Body temperature patterns during pregnancy and parturition in moose

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ABSTRACT

Gestation and lactation have high energetic requirements. Up to three-fourths of the gestation period in moose (*Alces alces*) overlaps with the food-scarce period in winter. During this period, moose deal with the limited forage resources available through hypometabolism with decreased heart rate and body temperature (T_b). Body temperature is also an indicator of oestrus, pregnancy and parturition, which is well documented in several domestic species. In this study, we sought to determine if moose displayed a similar T_b pattern during pregnancy and parturition to domesticated ruminants, and if we could detect parturition by combining T_b and activity data.

We studied the T_b pattern of 30 free-ranging adult female moose ($\geq$1.5 years old), equipped with ruminal temperature loggers and GPS collars. We documented a 0.13–0.19°C higher T_b in pregnant compared to non-pregnant moose, depending on the study area with the T_b difference increasing along a south-north gradient, and a drop in T_b and in activity when parturition was imminent. Detection of parturition was highly successful when combining T_b and activity data with an accuracy of 91.5%. Our findings demonstrate that T_b responses to pregnancy and parturition in a wild capital-breeding ruminant are similar to those of domesticated ruminants.

1. Introduction

Maintaining foetal homeothermy is a high priority in pregnant individuals. Alterations in maternal body temperature (T_b) due to stress, exercise, and alterations in ambient temperature require thermoregulatory strategies to keep a stable foetal T_b resulting in costs for both mother and foetus (Laburn et al., 2002). Reproduction, and especially parturition and lactation are energy consuming life events (Speakman, 2008). Food scarcity combined with low ambient temperature in winter has forced many species to adapt. Strategies vary from complete inactivity and sub-freezing body temperatures to migration to more suitable habitats. Moose (*Alces alces*) are capital breeders, with reproduction relying on their stored energy reserves, and the gestation period overlaps to large degree with the periods with the lowest food availability, particularly at northern latitudes (Ericsson et al., 2001; Markgren, 1969; Schwartz and Hundertmark, 1993). Moose and other ungulates, decrease T_b during winter to drastically reduce their metabolic needs -or to hypometabolism (Arnold et al., 2018; Græsli et al., 2020; Signer et al., 2011; Turbill et al., 2011).

Body temperature, as an indicator for oestrus, pregnancy and parturition is well documented in several domesticated species like cattle, sheep, horses and dogs (Auclair-Ronzaud et al., 2020; Ewbank, 1969; Godyń et al., 2018; Verstegen-Onclin and Verstegen, 2008). Fluctuations in T_b during pregnancy in cattle have been associated with fluctuations in hormone levels, and especially progesterone levels, due to the thermogenic effect of progesterone (Kornmatitsuk et al., 2002; Nabenishi and Yamazaki, 2017; Suthar et al., 2012). Progesterone, a steroid hormone mainly secreted by the corpus luteum and/or placenta, plays an important role in the oestrus cycle, and in the establishment and maintenance of pregnancy (Wiltbank et al., 2014). During pregnancy, the corpus luteum is maintained and produces high levels of progesterone, resulting in increased T_b (Suthar et al., 2012; Wiltbank et al., 2014).

Moose are polyoestral seasonal breeders, breeding from late September to early November (Malmsten et al., 2014; Niedziałkowska et al., 2022). The reported gestation lengths vary from 216 to 246 days, with a mean of 231 days resulting in a calving period in May and June (Markgren, 1969; Neumann et al., 2020; Schwartz, 1992; Schwartz and

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Hundertmark, 1993). In moose, progesterone levels increase the first 40-50 days after conception, thereafter it remains at the same level until it starts to decline 40-50 days pre-partum and in the last 4-6 days it declines sharply (Stewart et al., 1985). In cattle, corpus luteum regresses when parturition is imminent, resulting in decreased progesterone levels followed by a decrease in T_b (Cooper-Prado et al., 2011; Costa Jr et al., 2016; Kornmatitsuk et al., 2002; Suthar et al., 2012; Wrenn et al., 1958). The drop in T_b over the last days before parturition has therefore been used as a predictor of the onset of parturition in cattle (Costa Jr et al., 2016). Costa Jr et al. (2016) reported that a drop in daily mean ruminal temperature of $\geq 0.2°C$ from day -2 to -1 before parturition was a good indicator for calving in Holstein cattle. Earlier studies have used changes in movement and accelerometery data to predict parturition among ungulates, including moose (Chimienti et al., 2021; DeMars et al., 2013; Marchand et al., 2021; Nicholson et al., 2019; Severud et al., 2015). Changepoint analysis is a method to detect distributional changes in time series data (Killick et al., 2012). Activity derived from accelerometery data are demonstrated to decrease markedly during parturition in ungulate species like Mediterranean mouflon (*Ovis gmelini musimon* × *Ovis* sp.) and the Alpine ibex (*Capra ibex)*, where after it increase some days after the calving event (Marchand et al., 2021).

