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Physiological sensors in moose and other wildlife

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Tittel:			
Fysiologiske sensorer på elg og andre viltarter			

Forfattere:			
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Emneord:			
Alces alces, biologger, elg, fysiologi, hund, jakt, sensor, stress, vilt			

Sammendrag:

Et nøkkelspørsmål innen økologi er hvordan menneskelig aktivitet påvirker atferd og fysiologi hos viltlevende dyr. Utvikling av biologgere har muliggjort studier av ville dyr i deres naturlige miljø. Biologgere er sensorer som festes til dyret og som registrerer data om fysiologi, atferd, bevegelser og miljø. Ved å kombinere ulike biologgere, kan man øke kunnskapen og forståelsen av biologi, økologi og fysiologi hos viltlevende dyr og hvordan de tilpasser seg omgivelsene.

Fra 2010 har vi brukt biologgere i flere studier på ulike viltarter, inkludert bever (*Castor fiber)*, brunbjørn (*Ursus arctos*), elg (*Alces alces)* og jerv (*Gulo gulo)*. Vi har anvendt biologgere både i basal og anvendt forskning, inkludert å etablere normalverdier for kroppstemperatur, hjertefrekvens, bevegelser og aktivitet, avdekke sesongmessige variasjoner i disse parameterne og studere hvilken effekt menneskelig aktivitet har på dyrenes fysiologi og atferd.

Hovedfokus i denne rapporten var å vurdere hvordan jakt og andre menneskelige forstyrrelser påvirker fysiologi og atferd hos elg. Elgene ble instrumentert med GPS-halsbånd og biologgere for å registrere bevegelser, aktivitet, hjertefrekvens og/eller kroppstemperatur. Vi studerte effekten av eksperimentelle og reelle jaktsituasjoner med løshund, hvordan elgene reagerte på en skiløper, en person med hund i bånd, en person som sjekket kalvingsstatus og bedøvelse fra helikopter.

Vi fant at vellykkete eksperimentelle jaktsituasjoner med løshund (avstand elg-hund mindre enn 240 meter i mer enn 10 minutter) resulterte i høyere maksimal kroppstemperatur (0,88 °C høyere) og en gjennomsnittlig økning i hjertefrekvens på 24 slag per minutt sammenlignet med dagen etter jaktsituasjonen. Elgene hvilte i gjennomsnitt mer enn 90 minutter lengre dagen etter jakten. Resultatene viser at jakt med løshund øker individets energiforbruk og hviletid (og reduserer dermed også tilgjengelig tid for beiting). Helikopterfangst resulterte også i økt kroppstemperatur samme dag, mens det ikke ble registrert noen økning i kroppstemperaturen når elgen ble forstyrret av en skiløper. Vi fant at elgen beveget seg raskere og lenger den dagen de ble bedøvet fra helikopter og etter forstyrrelser av løshund og skiløper, sammenlignet med dagen etter. Noe av denne forskjellen skyldes økt hviletid dagen etter forstyrrelsen.

Andre studier med biologgere i denne rapporten:

Elg: Vi brukte biologgere for å studere hvordan kroppstemperaturen (T_b) varierte i løpet av året, i forskjellige områder og mellom kjønn og hvordan hjertefrekvensen (HR) og aktiviteten varierte i løpet av året. Elgene viste sesongmessige variasjoner i T_b, HR og aktivitet, med lavere verdier om vinteren og høyere verdier om sommeren. Høyeste gjennomsnittlige T_b og HR var 38,64 °C (10. juli) og 71,9 slag per minutt (26. juni) mens laveste gjennomsnittlige T_b og HR var 38,03 °C (17. mars) and 40,5 slag per minutt (6. mars). Kroppstemperaturen varierte også mellom forskjellige områder, okser hadde signifikant lavere gjennomsnittlig T_b (38,06 °C) enn kyr (38,29 °C).

Brunbjørn: Vi har anvendt biologgere i mer enn 10 år i ulike studier på brunbjørnens biologi, fysiologi og økologi. Vi har gjennomført studier i forbindelse med hibernering (bjørnens tid i hi), inkludert

tidspunkter og samspillet mellom miljø, atferd og fysiologi. Tidspunkt for higang så ut til å være tett koplet til reduksjon i stoffskiftet. Små bjørner hibernerte lengre enn store bjørner og forlot hiet senere. Vi fant ved hjelp av biologgerne at gjennomsnittlig drektighetslengde hos brunbjørn var 56 dager. Vi fant også at hjertefrekvensen og kroppstemperaturen varierte med tidspunkt på året, kroppsmassen og reproduksjonsstatus.

Bever: 36 bevere ble instrumentert med biologgere for å studere sesongmessig variasjon i kroppstemperatur og hjertefrekvens. Dyrene viste et sesongmessig mønster i gjennomsnittlig kroppstemperatur, med lavere verdier om vinteren (35,8 ± 0,15 °C i januar) enn om sommeren (36,3 ± 0,20 °C i juni, august og september). Vi fant et tilsvarende mønster for hjertefrekvensen, med lavere verdier om vinteren (gjennomsnittlig 78 ± 10 slag per minutt i januar) sammenlignet med sommeren 101 ± 5 slag per minutt i juni-juli). Vi fant også kjønnsforskjeller i de sesongmessige mønstrene for kroppstemperatur, sannsynligvis forårsaket av drektighet.

Jerv: Vi studerte daglig og sesongmessig variasjon i kroppstemperatur og aktivitet hos 14 jerver. Kroppstemperaturen og aktivitetsmønsteret endret seg sesongmessig. Jervene hadde distinkte aktivitetstopper i ved daggry og skumring. Gjennomsnittlig kroppstemperatur var 38,5 ± 0,2 °C, med en daglig variasjon på opptil 6 °C. Kroppstemperaturen varierte også med reproduksjonsstatus, med lavere verdier hos drektige tisper.

Bruk av biologgere for å studere viltlevende dyr har gitt ny innsikt i basal og anvendt økologi, biologi og fysiologi. Dette danner også grunnlaget for videre studier av dyrenes respons på klimaendringer, menneskelig aktivitet og forvaltningstiltak. Vi understreker at det er viktig å utføre pilotstudier for å kalibrere og validere metodene for hver enkelt dyreart, og at det kreves et stort antall individer, særlig når det skal kombineres data fra mer enn en biologger.

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Summary:

How human activity affects the behaviour and physiology of free-ranging animals in their natural environment is a key question in physiology. The development of biologging techniques has enabled researchers to collect data from free-ranging animals under undisturbed conditions. Biologgers are animal-attached sensors obtaining data about the physiology, behaviour, movement and/or environmental conditions of animals. Combination of different types of biologgers can increase our knowledge and understanding of the biology, ecology and physiology of free-ranging animals, and how they adapt to their environment.

Since 2010, we have used biologgers in several studies in different wildlife species including beavers (*Castor fiber)*, brown bears (*Ursus arctos*), moose (*Alces alces)* and wolverines (*Gulo gulo)*. We have used biologgers in both basic and applied sciences; obtaining body temperature, heart rate, movement and activity data to establish baseline values, and to study how it varies among different seasons and life events, with metabolic rate, and to assess how human activity affects physiology and behaviour.

The main focus of this report was to assess how hunting activity and other human disturbance affects the physiology and behaviour of moose. Each moose was instrumented with a GPS collar, heart rate logger and body temperature logger for simultaneous collection of data on movement, activity, heart rate and body temperature. We studied the effect of experimental and real hunting approaches with dogs, ski approaches, dog-on-leash approaches and two types of research activity, calf checks and chemical immobilisation from a helicopter.

We found that successful experimental hunting approaches (moose and dog were within 240 m for > 10 min) resulted in higher maximum body temperature (0.88°C higher) and a mean increase in heart rate of 24 beats per minute at the day of the approach compared to the day after. The moose rested on average > 90 min longer the day after the approach compared to the day of the approach. These results demonstrate that hunting with dogs increased moose energy expenditure and resting time (and consequently decreased time available for foraging) on an individual level. Captures from a helicopter also resulted in increased body temperature the day of the approach, while there was no significant increase in body temperature during ski approaches. We demonstrated higher maximum speed and longer travel distance on the day of captures, hunting and ski approaches compared to the day after. Some of this might be due to increased resting time the day after an approach, as demonstrated in successful hunting approaches.

Other studies included in this report using biologgers:

Moose: We used biologgers to study the temporal, spatial and gender variations in body temperature (T_b), and the temporal variation of heart rate and activity of moose. Moose displayed seasonal differences in T_b, HR and activity, with lower levels during winter and higher values during summer. The highest daily mean T_b and HR were 38.64°C (10 July) and 71.9 beats per minute (bpm; 26 June), whereas the lowest daily mean T_b and HR were 38.03°C (17 March) and 40.5 bpm (6 March). Moose

also displayed spatial variation in body temperature, and males had a significantly lower average T_b (38.06 °C) than females (38.29 °C).

Brown bear: We have used biologgers for more than ten years in different studies of brown bears' biology, physiology and ecology. We have performed several studies on hibernation, including the timing and the interplay between environmental, behavioural and physiological mechanisms. Timing of denning appeared to be tightly coupled with metabolic suppression. Smaller bears hibernated longer than larger bears, and left the den later. We used biologging techniques to describe the pregnancy of the brown bear and found a mean gestation length of 56 days. We also found that heart rate and body temperature varies with day of the year, body mass and reproductive state.

