on the reindeer in this study was granted by the Animal Experiment Board at the Regional State Administrative Agency in Finland (license ESAVI/3857/04.10.07/2017). Long-term climatic data are publicly available from the Finnish Meteorological Institute (<https://en.ilmatietaenlaitos.fi/download-observations/>). Curated biogger data and locally recorded weather data are available online (<https://figshare.com/s/c1044ce71c363ccc20b8>). The historical body mass data of females have been collected from the experimental reindeer herd at the Kutuharju Research Station by the Finnish Reindeer Herders' Association, who also own the reindeer herd and the station (<https://www.luke.fi/en/research/research-infrastructures/kutuharju-research-infrastructure>). Natural Resources Institute Finland updates, saves, and administrates this long-term reindeer herd data.

Literature Cited

- Aanes R., B.E. Sæther, F.M. Smith, E.J. Cooper, P.A. Wookey, and N. Areøritsland. 2002. The Arctic Oscillation predicts effects of climate change in two trophic levels in a high-Arctic ecosystem. *Ecol Lett* 5:445–453.
- Albon S.D., R.J. Irvine, O. Halvorsen, R. Langvatn, L.E. Loe, E. Ropstad, V. Veiberg, et al. 2017. Contrasting effects of summer and winter warming on body mass explain population dynamics in a food-limited Arctic herbivore. *Glob Change Biol* 23:1374–1389.
- Arnold W., T. Ruf, S. Reimoser, F. Tataruch, K. Onderschecka, and F. Schober. 2004. Nocturnal hypometabolism as an overwintering strategy of red deer (*Cervus elaphus*). *Am J Physiol* 286:R174–R181.
- Aublet J.-F., M. Festa-Bianchet, D. Bergero, and B. Bassano. 2009. Temperature constraints on foraging behaviour of male Alpine ibex (*Capra ibex*) in summer. *Oecologia* 159:237–247.
- Bårdsen B.J., P. Fauchald, T. Tveraa, K. Langeland, and M. Nieminen. 2009. Experimental evidence of cost of lactation in a low risk environment for a long-lived mammal. *Oikos* 118:837–852.
- Beatty D.T., A. Barnes, E. Taylor, D. Pethick, M. McCarthy, and S.K. Maloney. 2006. Physiological responses of *Bos taurus* and *Bos indicus* cattle to prolonged, continuous heat and humidity. *J Anim Sci* 84:972–985.
- Blix A.S. and H.K. Johnsen. 1983. Aspects of nasal heat exchange in resting reindeer. *J Physiol* 340:445–454.
- Brinkmann L., M. Gerken, and A. Riek. 2012. Adaptation strategies to seasonal changes in environmental conditions of a domesticated horse breed, the Shetland pony (*Equus ferus caballus*). *J Exp Biol* 215:1061–1068.
- Brivio F., M. Zurmühl, S. Grignolio, J. von Hardenberg, M. Apollonio, and S. Ciuti. 2019. Forecasting the response to global warming in a heat-sensitive species. *Sci Rep* 9:3048.
- Buckley L.B. and R.B. Huey. 2016. Temperature extremes: geographic patterns, recent changes, and implications for organismal vulnerabilities. *Glob Change Biol* 22:3829–3842.
- Burnham K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Vol. 172. Springer, New York.
- Chan-McLeod A.C.A., R.G. White, and D.E. Russell. 1999. Comparative body composition strategies of breeding and nonbreeding female caribou. *Can J Zool* 77:1901–1907.
- Cheng A. 2022. Extreme heat and humidity kill thousands of cattle in Kansas. *Washington Post* (June 16).
- Conradie S.R., S.M. Woodborne, S.J. Cunningham, and A.E. McKechnie. 2019. Chronic, sublethal effects of high temperatures will cause severe declines in southern African arid-zone birds during the 21st century. *Proc Natl Acad Sci USA* 116:14065–14070.
- Dash S., A.K. Chakravarty, A. Singh, A. Upadhyay, M. Singh, and S. Yousuf. 2016. Effect of heat stress on reproductive performances of dairy cattle and buffaloes: a review. *Vet World* 9:235–244.