Different biologging methods have been validated for continuous measurements of T_b in moose including both ruminal and vaginal implants (Herberg et al., 2018; Thompson et al., 2018). Studies of T_b patterns during the entire pregnancy including calving in wild ruminants are, to our knowledge, limited. Thompson et al. (2019) found a statistically higher T_b in pregnant compared to non-pregnant moose (0.18°C higher). Yet, the authors could not conclude if this was due to pregnancy because of the skewed ratio of pregnant and non-pregnant moose, and the T_b difference between groups was below the accuracy of the biologger. Here, we fitted female moose with ruminal temperature loggers

and GPS collars equipped with accelerometers providing fine scale data over up to two years per animal. We sought to determine if moose display a thermal pattern during pregnancy and parturition characteristic for domesticated ruminants (Costa Jr et al., 2016; Ewbank, 1969; Kornmatitsuk et al., 2002; Nabenishi and Yamazaki, 2017; Suthar et al., 2012). We also evaluated whether calving in moose could be identified based on changepoint analysis on a combination of thermal and activity data, as combination data has been previously documented to have higher accuracy for detecting parturition among ungulates than data from solely one source (Costa Jr et al., 2016; Ewbank, 1969; Marchand et al., 2021). We predicted higher T_b in pregnant moose compared to non-pregnant moose (Thompson et al., 2019). We also predicted a drop in ruminal temperature of $\geq 0.2°C$ when parturition is imminent (Costa Jr et al., 2016). And last, we predicted a drop in both T_b and activity in relation to calving, and thus detection of changepoints, due to the calving itself and the limited mobility of the calf during the first days (Costa Jr et al., 2016; Marchand et al., 2021; Testa et al., 2000).

2. Materials and methods

2.1. Study area and animals

From 2012 to 2017, we equipped 30 free-ranging female moose (≥ 1.5 years old) with ruminal temperature loggers and GPS collars in three different study areas in Sweden, ranging from 56° to 67° N latitude (see Fig. 1). The Northern alpine area is located in a high alpine area of northern inland Sweden (Nikkaluokta (67°N)), the Northern coastal area is located on the north-central coast (Nordmaling (63°N)), and the Southern island area is located in southeast Sweden on the island of Öland (56°N). Adult female moose were visually selected and immobilised from a helicopter in the three study areas, including ten in the
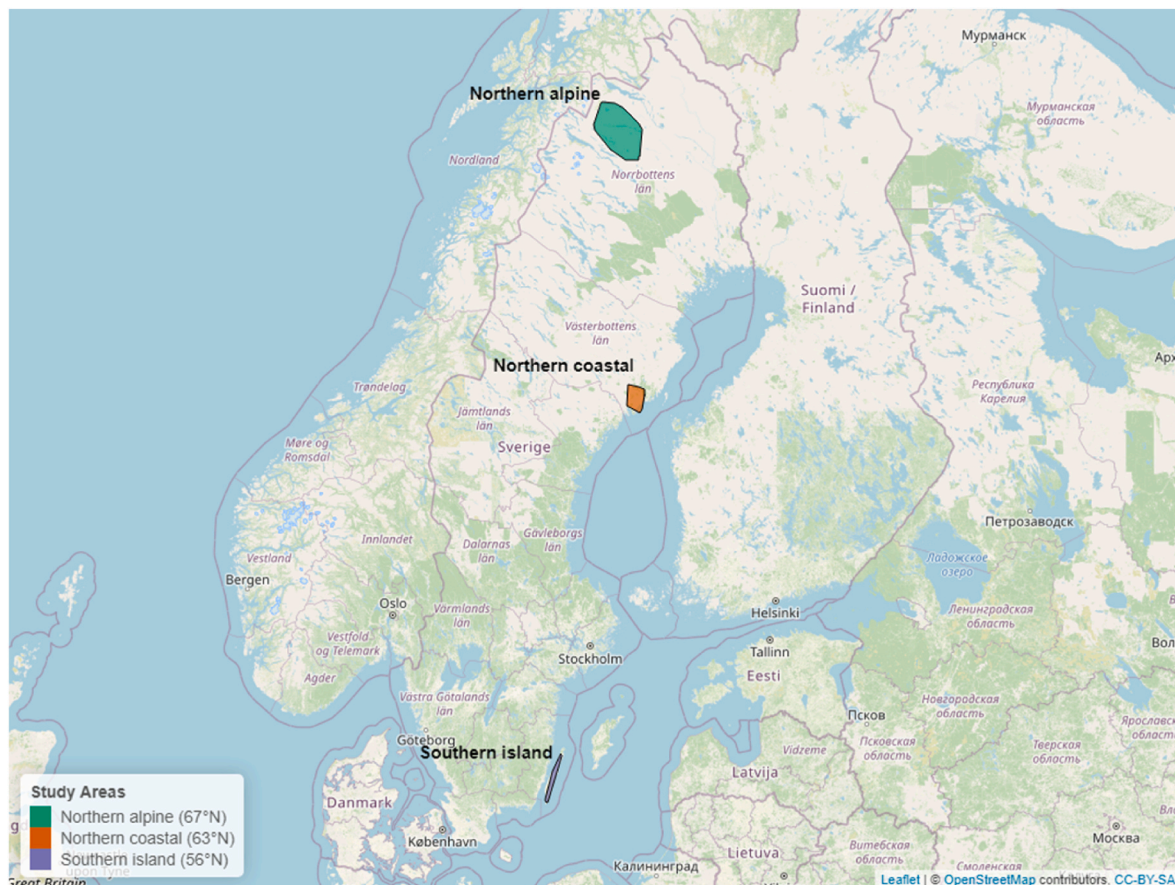