Beavers: Thirty-six beavers were instrumented with body temperature and heart rate loggers. They displayed a seasonal pattern in daily mean body temperature with lower body temperature in winter (35.8 ± 0.15 °C (mean ± SD) in January) than in summer (36.3 ± 0.20°C in June, August and September). The heart rate data indicate a similar pattern with lower heart rate in winter (mean nightly heart rate ± SD in January: 78 ± 10 beats per minute (bpm)) compared to summer (mean nightly heart rate ± SD in June and July 101 ± 5 bpm). We also found sexual difference in the seasonal body temperature patterns, likely due to gestation.

Wolverines: We studied the daily and seasonal variation in body temperature and activity patterns in a total of 14 wolverines. Body temperature and activity patterns changed seasonally, and they displayed distinct activity peaks during crepuscular hours. Average core body temperature were 38.5 ± 0.2 °C with a daily variation of up to 6°C. Body temperature patterns varied between reproductive states, with lower body temperature in pregnant females.

The use of biologging technology in studies of free-ranging animals has given us novel insight into their basic and applied ecology, biology and physiology. It has also provided a foundation for further studies to better understand the responses of the animals to climate change, human activity, conservation and management. We want to emphasise the use of pilot studies to calibrate and validate the methods applied to the given species, and that a high sample size is needed to get as reliable results as possible, especially when combining data from more than one biologger.

Content

Preface

This report summarizes the project «Fysiologiske sensorer som forvaltningsverktøy» [«Physiological sensors as a management tool»] funded by the Norwegian Environment Agency (grant #10040125 and grant #16040078).

The aim of the project was to test various physiological sensors (biologgers) and their applicability to free-ranging wildlife. The project was initiated in 2011 and started with pilot studies in 2012. The ambition was to use a new sensor implanted orally into the rumen, measuring temperature and activity. The sensor was developed by Vectronic (Germany), a telemetry company that collaborates with several wildlife projects in Scandinavia. At the same time, the project started using a heart monitor from Medtronic (USA) and two biologgers from StarOddi (Iceland), a temperature sensor and a combined heart rate/temperature monitor.

There are basically two main types of biologgers used in free-ranging mammals: 1) sensors that record and store data, e.g. body temperature and/or heart activity, and that requires retrieval of the unit for down-load of data when the instrumented animal is recaptured or dead; 2) sensors that record physiological variables and send data to a collar and/or to a server via the phone network or a satellite.

The project has focused on moose and brown bears. This report focuses on normal and stress physiology in moose. Parts of the brown bear study and results from other species are summarized in Chapter 5. Publications from the project are listed in Chapter 9.

Evenstad, 1 September 2021

Jon M. Arnemo, project leader

Forord

Denne rapporten avslutter prosjektet «Fysiologiske sensorer som forvaltningsverktøy» finansiert av Miljødirektoratet (kontraktsnr. 10040125 og kontraktsnr. 16040078).

Prosjektets formål har vært å teste ut ulike fysiologiske sensorer (biologgere) og anvendelsesområder for disse på viltlevende dyr i sitt naturlige miljø. Prosjektet ble initiert i 2011 og ble igangsatt i form av pilotstudier i 2012. Ambisjon var å ta i bruk en ny type sensor som legges ned i vomma via munnen på drøvtyggere og som måler temperatur og aktivitet. Sensoren ble utviklet av Vectronic (Tyskland), en samarbeidspartner innen telemetri for en rekke viltprosjekter i Skandinavia. Parallelt med dette tok prosjektet også i bruk andre sensorer som opereres inn i dyret, en hjertesensor fra Medtronic (USA) og to typer sensorer fra StarOddi (Island), henholdsvis en temperatursensor og en kombinert hjerte- og temperatursensor.

Det finnes en rekke tekniske løsninger for fysiologiske sensorer. Det er i prinsippet to ulike hovedtyper av biologgere som anvendes på viltlevende pattedyr: 1) sensorer som registrerer og lagrer data, f.eks. kroppstemperatur eller hjerteaktivitet, og som forutsetter at sensorene fås tilbake for avlesning ved gjenfangst av det aktuelle dyret eller når det instrumenterte dyret er dødt; 2) sensorer som registrerer fysiologiske parametre og sender data til et halsbånd for lagring og videresending via telefonnett eller satellitt.

Prosjektet har i hovedsak benyttet sensorer på elg og brunbjørn. Denne rapporten fokuserer på normalfysiologi og stressfysiologi hos elg. Deler av bjørnestudien og resultater fra bruk av fysiologiske sensorer på andre arter oppsummeres i kapittel 5. En oversikt over publikasjoner fra prosjektet er sammenstilt i kapittel 9.

Evenstad, 1. september 2021

Jon M. Arnemo, prosjektleder

1. Introduction

Moose (*Alces alces*) is a key herbivore species in the Scandinavian ecosystem and is ecologically, economically and culturally important. More than 110,000 moose are harvested annually in Scandinavia, and in Sweden >80 % of the moose mortality are attributed to hunting (Ericsson and Wallin, 2001). Concerns over animal welfare and stress related to hunting have been raised (Nelson et al., 2005; Paquet and Darimont, 2010), but so far, data is lacking to assess these issues.

A key ecological question is how human activity affects the behaviour and physiology of free-ranging animals in their natural environment. Human disturbance may induce both acute and chronic stress in an animal. Stress is a response to challenges in the body's homeostasis, and can be positive or negative – depending on the situation (Reeder and Kramer, 2005; McLaren et al., 2007). A stressor is the situation or stimulus causing stress, and it could be physical, psychological or both (Reeder and Kramer, 2005). Stress results in behavioural and physiological responses of the animal, and objective and quantitative measurements of stress are often used to assess animal welfare (McLaren et al., 2007). Both immediate and long-term responses to stress can potentially have life-threatening consequences. One behavioural response of an animal to stress is known as anti-predator behaviour. Stay, fight or flight when attacked, increasing home range area, shift to safer habitats and increasing nocturnal behaviour are examples of anti-predator behaviour. Behavioural responses to human activity have been studied in many different game species, including moose (Baskin et al., 2004; Neumann et al., 2009; 2010; Støen et al., 2010; Neumann et al., 2011a; Ericsson et al., 2015b; Sand et al., 2016), red deer (*Cervus elaphus*) (Sunde et al., 2009; Jarnemo and Wikenros, 2014), roe deer (*Capreolus capreolus*) (Cederlund and Kjellander, 1991; Benhaiem et al., 2008), and brown bears (*Ursus arctos*) (Støen et al., 2010; Ordiz et al., 2013; Hertel et al., 2016; Le Grand et al., 2019). Anti-predator behaviour can be studied from movement and activity data. Physiological responses to stress can be measured through changes in body condition, cortisol levels in blood, faeces, hair or saliva, physiological variables, such as heart rate and body temperature, and immunological and blood parameters (McLaren et al., 2007). Physiological responses to human activity have been studied in moose (Thompson et al., 2020), red deer (Bateson and Bradshaw, 1997) and brown bears (Støen et al., 2015; Le Grand et al., 2019). Studies of both behavioural and physiological responses are based upon established baseline ("normal") levels in undisturbed animals under natural conditions.

Biologgers are small tags attached to animals for measuring and/or relaying data about behaviour, physiology, movements and/or environmental conditions. Biologging technology extends the ability to observe and take measurements from free-ranging, undisturbed animals over long periods (Rutz and Hays, 2009). Such devices have been used to obtain body temperature or heart rate data in several ungulate species, including a few studies that simultaneously obtained body temperature and heart rate data from ungulates (Arnold et al., 2006; Signer et al., 2011; Turbill et al., 2011; Arnold et al., 2018; Riek et al., 2019; Græsli et al., 2020a).

The aim of this study was to use biologgers in free-ranging moose in order to establish reference (baseline) values of physiological variables and to assess how hunting activity and other human disturbance affect the physiology and behaviour. We instrumented each moose with a GPS collar and biologgers for simultaneous collection of data on movement, activity, heart rate and/or body temperature. We studied the effect of experimental and real hunting approaches with dogs, ski approaches, dog-on-leash approaches and two types of research activity, calf checks and chemical immobilisation from a helicopter.

2. Materials and Methods

2.1. Study animals and area

Twelve female moose (>1.5 years old) were included in this study, which was conducted in Nordmaling, Vännäs and Umeå municipalities in the county of Västerbotten, Sweden. The moose were equipped with a GPS Plus collar (Vectronic Aerospace GmbH, Berlin, Germany), ruminal temperature and mortality transmitter (MIT; Vectronic Aerospace GmbH, Berlin, Germany) and subcutaneous heart monitors (Reveal XT; Medtronic Inc., Minneapolis, Minnesota, USA and DST centi HRT; Star Oddi, Gardabaer, Iceland) during immobilisation.

The experiments were approved by the Animal Care Committee, Umeå, Sweden (Dnr A 14-15, Dnr A 3-16, Dnr A 28-17), and were carried out in accordance with Swedish legislation on animal research ethics. Experienced field personnel, pilots and veterinarians carried out captures, handling, collaring and surgeries, while experienced hunters, hunting dogs and field personnel carried out the approaches. None of the real hunts included in the study, resulted in a moose being shot.