- de Andrade Ferrazza R., H.D. Mogollón Garcia, V.H. Vallejo Aristizábal, C. de Souza Nogueira, C.J. Veríssimo, J.R. Sartori, R. Sartori, and J.C. Pinheiro Ferreira. 2017. Thermoregulatory responses of Holstein cows exposed to experimentally induced heat stress. *J Therm Biol* 66:68–80.
- Denryter K., R.C. Cook, J.G. Cook, K.L. Parker, and M.P. Gillingham. 2020. State-dependent foraging by caribou with different nutritional requirements. *J Mammal* 101:544–557.
- Desforges J.-P., G.M. Marques, L.T. Beumer, M. Chimienti, L.H. Hansen, S.H. Pedersen, N.M. Schmidt, and F.M. van Beest. 2021. Environment and physiology shape Arctic ungulate population dynamics. *Glob Change Biol* 27:1755–1771.
- Ditmer M.A., R.A. Moen, S.K. Windels, J.D. Forester, T.E. Ness, and T.R. Harris. 2018. Moose at their bioclimatic edge alter their behavior based on weather, landscape, and predators. *Curr Zool* 64:419–432.
- Dobricic S., S. Russo, L. Pozzoli, J. Wilson, and E. Vignati. 2020. Increasing occurrence of heat waves in the terrestrial Arctic. *Environ Res Lett* 15:024022.
- Folkow L.P. and J.B. Mercer. 1986. Partition of heat loss in resting and exercising winter- and summer-insulated reindeer. *Am J Physiol* 251:R32–R40.
- Fuller A., T. Dawson, B. Helmuth, R.S. Hetem, D. Mitchell, and S.K. Maloney. 2010. Physiological mechanisms in coping with climate change. *Physiol Biochem Zool* 83:713–720.

- Fuller A., D. Mitchell, S.K. Maloney, R.S. Hetem, V.F.C. Fonsêca, L.C.R. Meyer, T.M.F.N. van de Ven, and E.P. Snelling. 2021. How dryland mammals will respond to climate change: the effects of body size, heat load and a lack of food and water. *J Exp Biol* 224:jeb238113.
- Hetem R.S., A. Fuller, S.K. Maloney, and D. Mitchell. 2014. Responses of large mammals to climate change. *Temperature* 1:115–127.
- Hetem R.S., W.M. Strauss, L.G. Fick, S.K. Maloney, L.C.R. Meyer, M. Shobrak, A. Fuller, et al. 2012. Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? *Zoology* 115:411–416.
- Holmes S.M., J.P.G.M. Croomsigt, K. Danell, G. Ericsson, N.J. Singh, and F. Widemo. 2021. Declining recruitment and mass of Swedish moose calves linked to hot, dry springs and snowy winters. *Glob Ecol Conserv* 27:e01594.
- Hurley M.A., M. Hebblewhite, J.-M. Gaillard, S. Dray, K.A. Taylor, W.K. Smith, P. Zager, et al. 2014. Functional analysis of normalized difference vegetation index curves reveals overwinter mule deer survival is driven by both spring and autumn phenology. *Philos Trans R Soc B* 369:20130196.
- Igono M.O., G. Bjotvedt, and H.T. Sanford-Crane. 1992. Environmental profile and critical temperature effects on milk production of Holstein cows in desert climate. *Int J Biometeorol* 36:77–87.
- Irving L. and J. Krog. 1955. Temperature of skin in the Arctic as a regulator of heat. *J Appl Physiol* 7:355–364.
- Johnsen H.K., K.J. Nilssen, A. Rognmo, and A.S. Blix. 1990. Reindeer breathe less and save water in the cold. *Rangifer* 10:243–247.
- Johnson H.E., E.A. Lenart, D.D. Gustine, L.G. Adams, and P.S. Barboza. 2022. Survival and reproduction in Arctic caribou are associated with summer forage and insect harassment. *Front Ecol Evol* 10:899585.