Fig. 1. Location of the study areas in Sweden.

Northern alpine area (2012), twelve in the Northern coastal area (2017) and eight in the Southern island area (2015). The project was approved by the Regional Animal Ethics Committee for Northern Sweden in Umeå (Dnr A116–09, A12–12, A50–12, A205–12, A14-15) and was conducted following Swedish laws concerning animal research ethics. All personnel were trained and certified according to the standards of the Swedish Board of Agriculture.

2.2. Biologgers; programming and data collection

We fitted all moose with GPS Plus Collars (former version of VERTEX Plus) equipped with a global positioning system (GPS) receiver, a very high frequency (VHF) transmitter, an ambient temperature recorder, a global system for mobile (GSM) communication modem or IRIDIUM communication, and an acceleration sensor (Vectronic-Aerospace, Berlin, Germany) (Vectronic Aerospace, 2021). The collars were scheduled to record GPS positions at intervals ranging from 30 min to 3 h depending on other ongoing studies and used the GSM cell phone network or Iridium satellite communication to send the GPS position together with the most recently recorded ambient temperature to a database server, WRAM (Wireless Remote Animal Movement), for storage (Dettki et al., 2004). Acceleration was measured over two axes (X and Y) by the acceleration sensor integrated in the collar (hereafter referred to as "activity"). Activity was measured at a scale from 0 to 255 at 6 to 8 Hz at both axes and average values over 5-minuttes intervals are stored. The overall activity is presented as the sum of the activity on both axes, ranging from 0 to 510 with 0 representing no activity and 510 highest activity (Gervasi et al., 2006). In addition, we deployed mortality implant transmitters (MIT, Vectronic Aerospace GmbH, Berlin Germany), hereafter MIT, per os into the reticulorumen of the moose (Vectronic Aerospace, 2022). The MITs were programmed to obtain T_b at 5-min intervals, and the information was sent to the collar unit to be archived. Whenever the collar sent a GPS position message, the latest T_b archived was attached. The remaining data were downloaded upon collar retrieval. The accuracy of the MITs is 0.1°C, and they have a resolution of ±0.001°C (Herberg et al., 2018; Vectronic Aerospace, 2022).

2.3. Immobilisation procedure

We immobilised moose from a helicopter during wintertime (February–March) according to earlier described procedures (Evans et al., 2012; Græsli et al., 2020; Lian et al., 2014). We deployed MITs during immobilisation as previously described (Græsli et al., 2020; Minicucci et al., 2018). During captures, pregnancy status was determined by rectal palpation (Solberg et al., 2003). To retrieve the data obtained by the MIT, we recaptured the moose, according to the same procedure as the initial captures, and downloaded the stored MIT and activity data from the collar. Moose in the Northern alpine and Southern island areas were recaptured three years after the first capture, while moose in the Northern coastal area were recaptured the two following years after the initial capture, due to other ongoing studies.

2.4. Data preparation and analysis

One of the moose in the Southern island area died a few days post-capture and is excluded from the analyses. A necropsy was performed and no cause of death was identified, however, the MIT was missing from the rumen and was not found elsewhere, so we cannot rule out the possibility of improper placement of the device and subsequent expulsion. Three other moose died during the study period, two were shot during the annual moose hunt, and one died due to unknown reasons over one year after device deployment. For these moose, the MIT data were downloaded from the collar, and these data were included in the analyses. In addition, we lost GPS connection with two moose during the study period, and the received MIT data of nine and twelve months

duration, respectively, were included in the analysis. In total, we used 3,935,575 T_b measurements from 29 individual moose. We prepared and analysed the data using R version 4.0.0 (R Core Team, 2021), and considered *P* values <0.05 as significant.

We excluded the days of capture, recapture and three days post-capture/recapture from the analysis because the capture event and anaesthetics were expected to affect T_b (Kreeger and Arnemo, 2018; Thompson et al., 2020). Calving dates were determined based on GPS clustering, and subsequent visual observation of cow and offspring(s) in the field (Neumann et al., 2020). We defined the calving period as the calving date ±15 days. We used the mean gestation length of 231 days and calculated a conception date from the calving date (Schwartz and Hundertmark, 1993). To compare the T_b patterns between different reproductive states we used the mean calving date in the given area as a simulated calving date for non-pregnant moose. An overview of the study population with pregnancy status, years and study areas are shown in Table 1. We could verify birth of twins in 32% (*n* = 12) of the pregnant females (Northern alpine 9%, *n* = 1; Northern coastal 39%, *n* = 7; Southern island 50%, *n* = 4).