2.2. Immobilisation procedure

Moose were immobilised from a helicopter in February 2017 using a CO_2 powered rifle (Dan-Inject, Børkop, Denmark) with the drug combination of 50 mg xylazine (Xylased® 500 mg, Bioveta, a.s., Komenského 212, 68323 Ivanovice na Hané, Česká Republica) and 4.5 mg etorphine [Captivon® 98 Etorphine HCl 9.8 mg/ml, Wildlife Pharmaceuticals (PTY) Ltd., 38 Wilkens St., Rocky Drift, White River, South Africa], according to procedures previously described (Evans et al., 2012; Lian et al., 2014; Græsli et al., 2020a).

2.3. Biologgers and programming

The collars used for the moose, included a global positioning system (GPS) receiver, an ambient temperature recorder, a triaxial acceleration sensor (recording at six to eight Hertz), a mortality sensor, a very high frequency (VHF) transmitter, and a Global System for Mobile communication (GSM) modem (VectronicAerospace, 2019a). In addition, each collar was linked to external sensors, i.e. the MIT and proximity sensors UHF-ID tags (VectronicAerospace, 2019b; c) to monitor body temperature and to quantify proximity to the approaching source of disturbance (e.g. the hunting dog), respectively. The activity (i.e. moose head movement) was measured by an acceleration sensor within the collar and measures back-forward and right-left movement over two axes (X and Y) on a scale from 0 – 255 over five-minute recording intervals. Overall activity was presented as the sum of the activity data on the X- and Y-axes, ranging from 0 to 510 (Gervasi et al., 2006). We adjusted collar derived ambient temperatures according to the offsets described by Ericsson et al. (2015a) to represent a reliable index for the actual ambient temperatures experienced by the individual moose at given place and time. The collar recorded positions from one minute to every third hour, depending on the ongoing study. All GPS positions with additional information (ambient temperature, the most recently stored ruminal temperature and proximity contact) were sent via the GSM network to the Wireless Remote Animal Movement (WRAM) database for storage (Dettki et al., 2014). At recapture of the moose, all the data stored on the collar was manually downloaded and sent to the WRAM database.

The MIT was deployed in the rumen as described by Minicucci et al. (2018). MITs record the ruminal temperature at five-minute intervals and transmit the information to the collar unit for storage (VectronicAerospace, 2019b). In addition, the moose were fitted with surgically implanted subcutaneous heart monitors (Reveal XT and DST centi HRT). Reveal XTs continuously monitor the heart rate (HR) using an electrocardiogram (ECG), which converts the mean R-R interval (rate of a ventricular cycle) into HR, and store two-minute average values (Medtronic, 2017). DST centi HRT calculates a mean HR from a 4 second ECG strip with a 150 Hz measurement frequency, and stores the HR with a quality index of the signal clarity and the R-R interval regularity. The DST centi HRT and Reveal XT was surgically implanted subcutaneously at the left and right side, respectively, of the most

rostral part of sternum, and as described by Græsli et al. (2020a). We programmed and activated the Reveal XT after implantation, prior to the anaesthetic reversal.

Position data and estimates on ambient temperature were sent continuously via the GSM network, whereas data recorded by the collars, MITs and Reveal XTs were downloaded in the field during recaptures in February 2018 and in February 2019. The recaptures were carried out in the same way as the initial captures. During the recaptures in 2018 and 2019, we removed the DST centi HRTs (2018) and Reveal XTs (2019), following the same surgical procedures as for the implantation.

2.4.   Approaches
2.4.1.   Hunting approaches

Twenty-three approaches during real (n=6) and experimental (n=17) hunting situations were performed on eight individual female moose. The experimental hunts were performed after the national dog-on-leash requirement was lifted (21 August) and until the beginning of the annual moose hunt (first Monday in September in this area) in 2017 and 2018 (Länsstyrelserna, 2020). Real hunting situations were part of the regular moose hunt in the area from 4 – 24 September 2017. Twelve dogs of different breeds frequently used for moose hunting (Norwegian Elkhound: n=4, Jämthund: n=3, other breeds: n=5) conducted the hunting approaches in company with their dog handlers. All dogs were equipped with Garmin T5 or DC50 dog collars (Garmin Ltd., Olathe, Kansas, USA), and could be tracked directly via a hand-held GPS (Garmin Astro 320) (Garmin, 2019).

2.4.1.1.   *Experimental hunts*

The experimental hunts were simulating real hunting situations. The dog handler walked with a leashed dog towards the last known GPS position of the moose, and monitored its current position using a VHF tracking receiver. The dog was released and started tracking the moose while the handler monitored the dog via a hand-held GPS. Once the dog had been in close contact with the moose or was not able to find the moose, the handler leashed the dog and went back to the car.

2.4.1.2.   *Real hunts*

Dogs belonging to local hunting teams were equipped with UHF-ID tags (VectronicAerospace, 2019c). When near a collared moose from our study (300-400 meters), the UHF-ID tag sent a signal to the proximity sensors within the moose collar. A message with the ID tag number was sent from the collar together with the last GPS position to the WRAM database for storage (Dettki et al., 2014).

2.4.2.   Ski approaches

In February-March 2017, a master student approached the 12 moose on skis. A total of 45 approaches were performed. The student skied to the last known GPS position of the moose, recorded environmental data at the position, and tracked the moose on skis for 30 minutes afterwards. She recorded her tracks with a hand-held GPS (Garmin Ltd., Olathe, Kansas, USA). The experiments are described in detail elsewhere (Viljanen, 2019).

2.4.3.   Calf checks

To assess the reproduction success of the moose, a researcher sneaked into the animals' position shortly after calving, in order to confirm the number of calves. The researcher was equipped with a hand-held GPS in order to record his own tracks and walked towards the last known GPS position and tracked the moose via a VHF tracking receiver. These experiments were carried out in May-June in 2017 and 2018. A total of 31 calf checks were performed.

2.4.4.   On-leash approaches

The on-leash approaches were performed as a preliminary experiment, in order to test the equipment before the hunting approaches started. Eight on-leash approaches were performed in August 2017.

The moose were tracked with a dog walked on-leash. The dogs were equipped with Garmin T5 or DC50 dog collars and UHF proximity tags, as the dogs also took part in the experimental hunting approaches.

2.4.5. Captures and chemical immobilisation

In February 2018, ten out of 12 moose were recaptured for collar data download, DST centi HR device removal and download of data of the Reveal XT device. In addition to the moose GPS positions, which were recorded every 3 hours in that period, we had detailed GPS tracks of the helicopter capturing the animals.

2.5. Data preparation

The parameters analysed for the different types of approaches and captures in order to assess the behavioural and physiological effects on moose, are summarized in Table 1. For all types of approaches we had to exclude some events due to lack of sufficient data.

Table 1: Parameters analysed for the different types of approaches to assess the physiological and behavioural effects, and the number of approaches included when analysing the parameters (n). FID: flight initiation distance.

Approach	Parameters	n
Hunting approaches	Maximum body temperature	14
	Total distance travelled per day	13
	Maximum speed	13
	Mean Heart rate	14
	Total resting time per day	14
	FID – activity	16
	FID – body temperature	16
Ski approaches	Maximum body temperature	28
	Total distance travelled per day	28
	Maximum speed	28
	FID – activity	28
	FID – movement (speed)	28
Calf checks	FID – activity	31
	FID – body temperature	31
On-leash approaches	FID – activity	8
	FID – body temperature	8
Captures	Maximum body temperature	10
	Total distance travelled	9

2.5.1. Hunting approaches

Based on the distance between the moose and the dog as well as the duration of the contact, we classified hunts into three categories:

- **Successful** – moose and dog were within 240 meters for at least 10 minutes, i.e. the dog followed the moose closely for an extended time and thus the moose was successfully approached by the dog
- **Disturbed** – moose and dog were within 240 meters for less than 10 minutes, i.e. the dog did not follow the moose as closely as in an approach classified as successful but the it was still likely that moose was disturbed by the presence of the dog in the area
- **Not disturbed** – moose and dog were never within 240 meters

Høgskolen
i Innlandet

This classification is based on the maximum flight initiation distances (FID) found during skiing approaches of the same moose, but during a different season (Viljanen, 2019).

We only included approaches classified as successful or disturbed in the analyses.

2.6.   Data analyses

All the data were prepared and analysed using R version 3.6.1 (RCoreTeam 2019). P-values <0.05 were considered significant.

2.6.1.   Body temperature (T_b), movement of the moose and resting time

Our general approach for the analysis was to compare the actual day of the experimental approach or capture with a reference time before and the day after.

To investigate the effects of our experimental approaches and captures on the maximum body temperature of the moose we used linear models from the lme4 package (Bates et al., 2015) to model the maximum T_b (response variable), considering the explanatory variables Period (factor with three levels; reference period, day of approach and day after approach) and Success (factor with two levels; disturbed and successful). Not every moose was experimentally approached repeatedly which resulted in too few data points to include the individual moose ID as a random structure. Model selection was based on Akaike's information criterion corrected for small sample size (AICc) and carried out with the function lCtab from the bbmle package (Bolker and RCoreTeam, 2017). We picked the most parsimonious model within ΔAICc ≤2 and applied a post-hoc test with estimated marginal means from the emmeans package (Lenth et al., 2019) to estimate which levels of the categorical variables were significantly different from each other. When analysing the movement data for the experimental approaches, we used ten-minutes GPS positions, whereas for ski approaches, GPS positions were recorded every 30 min. We switched to acquiring 5 min positions in the morning of the scheduled ski approach and recorded positions every minute during the approach. We linearly interpolated the 30 min GPS positions and any missing positions (0.08 %) with the 'na.approx' function from the zoo package in R (Zeileis and Grothendieck, 2005) and standardised the 1 and 5 min GPS positions to 10 min GPS positions in order to make them homogeneous. GPS fix rate around the period of captures was 3 hours.