- Kueh M.T. and C.Y. Lin. 2020. The 2018 summer heatwaves over northwestern Europe and its extended-range prediction. *Sci Rep* 10:19283.
- Langrock R., R. King, J. Matthiopoulos, L. Thomas, D. Fortin, and J.M. Morales. 2012. Flexible and practical modeling of animal telemetry data: hidden Markov models and extensions. *Ecology* 93:2336–2342.
- Lust A., A. Fuller, S.K. Maloney, D. Mitchell, and G. Mitchell. 2007. Thermoregulation in pronghorn antelope (*Antilocapra americana*, Ord) in the summer. *J Exp Biol* 210:2444–2452.
- Mason T.H.E., F. Brivio, P.A. Stephens, M. Apollonio, and S. Grignolio. 2017. The behavioral trade-off between thermoregulation and foraging in a heat-sensitive species. *Behav Ecol* 28:908–918.
- McClintock B.T. and T. Michelot. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol Evol* 9:1518–1530.
- McNab B.K. 2002. The physiological ecology of vertebrates: a view from energetics. Cornell University Press, New York.
- Mesteig K., N.J.C. Tyler, and A.S. Blix. 2000. Seasonal changes in heart rate and food intake in reindeer (*Rangifer tarandus tarandus*). *Acta Physiol Scand* 170:145–151.
- Mitchell D., E.P. Snelling, R.S. Hetem, S.K. Maloney, W.M. Strauss, and A. Fuller. 2018. Revisiting concepts of thermal physiology: predicting responses of mammals to climate change. *J Anim Ecol* 87:956–973.
- Mörschel F.M. and D.R. Klein. 1997. Effects of weather and parasitic insects on behavior and group dynamics of caribou of the Delta Herd, Alaska. *Can J Zool* 75:1659–1670. <https://doi.org/10.1139/z97-793>.
- Nilsson A., B. Åhman, H. Norberg, I. Redbo, E. Eloranta, and K. Olsson. 2006. Activity and heart rate in semi-domesticated reindeer during adaptation to emergency feeding. *Physiol Behav* 88:116–123.
- Parker K.L. and C.T. Robbins. 1984. Thermoregulation in mule deer and elk. *Can J Zool* 62:1409–1422.
- Peters W., A. Bastos, P. Ciais, and A. Vermeulen. 2020. A historical, geographical and ecological perspective on the 2018 European summer drought. *Philos Trans R Soc B* 375:20190505.
- Pigeon G., S. Albon, L.E. Loe, R. Bischof, C. Bonenfant, M. Forchhammer, R.J. Irvine, E. Ropstad, V. Veiberg, and A. Stien. 2022. Context-dependent fitness costs of reproduction despite stable body mass costs in an Arctic herbivore. *J Anim Ecol* 91:61–73.
- Pörtner H.-O., D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, et al., eds. 2019. IPCC special report on the ocean and cryosphere in a changing climate. Cambridge University Press, Cambridge.
- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Rantanen M., A.Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma, and A. Laaksonen. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Commun Earth Environ* 3:168.
- Røed K.H., Ø. Flagstad, M. Nieminen, Ø. Holand, M.J. Dwyer, N. Røv, and C. Vilà. 2008. Genetic analyses reveal independent domestication origins of Eurasian reindeer. *Proc R Soc B* 275:1849–1855.
- Sarmiento W., M. Biel, and J. Berger. 2019. Seeking snow and breathing hard—behavioral tactics in high elevation mammals to combat warming temperatures. *PLoS ONE* 14:e0225456.
- Schmidt-Nielsen K. 1997. Animal physiology: adaptation and environment. Cambridge University Press, Cambridge.
- Semenzato P., F. Cagnacci, F. Ossi, E. Eccel, N. Morellet, A.J.M. Hewison, E. Sturaro, and M. Ramanzin. 2021. Behavioural heat-stress compensation in a cold-adapted ungulate: forage-mediated responses to warming Alpine summers. *Ecol Lett* 24:1556–1568.