We used the method described by Thompson (2020) to filter out drinking events, as the ruminal temperature is shown to be a good predictor for body temperature when drinking events are filtered out (Herberg et al., 2018). Thus, every $T_b \leq 37.54$°C and the following 40 min, in addition to every drop in $T_b > 0.25$°C within 5 min (from the previous regular measurement) were classified as drinking events and filtered out.

2.4.1. Body temperature patterns associated with pregnancy

To investigate T_b patterns, and to test for differences of T_b in relation to different reproductive states throughout the year, we fitted generalised additive mixed models (GAMMs) with daily mean T_b as the response variable (Wood, 2017). We used the following explanatory variables to build a set of candidate models: 1) Pregnant (factor with two levels; yes (pregnant) or no (non-pregnant)), describing the reproductive state of the animal; 2) "day of gestation" (DOG, continuous 1–231), a measure of days from the estimated conception date and 3) area (factor with three levels: Northern alpine, Northern coastal and Southern island), which includes our three study areas. We set up a list of candidate models with all possible additive combinations as well as the interactions between DOG and Pregnant and Area and Pregnant. We included these combinations because we expected different patterns over time between different reproductive states, due to changes in progesterone levels during the pregnancy in moose (Stewart et al., 1985), and because we expected differences in environmental conditions like climate and food availability and quality between areas, which could be reflected in differences in body condition between pregnant and non-pregnant in capital breeders like moose (Holmes et al., 2021).

We fitted a smooth term for DOG, due to the non-linear relationship with the default thin plate regression spline. Area was included due to a reported latitudinal difference in daily mean T_b (Fohringer, 2021). Due to the high number of T_b measurements, we used the function "bam" from the R package *mgcv* (Wood and Wood, 2015). We used model selection based on Akaike's Information Criterion (AIC) to select the highest ranked model for our data within ΔAIC <2, carried out with the function lCtab from the bbmle package (Bolker and RCoreTeam, 2017).

Table 1

Overview over study population, pregnancy status, year and location.

Study area	Year	*n*	Pregnant	Non-pregnant
Northern alpine	2012	10	5	5
	2013	9	6	3
Northern coastal	2017	12	11	1
	2018	8	7	1
Southern island	2015	7	6	1
	2016	4	2	2
Total		50	37	13

Moose ID was included as a random intercept and slope in all models. To account for detected temporal autocorrelation, we added an autoregressive order 1 (AR1) model structure (Pinheiro and Bates, 2000). To choose adequate basis dimensions of the parameter k, we applied the "gam.check" function (Wood, 2017). We applied a post-hoc test with estimated marginal means from the emmeans package to estimate which levels of the categorical variables were significantly different from each other (Lenth et al., 2019).

2.4.2. Body temperature patterns associated with calving

We calculated hourly mean T_b during the calving period for all moose ($n = 50$). From the hourly means, we calculated a rolling 24 h mean T_b for every hour during the day (from 06.00 one day to 05.59 the day after, from 07.00 to 06.59 etc.). We did that to ensure that we were able to detect drops in the variables throughout the day, as we did not have the exact time of calving. We thereafter calculated drops in the 24 h mean body temperatures for each hour during the day, and detected drops in the 24 h mean T_b $\geq 0.2°C$ in relation to the calving date estimated from GPS-clustering among the pregnant females.

2.4.3. Prediction of parturition based on body temperature and activity data

We calculated rolling 24 h activity means according to the same method as used to calculate rolling 24 h T_b means for all moose. We used changepoint analysis among the pregnant females to detect specific time points in the calving period, with major changes in the activity and T_b data. We only included moose with both activity and T_b data in our changepoint analysis ($n = 47$), and therefore excluded three moose lacking activity data. We used the R package "changepoint.np" due to the non-parametric distribution of the data (Haynes et al., 2021). We used the PELT (Pruned Exact Linear Time) method and the CROPS (The Changepoints for a Range of PenaltieS) algorithm in the "cpt.np" function of the R-package to find the optimal segmentations and locations of multiple changepoints in the time-series data (Haynes et al., 2014; Killick et al., 2012). To avoid overfitting or underfitting of the number of changepoints, we used diagnostic plots as described in the method by Lavielle (2005) to identify the appropriate penalty constant. The number of changepoints was selected as the elbow in the curve in the diagnostic plot of the unpenalised cost versus the number of changepoints. We thereby found the location of the selected number of changepoints and plotted the detected changepoints on time series graphs, one for each parameter, to visualise changepoints in activity and T_b in the calving period. We used the detected changepoints around the calving date detected by GPS-clustering to describe the pattern of T_b and activity in relation to parturition. We calculated the number of individuals with the same type of pattern in relation to the parturition to identify the number of events detected as true-positive parturition events, but also the number of false-positive events and calving events not detected by this method.