We used the AdehabitatLT package (Calenge, 2006) to calculate the Euclidean distance between consecutive GPS positions and calculated the total distance travelled per day (m) and the maximum speed (m/min). We modelled the maximum speed and the total distance travelled per day (response variables), using gamma distributed generalised linear models with identity link function. Explanatory variables are presented in Table 2, and the model selection followed the same approach as for body temperature. Due to differing GPS fix rates before the experimental hunting approaches, we were not able to include a reference period in the movement analysis and only compared the day of the approach with the day after, whereas we compared estimates on moose resting behaviour and body temperature to estimates during the reference period and the day after the approach.

Table 2: Explanatory variables included in the linear model combinations to evaluate body temperature, movement (distance travelled and maximum speed) and resting behaviour (active versus inactive) of moose approached by hunting dogs and human on skis

Explanatory variable	Description	Approach
Period	Factor with three* levels (reference period, day of approach, day after approach)	Dog, Ski, Captures
Success	Factor with two levels (disturbed, successful)	Dog
Calf	Factor with two levels (with/without calf)	Ski, Captures

*For movement two levels, the reference period was excluded. For hunting approaches the reference period was seven days, for ski approaches one day

To investigate the effects of experimental hunts on the activity level of moose we classified moose behaviour into 1) inactive (i.e. resting) and 2) active by fitting separate hidden Markov models (HMMs) to each individuals' observed activity data (i.e. summed acceleration of X- and Y-axes). HMMs are time-series models that assume animals' observed movement or activity patterns to be determined by an underlying 'hidden' finite state sequence, where the states can be interpreted as proxies for the unobserved behavioural modes of an animal (Patterson et al., 2009; Langrock et al., 2012). We modelled activity using a state-dependent gamma distribution. To account for potential effects of temporal patterns and temperature on moose behaviour, the state transition probabilities were expressed as functions of the time of day, light conditions (dark, light or twilight at time of observation), day of the year and corrected collar derived ambient temperature using a binomial logit link function (i.e. with the categories representing the two different states the process might switch to). We used forward selection based on Aikaike's Information Criterion (AIC) to determine the influence of these covariates considered in each of the individual HMMs. For cyclic covariates (day of year and time of day), we included sine and cosine terms. All HMMs were fitted via numerical likelihood maximisation using the momentuHMM R package (McClintock and Michelot, 2018). Each model was run with 30 sets of random starting values to avoid local maxima (always choosing the model with the highest log-likelihood value). We then determined the most likely state sequence from each HMM using the Viterbi algorithm and calculated the total time spent resting per day (min) based on these results. Subsequently, we ran a linear model with resting time as response variable and performed model selection, following the same approach as for body temperature analysis (explanatory variables are presented in Table 2).

2.6.2. Heart rate (HR)

The Reveal XT calculated the HR based on recognition of R peaks in the ECG, and the ECGs were deleted while the HR data was stored in the memory of the logger (Medtronic, 2017). The algorithm used for detection for R peaks was not always correct, likely because the Reveal XT is designed for use in human medicine, and heart anatomy and physiology of humans and moose differ. Because of that, some of the heartbeats were not detected and sometimes one heartbeat was detected as two (double counting). The minimum HR of a moose resting during winter was found to be above 37.5 bpm (Græsli et al., 2020a), so all values lower than that were removed. Based on comparisons of the HR data from the Reveal XT with manually calculated HRs from ECGs obtained by another HR logger (DST centi HRT, which was deployed additionally as part of a second study) and accelerometer data from the same moose, we found no correlation between activity level and heart rate accuracy and concluded that the algorithm performed similarly during both active and passive phases. Consequently, we used the obtained raw HR data and only corrected for impossible low HRs, based on results of minimum HR in winter according to Græsli et al. (2020a). By doing this, we were able to calculate differences in HR and identify significant changes in HR over time. However, we were unable to account for potential double-counting and can therefore not report any mean or maximum HR values.

All experiments were carried out between 08.00 and 14.00 local time, and we, therefore, compared the HR measurements during this period of the day. To compare the HR data between the different periods, we built a linear mixed effect model (nlme package) with the HR data and included the variable period (reference time, day of approach and day after approach) as a fixed factor (Pinheiro et al., 2019). The HR data was autocorrelated, which was considered in the model by including an autocorrelation structure (corCAR1). Moose ID was included as a random factor to account for repeated measures of the same moose.

2.6.3. Behavioural responses

In order to detect flight initiation distances, FID – how close the dog was when the moose started to react behaviourally (based on collar activity/accelerometer data) or physiologically (based on body temperature) and to be able to find out for how long collar activity levels and T_b were affected by the approaches (i.e. how long it takes for both metrics to return back to the 'normal' pre-approach state),

we applied a 'changepoint' analysis that identifies time periods when a significant change in the time series observations of a variable occurs, based on a defined moving window. Simply put, a changepoint is an instance in time where the statistical properties before and after this time point differ. With potential changes naturally occurring in data and many statistical methods assuming a "no change" setup, changepoint analysis is important in both applied and theoretical statistics. We used the R package *changepoint* (Killick and Eckley, 2014) on collar activity and T_b-data. We identified two change-points (Bin Seg method) based on the variance in the activity data and the mean and the variance in the body temperature data, which should ideally correspond to the start (time of FID) and end (settling down of the moose) of the behavioural and physiological response. For the ski approaches, we had a finer scaled GPS data resolution (data recorded every minute) and did changepoint analysis (PELT algorithm) on the mean and variance of the speed in addition to activity data.

We then calculated the time the moose was affected (hereafter: time affected = time between the two changepoints), compared the times of the changepoints with the GPS data of the dogs/human and calculated FID (euclidean distance), i.e. how close the approacher/dog was when the moose started to react. In addition, we calculated the time affected after an approach ended (the difference between the time of the second changepoint and the time the approach ended (found in the protocol).

3. Results

3.1. Experimental hunting approaches

3.1.1. Body temperature (T_b), movement of the moose, heart rate (HR) and resting time

Our results highlighted changes in moose behaviour and physiology represented by increased movement, T_b and HR during successful experimental hunting situations (Figure 1). Hunting dogs followed moose tracks closely (e.g. Animation 1).

Figure 1: Example of activity (A), heart rate (B) and body temperature (C) during a day of an experimental hunting approach on a female moose in the study area around Nordmaling. The time of the hunting approach are highlighted in blue.
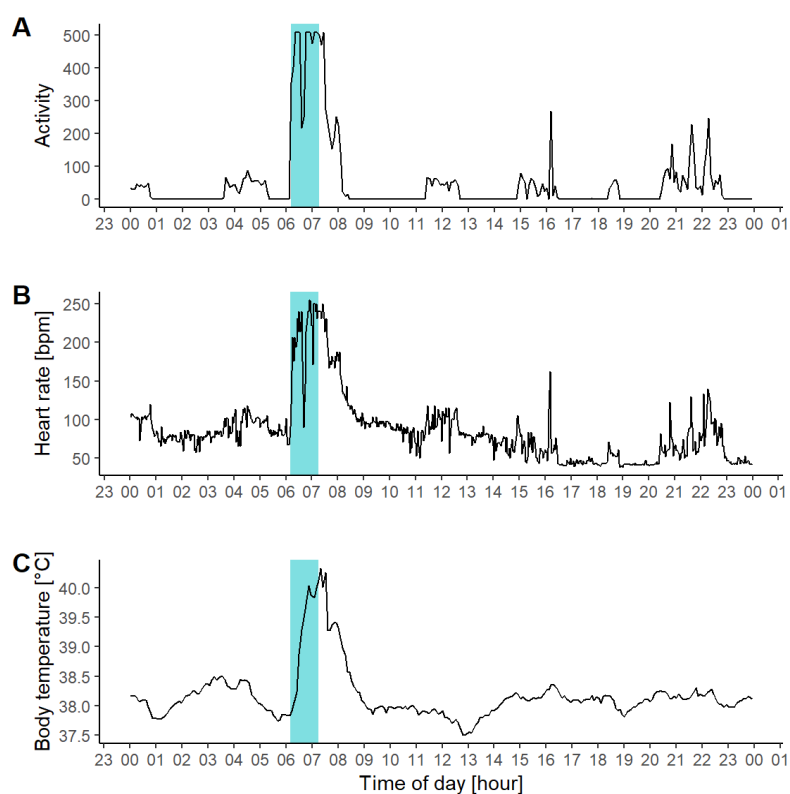
Animation 1:
Animation (A) of GPS positions of a moose (red) during the day of a successful experimental hunting approach with a baying dog (blue) in Nordmaling study area. Activity (B), heart rate (C) and body temperature (D) are displayed on the right side of the panel. The vertical black line is synchronized with the animation and the area highlighted in grey indicates the time of the hunting approach. Please click the link below to be directed to the rpubs webpage to see the animation.
https://rpubs.com/Ecophys_Evenstad/587135

Table 3: Log-likelihood (logLik and ΔlogLik), Akaike's information criterion corrected for small sample size (AICc and ΔAICc), number of parameters (n) and model weight (weight) for the top-ranked model combinations evaluating body temperature, movement (distance travelled and maximum speed) and resting behaviour (active vs inactive) of moose approached by hunting dogs

Model combinations	logLik	AICc	ΔlogLik	ΔAICc	n	weight
Body temperature						
Period*Success	-12.1	41.5	14.9	0.0	8	0.55
Period	-16.8	42.6	10.3	1.1	5	0.32
Period+Success	-16.3	44.4	10.7	2.8	6	0.13
Distance						
Period	-235.0	477.0	7.9	0.0	4	0.49
Period*Success	-232.2	477.5	10.6	0.5	6	0.38
Period+Success	-234.9	479.7	7.9	2.7	5	0.13
Speed						
Period	-119.8	246.7	12.7	0.0	4	0.62
Period*Success	-118.0	248.9	14.5	2.2	6	0.20
Period+Success	-119.7	249.2	12.8	2.5	5	0.18
Resting						
Period*Success	-201.4	420.5	11.4	0.0	8	0.56
Period+Success	-205.2	422.2	7.7	1.7	6	0.24
Period	-206.7	422.6	6.1	2.2	5	0.19

Results of the model selection processes for T_b, Distance travelled, Speed and Resting are presented in Table 3. The test statistics for the selected models are presented in Table 4. Test statistics for the linear mixed model evaluating HR are also presented in Table 4.