- Shepard E.L.C., R.P. Wilson, L.G. Halsey, F. Quintana, A. Gómez Laich, A.C. Gleiss, N. Liebsch, A.E. Myers, and B. Norman. 2008. Derivation of body motion via appropriate smoothing of acceleration data. *Aquat Biol* 4:235–241.
- Shively R.D., J.A. Crouse, D.P. Thompson, and P.S. Barboza. 2019. Is summer food intake a limiting factor for boreal browsers? diet, temperature, and reproduction as drivers of consumption in female moose. *PLoS ONE* 14:e0223617.

- Shrestha A.K., S.E. van Wieren, F. van Langevelde, A. Fuller, R.S. Hetem, L. Meyer, S. de Bie, and H.H.T. Prins. 2014. Larger antelopes are sensitive to heat stress throughout all seasons but smaller antelopes only during summer in an African semi-arid environment. *Int J Biometeorol* 58:41–49.
- Sinclair V.A., J. Mikkola, M. Rantanen, and J. Räsänen. 2019. The summer 2018 heatwave in Finland. *Weather* 74:403–409.
- Skogland T. 1980. Comparative summer feeding strategies of arctic and alpine rangifer. *J Anim Ecol* 49:81–98.
- Speakman J.R. and E. Król. 2010. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *J Anim Ecol* 79:726–746.
- Stillman J.H. 2019. Heat waves, the new normal: summertime temperature extremes will impact animals, ecosystems, and human communities. *Physiology* 34:86–100.
- Thompson D.P. and P.S. Barboza. 2014. Nutritional implications of increased shrub cover for caribou (*Rangifer tarandus*) in the Arctic. *Can J Zool* 92:339–351.
- Thompson D.P., J.A. Crouse, S. Jaques, and P.S. Barboza. 2020. Redefining physiological responses of moose (*Alces alces*) to warm environmental conditions. *J Therm Biol* 90: 102581.
- Trondrud L.M. 2021. Energetics in seasonal environments: reindeer as a case study. PhD diss. Norwegian University of Life Sciences, Ås, Norway.
- Trondrud L.M., G. Pigeon, S. Albon, W. Arnold, A.L. Evans, R.J. Irvine, E. Król, et al. 2021. Determinants of heart rate in Svalbard reindeer reveal mechanisms of seasonal energy management. *Philos Trans R Soc B* 376:20200215.
- Turbill C., T. Ruf, T. Mang, and W. Arnold. 2011. Regulation of heart rate and rumen temperature in red deer: effects of season and food intake. *J Exp Biol* 214:963–970.
- van Beest F.M. and J.M. Milner. 2013. Behavioural responses to thermal conditions affect seasonal mass change in a heat-sensitive northern ungulate. *PLoS ONE* 8:e65972.
- van Beest F.M., B. Van Moorter, and J.M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim Behav* 84:723–735.
- Williamson L., G. Pigeon, A. Mysterud, A. Stien, M. Forchhammer, and L.E. Loe. 2019. Keeping cool in the warming Arctic: thermoregulatory behaviour by Svalbard reindeer (*Rangifer tarandus platyrhynchus*). *Can J Zool* 97:1177–1185.
- Wilson R.P., L. Börger, M.D. Holton, D.M. Scantlebury, A. Gómez-Laich, F. Quintana, F. Rosell, et al. 2020. Estimates for energy expenditure in free-living animals using acceleration proxies: a reappraisal. *J Anim Ecol* 89:161–172.
- Wood S.N. 2017. Generalized additive models: an introduction with R. CRC, Boca Raton, FL.
- Young T.P. 1994. Natural die-offs of large mammals: implications for conservation. *Conserv Biol* 8:410–418.
- Zhao Z.-J., C. Hambly, L.-L. Shi, Z.-Q. Bi, J. Cao, and J.R. Speakman. 2020. Late lactation in small mammals is a critically sensitive window of vulnerability to elevated ambient temperature. *Proc Natl Acad Sci USA* 117:24352–24358.
- Zhou W., M. Wang, K. Gao, H. Gao, F. Wei, and Y. Nie. 2022. Behavioural thermoregulation by montane ungulates under climate warming. *Divers Distrib* 28:2229–2238.