We repeated the procedure for non-pregnant individuals to look for the same pattern among those, and thus find the number of females identified as non-parturient, but also the number of false positive parturition events in the calving period. The calving period was defined as the mean estimated calving date (of the pregnant females) in the area ± 15 days for non-pregnant individuals.

We calculated the sensitivity (proportion of correctly identified parturient females), specificity (proportion of correctly identified non-parturient females) and accuracy (overall rate of true predictions) of the use of changepoints to detect parturition.

3. Results

3.1. Body temperature patterns associated with pregnancy

Body temperature varied with reproductive states, and was higher in pregnant compared to non-pregnant moose throughout the entire gestation period (Fig. 2). The highest ranked model to explain variation in T_b included reproductive state, area, the interaction between them, DOG and the interaction between reproductive state and the DOG (Tables 2 and 3). Post-hoc analysis revealed a 0.19°C (SE 0.02°C, p-value <0.0001), 0.13°C (SE 0.02°C, p-value <0.0001) and 0.13°C (SE 0.02°C, p-value <0.0001) higher daily mean T_b in pregnant moose compared to non-pregnant in the Northern alpine area, Northern coastal and Southern island study areas, respectively.

3.2. Body temperature patterns associated with calving

T_b decreased when parturition was imminent (Fig. 3). We detected a drop in the rolling 24 h mean T_b $\geq 0.2°C$ associated with calving in 59.5% ($n = 22$) of all moose (Northern alpine = 27.3%, $n = 3$; Northern coastal = 77.8%, $n = 14$; Southern island = 62.5%, $n = 5$). Twelve of the remaining moose, which were observed with new-born calves, had a drop in the rolling 24 h mean T_b between 0.1°C and 0.2°C, while the last three moose had a T_b drop $\leq 0.1°C$ (Supplementary file 1).

3.3. Prediction of parturition based on body temperature and activity data

We detected a changepoint in a decreasing trend in the body temperature followed by a changepoint in a decreasing trend in the activity in relation to the calving date (estimated from GPS clustering) in 31 of 35 pregnant individuals (Fig. 3). This gives a sensitivity of this method of 88.6%. The changepoint in T_b occurred the day before the parturition (mean: day -1, range: day -3 – 0), while the changepoint in activity occurred at the parturition date (mean: day 0, range: day -1 – 1). This pattern was only detected in relation to parturition, and not elsewhere during the calving period. All four parturient individuals not showing this pattern were from the Northern alpine area. We could not detect a pattern indicating parturition in any of the non-pregnant females ($n = 12$) in the calving period (mean calving date in the area ± 15 days) (Fig. 4), resulting in a lack of parturition date for all non-pregnant females and thus a 100% specificity of the method. The overall accuracy of this method to detect parturition in moose, including pregnant and non-pregnant ones, was 91.5%.

4. Discussion

Our study showed that the body temperature patterns displayed in wild and free-ranging moose during pregnancy and parturition, with a significantly higher T_b in pregnant compared to non-pregnant animals, and a decline in T_b when parturition is imminent, are similar to that reported in domesticated cattle (Costa Jr et al., 2016; Suthar et al., 2012; Wrenn et al., 1958). The daily mean body temperatures were between 0.13 and 0.19°C higher in pregnant compared to non-pregnant moose, depending on the study area with body temperature difference increasing along a south-north gradient (i.e. from the Southern island and Northern coastal areas to the Northern alpine area). Our results are in line with a study of North American moose that reported a difference in core body temperature of 0.18°C between the pregnancy states (Thompson et al., 2019).