Table 4: Model parameter estimates, standard errors (SE), t-values and p-values for variables in the models evaluating body temperature, movement (distance travelled and maximum speed), resting behaviour (active versus inactive) and heart rate of moose approached by hunting dogs.

| Model parameters	Estimate (β)	SE	t-value	p-value
Body temperature				
(Intercept)	39.40	0.20	195.68	<0.001
Period at	-0.24	0.28	-0.83	0.41
Period after	-0.27	0.28	-0.96	0.34
Success successful	-0.07	0.23	-0.31	0.76
Period at : Success successful	0.71	0.32	**2.22**	0.03
Period after : Success successful	-0.13	0.32	-0.41	0.69
Distance				
(Intercept)	7123	1008	7.06	<0.001
Period after	-4145	1093	**-3.79**	<0.001
Speed				
(Intercept)	99.6	14.1	7.07	<0.001
Period after	-76.5	14.5	**-5.28**	<0.001
Resting				
(Intercept)	801.9	26.6	30.18	<0.001
Period at	-33.6	37.6	-0.89	0.378
Period after	-46.9	37.6	-1.25	0.221
Success successful	11.4	30.3	0.38	0.709
Period at : Success successful	-23.2	42.8	-0.54	0.591
Period after : Success successful	84.6	42.8	**1.97**	0.057
Heart rate				
(Intercept)	65.25	4.32	15.10	<0.001
Period at	24.46	3.29	**7.43**	<0.001
Period reference	2.85	2.49	1.15	0.25

We observed a significantly higher maximum T_b [0.9°C higher (SE 0.15°C, p-value <0.001)] at the day of the approach compared to the day after for the successful approaches (Figure 2 B). In addition, the maximum T_b on the day of the approach was 0.5°C higher (SE 0.15°C, p-value 0.031) compared to the reference time. Highest T_b measured in the study was 40.8°C which was recorded during a successful approach (Figure 2 A). We did not detect any differences in T_b between the reference period, the day of the approach and the day after the approach among the disturbed moose (Figure 2 B, Animation 2), in which the dog did not follow the moose closely but was only present in the vicinity for < 10 min.

Animation 2:
Animation (A) of GPS positions of a moose (red) during the day of an experimental hunting approach with a baying dog (blue) in Nordmaling study area, which was classified as disturbed only. Activity (B), heart rate (C) and body temperature (D) are displayed on the right side of the panel. The moving vertical black line is synchronized with the animation and the area highlighted in grey indicates the time of the hunting approach. Please click the link below to be directed to the rpubs webpage to see the animation.
https://rpubs.com/Ecophys_Evenstad/587137

*Figure 2: **(A)** Maximum body temperature T_b (°C) during different periods (Reference, At, After) between different success states (Disturbed only in red, Successful approach in blue) for moose approached by hunting dogs. **(B)** Estimated marginal means (emmeans) for maximum body temperature T_b (°C) for different success states (Successful, Disturbed) before (Reference), during (At) and after (After) experimental hunting approaches. The black dots represents the marginal means, the purple area represents 95 % confidence interval and an overlap of the red arrows indicates non-significant differences.*
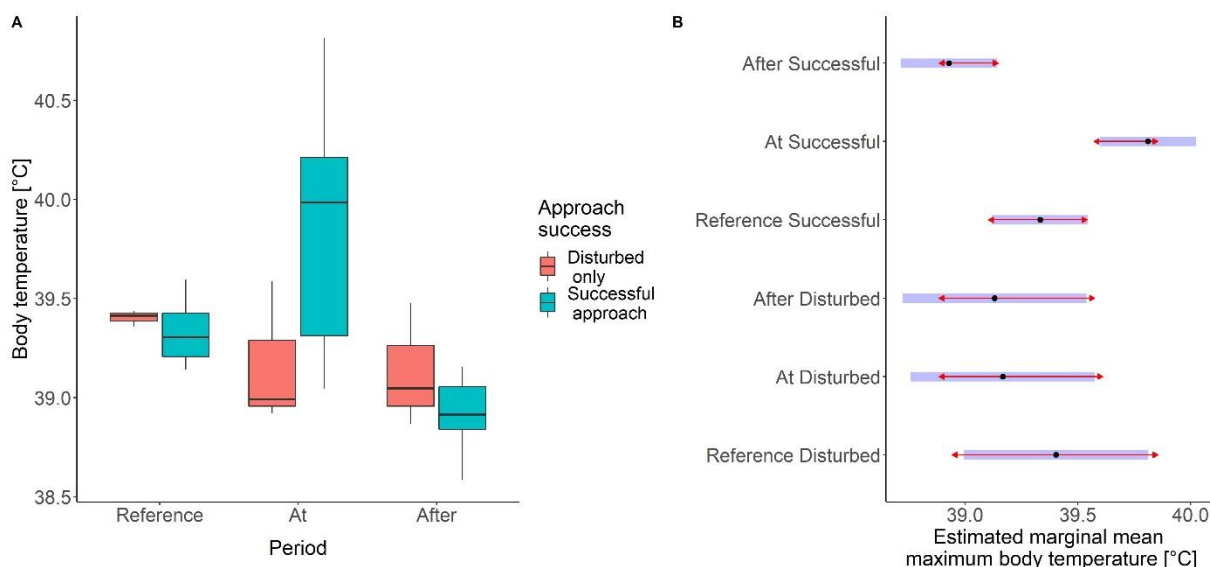
We found a higher maximum speed [77 m/min higher (SE 14.5 m/min, p-value <0.001), Figure 3 A and B] and a longer distance travelled (4.1 km longer (SE 1.1 km, p-value <0.001), Figure 3 C and D) at the day of the approach compared to the day after the approach for all moose.

Figure 3: (A) Maximum speed (m/min) and (C) total distance travelled per day (m) during different periods (At, After) for moose approached by hunting dogs. Estimated marginal means (emmeans) are presented for (B) maximum speed (m/min) and (D) total distance travelled (m) during (At) and after (After) experimental hunting approaches. The black dots represents the marginal means, the purple area represents 95 % confidence interval and an overlap of the red arrows indicates non-significant differences.
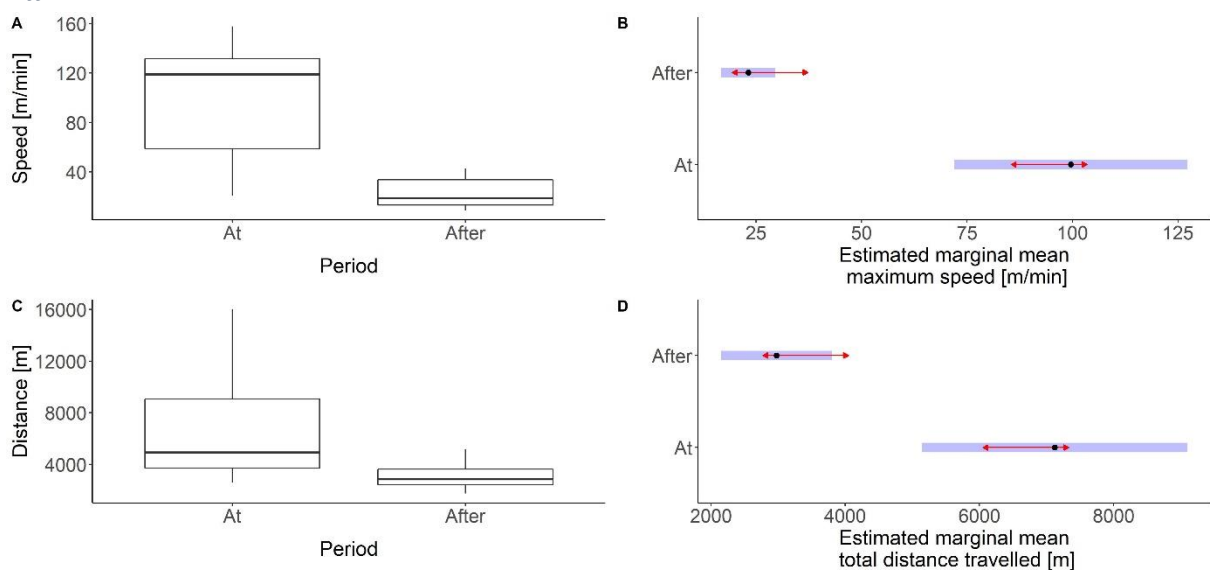
HR values for the day of the approach were significantly higher compared to the reference period and the day after the approach (22 and 24 bpm, respectively). Highest HR measured in the study was 195 bpm (confirmed from stored ECG episodes).