Our documented differences in T_b between the two reproductive states with higher T_b in pregnant than non-pregnant is in line with previous reports from muskoxen (*Ovibos moschatus*) and Svalbard reindeer (*Rangifer tarandus platyrhynchus*), two other capital breeders living in cold and seasonal environments (Arnold et al., 2018; Schmidt et al., 2020). In muskoxen, the linkage between reproductive state and T_b was suggested due to hypometabolism, as hypometabolism was only displayed in non-pregnant muskoxen (Schmidt et al., 2020). This is in contrast to moose where hypometabolism is documented in both pregnant and non-pregnant moose (Fohringer, 2021; Græsli et al., 2020). Schmidt et al. (2020) suggested that there was a trade-off in female muskoxen between hypometabolism and sustaining foetal growth. Fluctuations in maternal T_b during pregnancy disturbs the foetal T_b, but
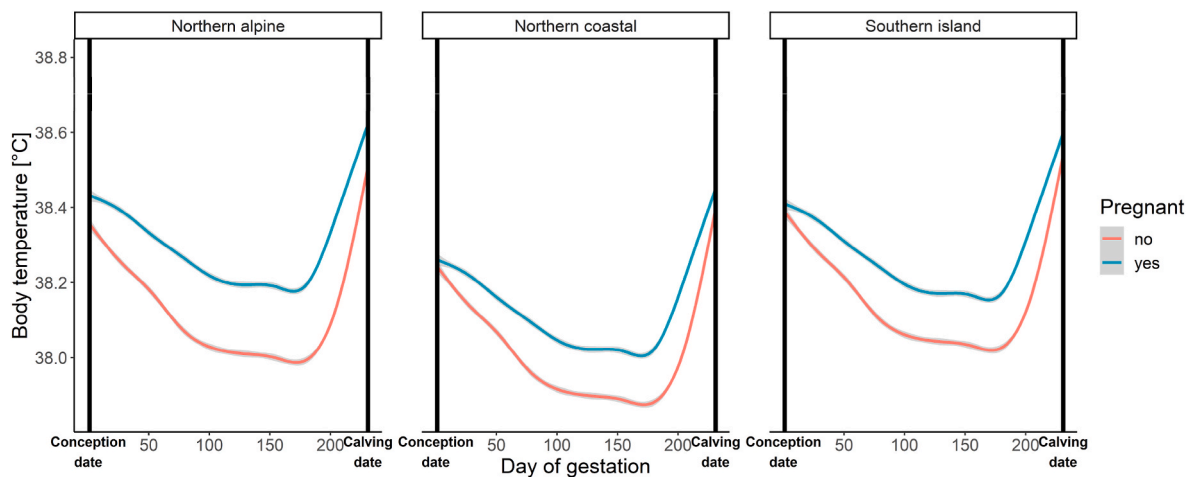
Fig. 2. Daily mean body temperature patterns during pregnancy in moose between different reproductive states and areas predicted from generalised additive mixed models (GAMMs). Grey areas around the lines represents the 95% confidence intervals.

Table 2

Log-likelihood (logLik), Akaike's information criterion (ΔAIC), degrees of freedom (df) and model weight (weight) for the model combinations evaluating daily mean body temperature (T_b) of female moose during pregnancy, considering the explanatory variables Pregnant (factor with two levels; yes or no), "day of the gestation" (DOG, 1–231) and Area (factor with three levels: Northern alpine, Northern coastal and Southern island). "s" is the smoother term assessing the linearity or non-linearity of the response variable. Moose ID was included as a random intercept and slope in all models. The best-fitted model were selected as the model with the lowest AIC score (most parsimonious model). To account for detected temporal autocorrelation, we added an autoregressive order 1 (AR1) in the selected model.

Model combinations	logLik	ΔAIC	df	weight
Pregnant * Area + s(DOG) + s(DOG * Pregnant)	7564.6	0.0	96.6	1
Pregnant + Area + s(DOG) + s(DOG * Pregnant)	7537.8	49.4	94.4	<0.001
Pregnant + s(DOG) + s(DOG * Pregnant)	7537.7	49.6	94.5	<0.001
Pregnant + Area + s(DOG)	7474.6	158.7	85.9	<0.001
Pregnant + s(DOG)	7474.5	158.9	86.0	<0.001
Area + s(DOG) + s(DOG * Pregnant)	7193.7	734.8	93.1	<0.001
s(DOG) + s(DOG * Pregnant)	7193.6	735.0	93.1	<0.001
Area + s(DOG)	6670.7	1760.9	83.1	<0.001
s(DOG)	6670.5	1761.2	83.2	<0.001
Pregnant * Area	3609.0	7839.9	61.0	<0.001
Pregnant + Area	3605.7	7842.6	59.0	<0.001
Pregnant	3605.6	7842.8	59.0	<0.001
Area	3277.2	8497.3	57.8	<0.001
Null model	3277.0	8497.8	57.9	<0.001

Table 3

Results of the generalised additive mixed model (GAMM) testing for effects of reproductive state, study area and day of gestation on mean daily T_b. The adjusted R^2 for the model was 0.782. The intercept represents non-pregnant females in the Northern alpine area.

Term	Estimate	SE[a]	t-value[b]	p-value
Intercept	38.123	0.049	773.447	<0.0001
Pregnant (yes)	0.182	0.015	12.065	<0.0001
Area (Northern coastal)	−0.113	0.064	−1.765	0.0776
Area (Southern island)	0.032	0.073	0.440	0.6597
Pregnant (yes) Area (Northern coastal)	−0.059	0.020	−2.884	0.0039
Pregnant (yes) Area (Southern island)	−0.055	0.018	−3.009	0.0026

Term		EDF[c]	F-value	p-value
s(DOG)		22.75	71.75	<0.0001
s(DOG):pregnant no		7.43	6.49	<0.0001
s(DOG):pregnant yes		0.0008	0.03	0.996
s(Object_ID)		24.07	5460.39	<0.0001
s(Object_ID, DOG)		24.88	4525.36	<0.0001

[a] SE = standard error.
[b] t-value = test statistic.
[c] EDF = effective degrees of freedom.