Moose rested significantly longer (95 min (SE 20.6 min, p-value<0.001)) the day after a successful approach compared to the day of the approach. In addition, we demonstrated that the successfully approached moose rested 96 minutes longer (SE 30.3 min, p-value 0.036) than the disturbed moose (i.e. moose without a direct contact with hunting dog, but that showed signs of disturbances) the day after the approach (Figure 4). The mean resting time per day in the reference period was 13.5 hours.

Figure 4: (A) Time spend resting (min) during different periods (Reference, At, After) between different success states (Disturbed only in red, Successful approach in blue) for moose approached by hunting dogs. (B) Estimated marginal means (emmeans) for time spend resting (min) for different success states (Successful, Disturbed) before (Reference), during (At) and after (After) experimental hunting approaches. The black dots represents the marginal means, the purple area represents 95 % confidence interval and an overlap of the red arrows indicates non-significant differences.
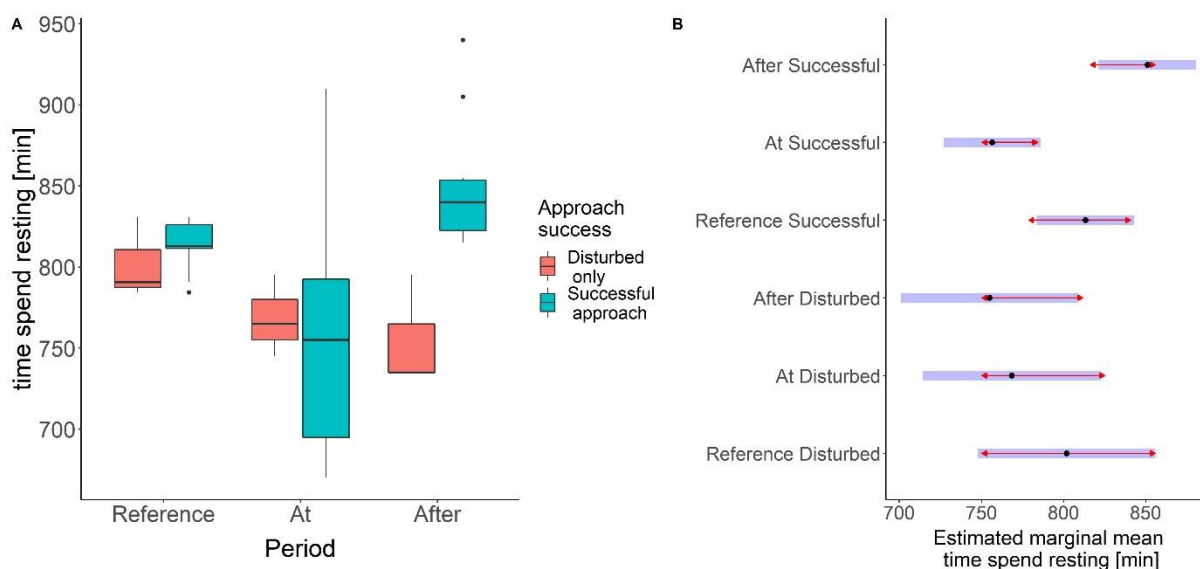
3.1.2. Behavioural responses

Based on collar activity (accelerometer) data, we detected changepoints (Figure 5 A) in ten of the sixteen approaches (disturbed n=1, successful n=9). Changepoints on T_b data were detected in three successful approaches (Figure 5 B).

For the successful approaches, the average FID was 142 m (median) (range 86 – 248 m). The collar activity was at the same level as before the approach 54 min (median) after an approach ended (range 27 – 114 min). We found that total time T_b was affected, was 14.5 min longer compared to the time the collar activity was affected (median total time T_b 132 min (range 124 – 160 min) versus collar activity 117.5 min (range 25 – 180 min). The average time affected after an approach ended was 8 minutes longer for T_b compared to activity (median time T_b 62 min (range 36 – 81 min) vs activity 54 min (range 27 – 114 min). Most of the changepoints in T_b detected corresponded to drinking episodes (based on graphical visualisation of the T_b dropping up to 2°C in a short period of time) instead of indicating the time point when the moose settled down after an approach (see Figure 6).

Figure 5: Example of an experimental hunting approach with dogs (grey area) on a female moose and detected changepoints (red line) for activity (A) and body temperature (B) data.
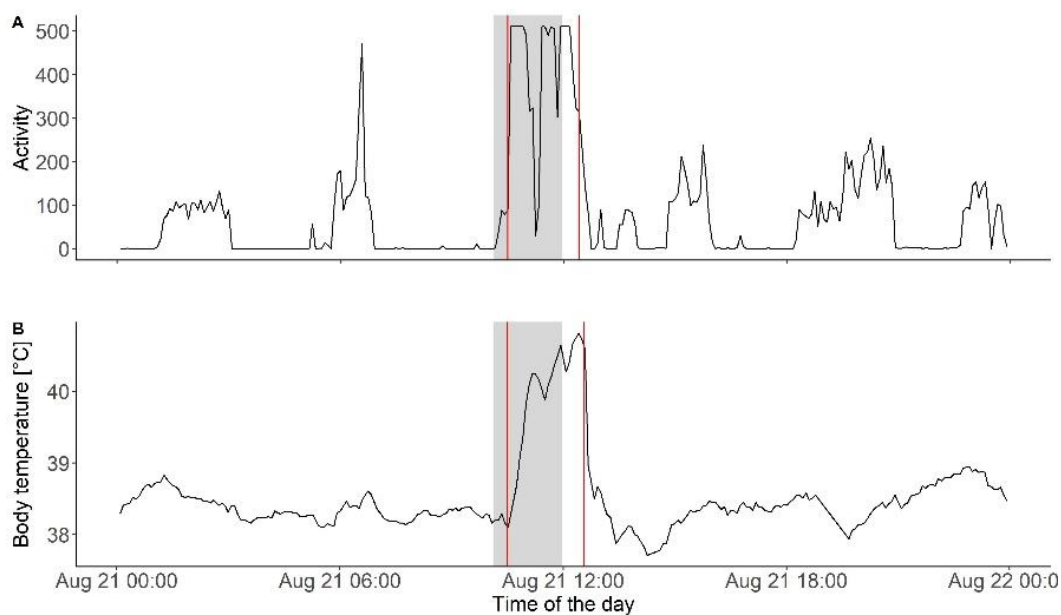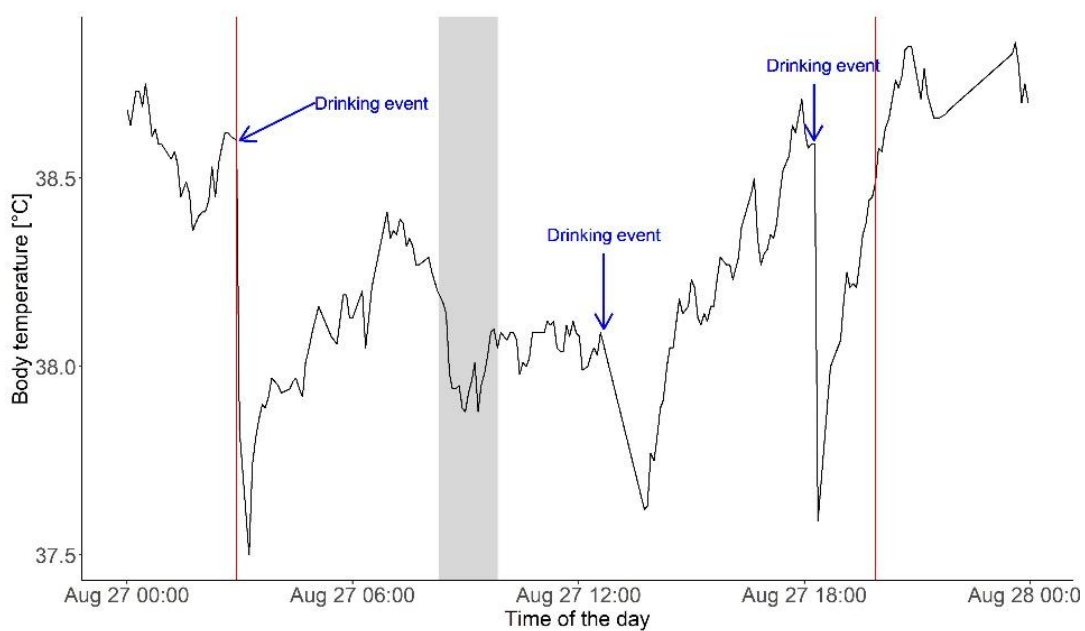

Figure 6: Illustration of the impact of a drinking event (blue) on the detection of changepoints (red) on body temperature data related to an experimental hunting approach with dogs (grey area).

3.3. On-leash approaches and calf checks

3.3.1. Behavioural responses

Based on collar activity (accelerometer) data, we detected changepoints in three out of eight on-leash approaches (Animation 3) and 15 out of 31 calf checks (Animation 4). Changepoints on T_b data could not be detected in any of the approaches.