We therefore suggest that the difference in T_b between pregnant and non-pregnant moose reflects the higher progesterone levels during pregnancy, based on the progesterone fluctuations documented in moose during pregnancy and the thermogenic effect of progesterone.

About 60% of the moose in our study displayed a drop in daily mean $T_b \geq 0.2°C$ associated with calving, as earlier reported in domestic cattle (Costa Jr et al., 2016). The probability of a T_b drop $\geq 0.2°C$ associated with calving varied between areas, with highest probability in Northern coastal area (77.8%), and lowest in the Northern alpine area (7.3%). The differences between areas indicates that animals in different environmental settings encounter different limitations and margins especially with respect to food availability and quality, and climatic conditions such as ambient temperature, precipitation and snow conditions. Similarly, annual variations in environmental conditions, food availability and quality could explain differences between areas as the study years differs between the areas (Holmes et al., 2021). We recommend future research to study more deeply possible environmental factors explaining observed differences in T_b and their ecological implications. Costa Jr et al. (2016) reported an average difference of 0.32°C (primiparous) and 0.36°C (parous) in Holstein cattle. The different results between our and the study of Costa Jr et al. (2016) are likely species-specific, and/or
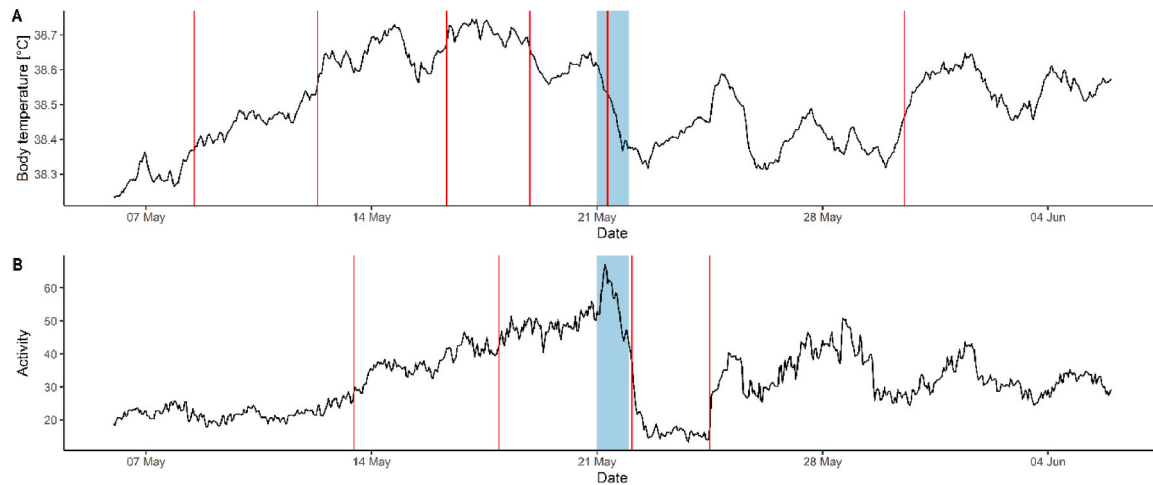
the excursions can be attenuated by changes in the heat production of the foetus or the thermal conductance of the placenta (Laburn et al., 2002). In moose, hypometabolism is a strategy to save energy during periods with colder climate and limited resources available, in both pregnant and non-pregnant moose, as well as in males (Fohringer, 2021; Græsli et al., 2020). The lowest daily mean T_b in winter was 0.6°C lower than the highest daily mean T_b in summer in pregnant females in the Northern coastal area (Græsli et al., 2020). The consequences for the foetus of maternal exposure to hot temperatures are more severe than to cold ones (Laburn et al., 2002). We therefore assume that the hypometabolism displayed during winter is well tolerated by both the foetus and the pregnant moose. The connection between fluctuations in T_b and hormone levels, and especially progesterone levels (due to the thermogenic effect of progesterone) is well documented in domestic ruminants (Suthar et al., 2012; Wrenn et al., 1958). Progesterone levels in moose increase in the beginning of the pregnancy, and then remain stable until they decline during the last part of the pregnancy (Stewart et al., 1985).