Animation 3:
Animation (A) of GPS positions of a moose (red) during the day of an on-leash approach with a dog (blue) in Nordmaling study area. Activity (B), heart rate (C) and body temperature (D) are displayed on the right side of the panel. The moving vertical black line is synchronized with the animation and the area highlighted in grey indicates the time of the hunting approach. Please click the link below to be directed to the rpubs webpage to see the animation.
https://rpubs.com/Ecophys_Evenstad/587140

Animation 4:
Animation (A) of GPS positions of a moose (red) during the day of a calf check by field personnel (blue) in Nordmaling study area. Activity (B), heart rate (C) and body temperature (D) are displayed on the right side of the panel. The moving vertical black line is synchronized with the animation and the area highlighted in grey indicates the time of the hunting approach. Please click the link below to be directed to the rpubs webpage to see the animation.
https://rpubs.com/Ecophys_Evenstad/587146

Moose were on average affected for 15 min (median) after an on-leash approach. However, one moose was behaviourally affected for 66 min after the approach ended. Malfunctioning of the proximity sensor resulted in missing moose GPS positions for one approach. Median FID for the remaining two on leash approaches was 180 m (range 121 – 238 m). Median FID for the calf checks was 99 m (range 20 – 357 m).

3.4. Ski approaches

3.4.1. Body temperature (T_b) and movement of the moose

Experimental ski approaches on female moose (Animation 5) did not result in any significant increases in T_b (Table 5).

Animation 5:
Animation (A) of GPS positions of a moose (red) during the day of an experimental ski approach by a master student (blue) in Nordmaling study area. Activity (B), heart rate (C) and body temperature (D) are displayed on the right side of the panel. The moving vertical black line is synchronized with the animation and the area highlighted in grey indicates the time of the hunting approach. Please click the link below to be directed to the rpubs webpage to see the animation.
https://rpubs.com/Ecophys_Evenstad/587260

Table 5: Log-likelihood (logLik and ΔlogLik), Akaike's information criterion corrected for small sample size (AICc and ΔAICc), number of parameters (n) and model weight (weight) for the top-ranked model combinations evaluating body temperature, movement (maximum speed and total distance travelled per day) of moose approached by skier.

| Model combinations	logLik	AICc	ΔlogLik	ΔAICc	n	weight
Body temperature						
Null model	29.7	-55.2	0.0	0.0	1	0.408
Period	31.4	-54.4	1.7	0.8	3	0.271
Calves	29.9	-53.6	0.2	1.6	2	0.182
Period + Calves	31.6	-52.6	2.0	2.4	4	0.120
Period * Calves	32.1	-49.1	2.4	6.1	6	0.019
Speed						
Period + Calves	-341.1	692.9	52.6	0.0	4	0.808
Period * Calves	-340.5	696.3	53.2	3.4	6	0.148
Period	-345.1	698.7	48.6	5.8	3	0.044
Null model	-393.7	791.5	0.0	98.6	1	<0.001
Calves	-393.6	793.5	0.1	100.6	2	<0.001
Distance						
Period + Calves	-767.5	1545.6	23.1	0.0	4	0.542
Period * Calves	-765.4	1546.1	25.2	0.4	6	0.439
Period	-771.9	1552.3	18.6	6.7	3	0.019
Calves	-786.6	1579.4	3.9	33.8	2	<0.001
Null model	-790.5	1585.2	0.0	39.5	1	<0.001

The most parsimonious movement models included Period and Calf as explanatory variables (Table 5). The test statistics for the selected models are presented in Table 6.

Table 6: Model parameter estimates, standard errors (SE), t-values and p-values for variables in the models evaluating movement (distance travelled and maximum speed of moose approached by skier.

Model parameters	Estimate (β)	SE	t-value	p-value
Speed				
(Intercept)	9.97	1.46	6.84	<0.001
Period at	48.87	7.42	**6.59**	<0.001
Period after	2.62	1.60	1.63	0.1059
Calves yes	-4.36	1.61	**2.71**	0.0081
Distance				
(Intercept)	1606	198	8.13	<0.001
Period at	1827	378	**4.83**	<0.001
Period after	315	226	1.39	0.167
Calves yes	-579	216	**-2.76**	0.007

We observed a significantly higher maximum Speed (49 m/min higher (SE 7.41 m/min, p-value <0.001), Figure 7 A and B) and longer distance travelled (1826 m longer (SE 377.8 m, p-value <0.001), Figure 7 C and D) for moose without a calf, at the day of the approach compared to the day after.

Figure 7: (A) Maximum speed (m/min) and (C) total distance travelled per day (m) during different periods (Reference, At, After) between for moose with and without a calf approached by a skier. Estimated marginal means (emmeans) are presented for (B) maximum speed (m/min) and (D) total distance travelled per day (m) for moose with and without a calf before (Reference), during (At) and after (After) experimental skiing approaches. The black dots represents the marginal means, the purple area represents 95 % confidence interval and an overlap of the red arrows indicates non-significant differences.
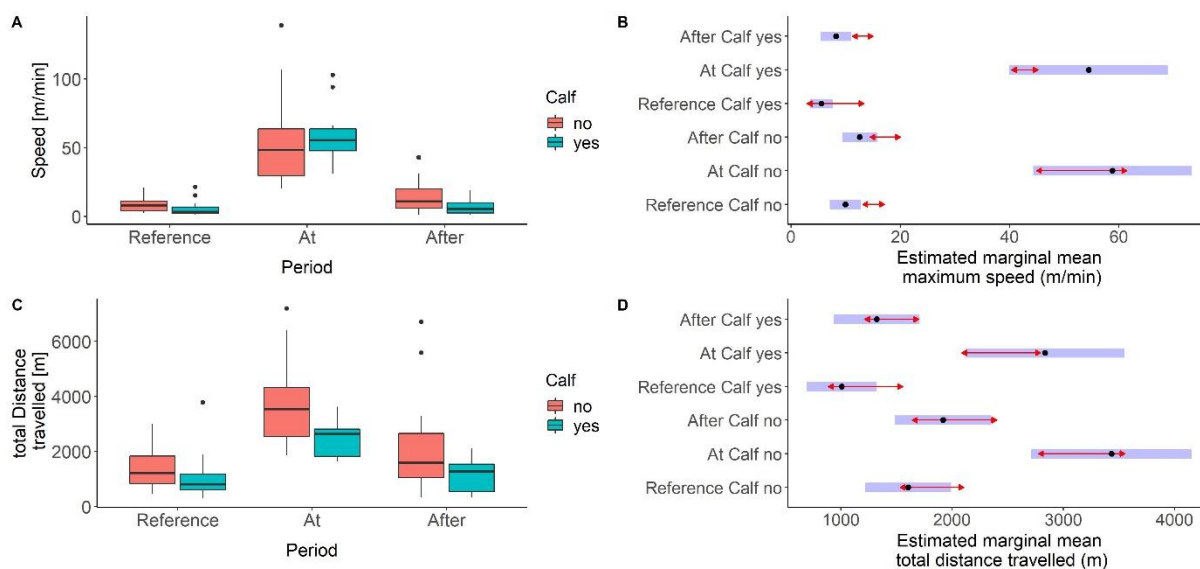

The day before a ski approach and the day after did not significantly differ from each other (Figure 7 B and D). Generally, moose without a calf travel 4.4 m/min faster (SE 1.61 m/min, p-value <0.01) and 597 m longer (SE 216 m, p-value <0.01) than moose with a calf (Figure 7 B and D).

3.4.2. Behavioural responses

Based on collar activity (accelerometer) and movement (speed) data, we detected changepoints in all 28 ski approaches (Figure 8). Median FID based on activity data was 276 m (range 83 m – 686 m), whereas the finer scaled resolution speed data resulted in a median FID of 136 m (range 84 m – 360 m). The average detection of changepoints differed by four minutes and 140 m, which essentially represents the difference in data resolution.

Figure 8: Comparison of changepoint detection (red lines) for one experimental ski approach (grey area) on a female moose for speed (m/min) data with one minute resolution and PELT algorithm (A) and activity data with five minute resolution and Bin Seg algorithm (B). Times of the first detected changepoint (FID) are displayed in the plots.
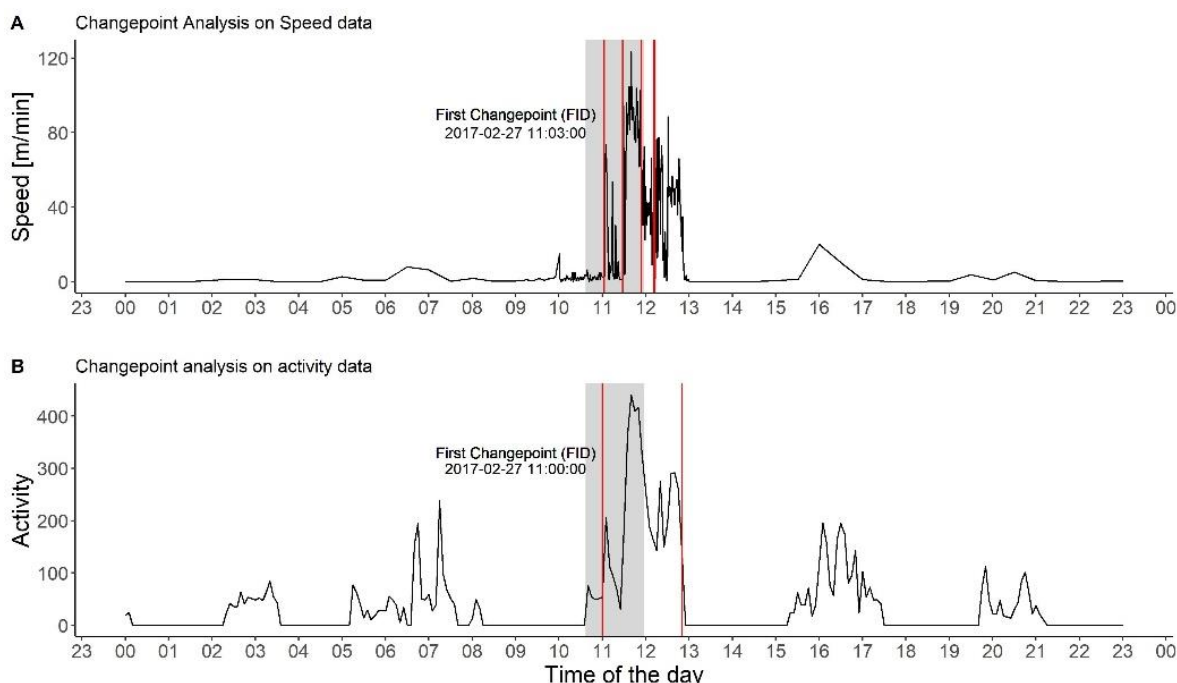
3.5. Captures and chemical immobilisation