Fig. 3. Changepoints (red vertical lines) in the rolling 24 h mean body temperature (A) and activity (B) in the calving period (calving date estimated from GPS-clustering ± 15 days) for one pregnant female moose. The calving date is presented as a vertical blue bar.
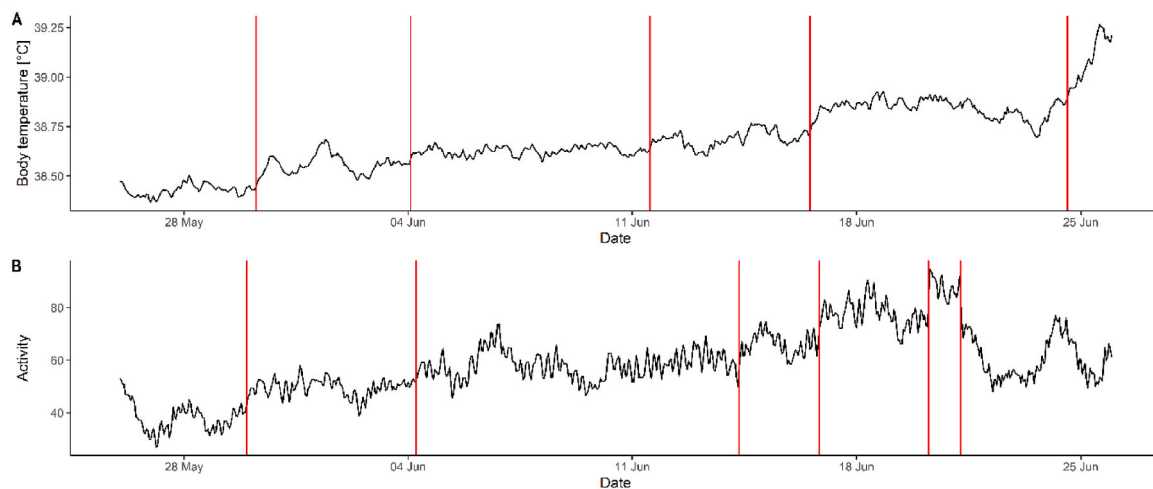

Fig. 4. Changepoints (red vertical lines) in the rolling 24 h mean body temperature (A) and activity (B) in the calving period (mean calving date in the area estimated from GPS-clustering ± 15 days) for one non-pregnant female moose.

linked to differences in experimental set-up, methods, and ruminal sensors used.

We demonstrated a changepoint in a decreasing trend in T_b the day before the calving, followed by a changepoint in a decreasing trend in activity on the day of the calving. This was a highly successful method of detecting parturition in moose (accuracy 91.5% (percentage of correct assessments), sensitivity 88.6% (percentage of true positive assessments) and specificity 100% (percentage of true negative assessments). When interpreting this result one should bear in mind that the parturition date is based on an estimation from GPS-clustering, and subsequent visual observation of mother and offspring(s) in the field (Neumann et al., 2020), and the precision of this method is not validated. The accuracy of our method are, however, similar to the accuracy of other methods using GPS data alone or in combination with activity data to predict parturition in ungulates (DeMars et al., 2013; Marchand et al., 2021; Nicholson et al., 2019). By combining T_b and activity data as a combination of the individuals' physiological and behavioural response, we were able to get more accurate results than the use of activity or T_b alone, as the use of them alone would have resulted in several false positives. This is likely due to other sources of fluctuations in activity and thus mainly movement, and ruminal T_b such as heat increment of feeding, drinking events, the location of the ruminal sensor, increased

activity, stress and infections (Beatty et al., 2008). We cannot rule out that there might be more efficient and less invasive methods to infer the parturition in moose, more research is needed to investigate this.

Age, body mass, population density and climatic conditions are known to affect fecundity in female moose, and moose in northern-Sweden living under harsh climatic conditions have a lower number of offspring per female moose compared to moose further south (Sand, 1996; Sæther and Haagenrud, 1983). Progesterone concentrations during pregnancy are higher in female moose with twins compared to singletons (Stewart et al., 1985). Due to the thermogenic effect of progesterone, one would expect that this was reflected in the T_b, as shown in cattle where cows with twins had higher T_b compared to those with singletons (Scanavez et al., 2018). Due to the skewed ratio between females with singletons and twins within the different areas, we were not able to investigate the correlation between the number of offspring per female and the T_b pattern. Considering the potential connection between T_b and progesterone levels, we also expect that the differences in progesterone levels during oestrus will influence the T_b levels, as reported in cattle (Cooper-Prado et al., 2011; Wrenn et al., 1958). A variety of gestation lengths of moose have been reported, varying from 216 to 246 days (Markgren, 1969; Schwartz, 1992; Schwartz and Hundertmark, 1993). We would suggest further development of this study,

by investigating the T_b and activity patterns during oestrus in captive moose, to see if the conception date could be identified by T_b and activity and possibly determine a more accurate gestation length based on the conception and parturition dates. This is relevant information for monitoring reproductive patterns in moose in a changing climate and vegetation phenology.

5. Conclusion

Here we documented T_b patterns of female moose in three different environmental settings in Sweden during the entire pregnancy, including parturition. We found a significant higher T_b in pregnant compared to non-pregnant moose, and T_b decreased when parturition was imminent. We also found site-specific change in temperature with larger change at more northern latitudes. About 60% of the pregnant moose displayed a drop in daily mean $T_b \geq 0.2°C$ associated with calving. A combination of T_b and activity data allowed successful detection of parturition with a high accuracy (91.5%).

Author statement

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There are no conflicts of interest.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2022.103334.

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