3.5.1. Body temperature (T_b) and movement of the moose

We selected the most parsimonious models for the body temperature and movement (total distance travelled) models, which included Period as explanatory variable (Table 7). The test statistics for the selected models are presented in Table 8. Our results emphasize that the day of capture increased maximum body temperature by 0.5 °C (SE 0.15 °C , p-value < 0.01, Figure 9 A and B) and total distance travelled by 3904 m (SE 960 m, p-value < 0.001, Figure 9 C and D) compared to the reference period before. The max body temperature during the reference period before and the day after did not differ significantly, whereas the total distance travelled was still significantly longer (1891 m longer, SE 555.2 m, p-value < 0.005, Figure 9 D) the day after a capture event compared to the reference time before.

Table 7: Log-likelihood (logLik and ΔlogLik), Akaike's information criterion corrected for small sample size (AICc and ΔAICc), number of parameters (n) and model weight (weight) for the top-ranked model combinations evaluating body temperature, and distance travelled of moose which were captured.

Model combinations	logLik	AICc	ΔlogLik	ΔAICc	n	weight
Body temperature						
Period	-6.9	23.7	8.5	0.0	3	0.9959
Null model	-15.4	35.4	0.0	11.7	1	0.0029
Calves	-15.1	37.2	0.3	13.5	2	0.0012
Distance						
Period	-227.3	464.4	12.3	0.0	3	1
Null model	-239.5	483.6	0.0	19.2	1	<0.001
Calves	-2395	486.0	0.0	21.7	2	<0.001

Table 8: Model parameter estimates, standard errors (SE), t-values and p-values for variables in the models evaluating movement (distance travelled per day (m)) of moose which were captured.

Model parameters	Estimate (β)	SE	t-value	p-value
Body temperature				
(Intercept)	38.57	0.111	348.70	<0.001
Period at	0.51	0.156	**3.27**	0.0033
Period after	-0.180	0.156	-1.15	0.2615
Distance				
(Intercept)	715	147	4.87	<0.001
Period at	3904	960	**4.07**	<0.001
Period after	1891	555	**3.41**	0.00232

Figure 9: (A) Maximum body temperature (°C) and (C) total distance travelled per day (m) during different periods (Reference, At, After) for moose being captured by helicopter. Estimated marginal means (emmeans) are presented for (B) maximum body temperature (°C) and (D) total distance travelled per day (m) for moose before (Reference), during (At) and after (After) captured by helicopter. The black dots represent the marginal means, the purple area represents 95 % confidence interval and an overlap of the red arrows indicates non-significant differences.

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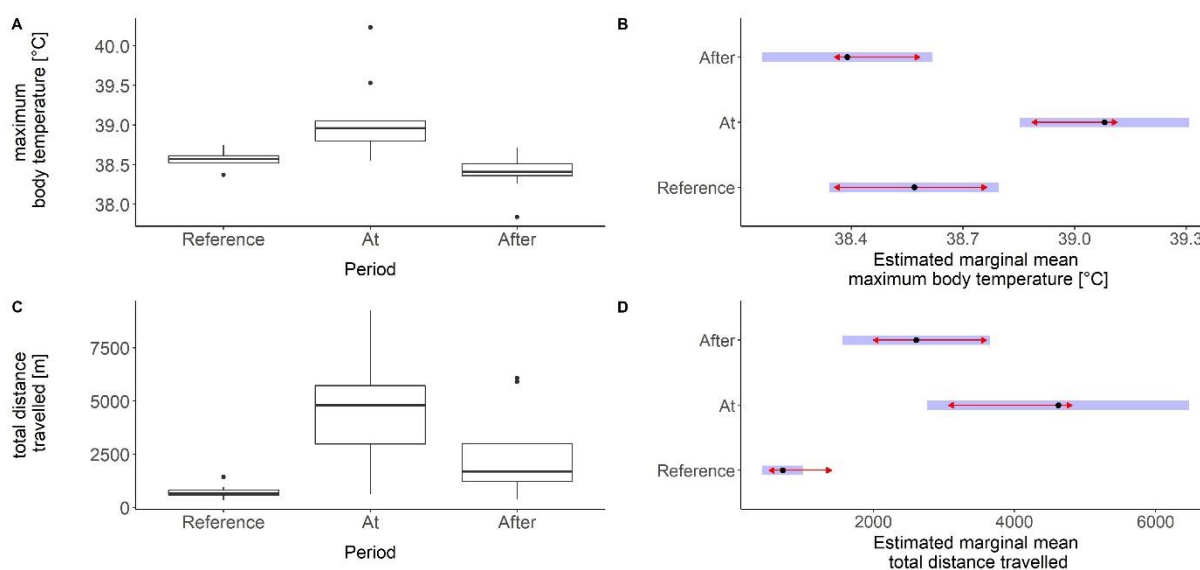
Visually inspected, movement rates are affected for 2 – 4 days after a capture event (Figure 10) before they return to pre-capture rates.

Figure 10: Boxplots of total distance travelled (m) per day ten days before and ten days after captures (day 0, red boxplot).
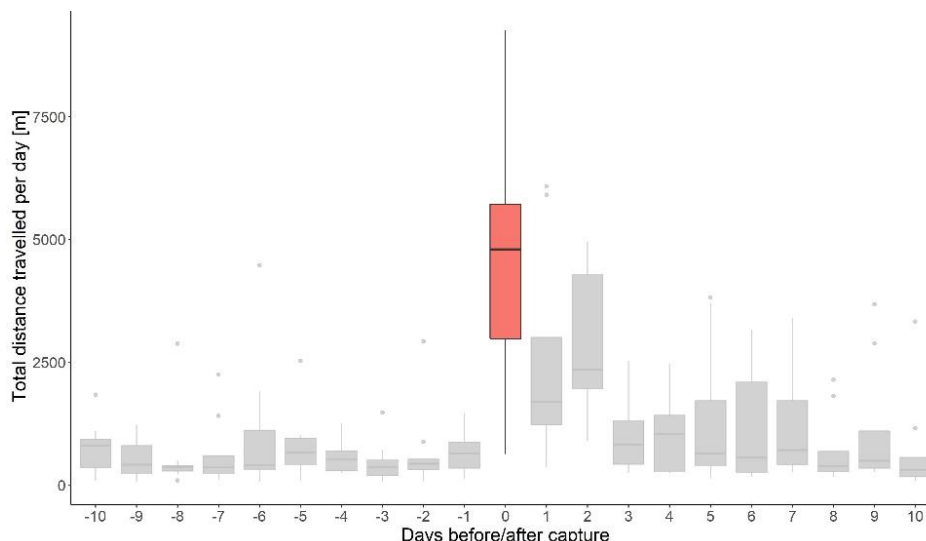
3.6.   Comparison of the effects of disturbances on body temperature (T_b)

Moose display seasonal hypometabolism with higher body temperatures and heart rates in summer than in winter (Græsli et al., 2020a). To compare the physiological effects of three disturbances (captures, experimental hunts, ski approaches), we extracted the differences in maximum body temperature from one period to the other (Figure 11 A) to account for underlying seasonal differences. Capture and experimental hunting approaches caused a similar increase in maximum T_b at the day of the capture or hunt (0.5°C increase) compared to the reference period, whereas skiing approaches did not result in an increase in maximum T_b (Figure 11 B "Reference – At"). Experimental hunting approaches caused a bigger decrease in maximum T_b the day after an approach (0.9°C decrease) than captures with a 0.7°C decrease the day after a capture event (Figure 11 B "At – After"). Ski approaches increased max T_b by 0.1°C the day after an approach, which however was not significant. Moose, which were hunted experimentally or captured had lower max T_b the day after a hunt or capture compared to the reference period. However, these results were not significant (Figure 11 B "Reference – After").

Figure 11: Panel (A) compiles the maximum body temperatures (°C) during the different disturbance types (captures, successful experimental hunting approaches and skiing approaches) on female moose, compared between the reference period, the day of capture/approach and the day after. Panel (B) summarizes the differences in maximum body temperature (°C) from one period to the other and disturbance type (e.g. difference in maximum body temperature between the reference period before a capture and the day of capture ("Reference – At"). The black line at 0.0 represent 0 °C difference in body temperature between two periods. Significance levels are indicated by *** ≤ 0.001, ** ≤ 0.01, * ≤ 0.05, ns = not significant.

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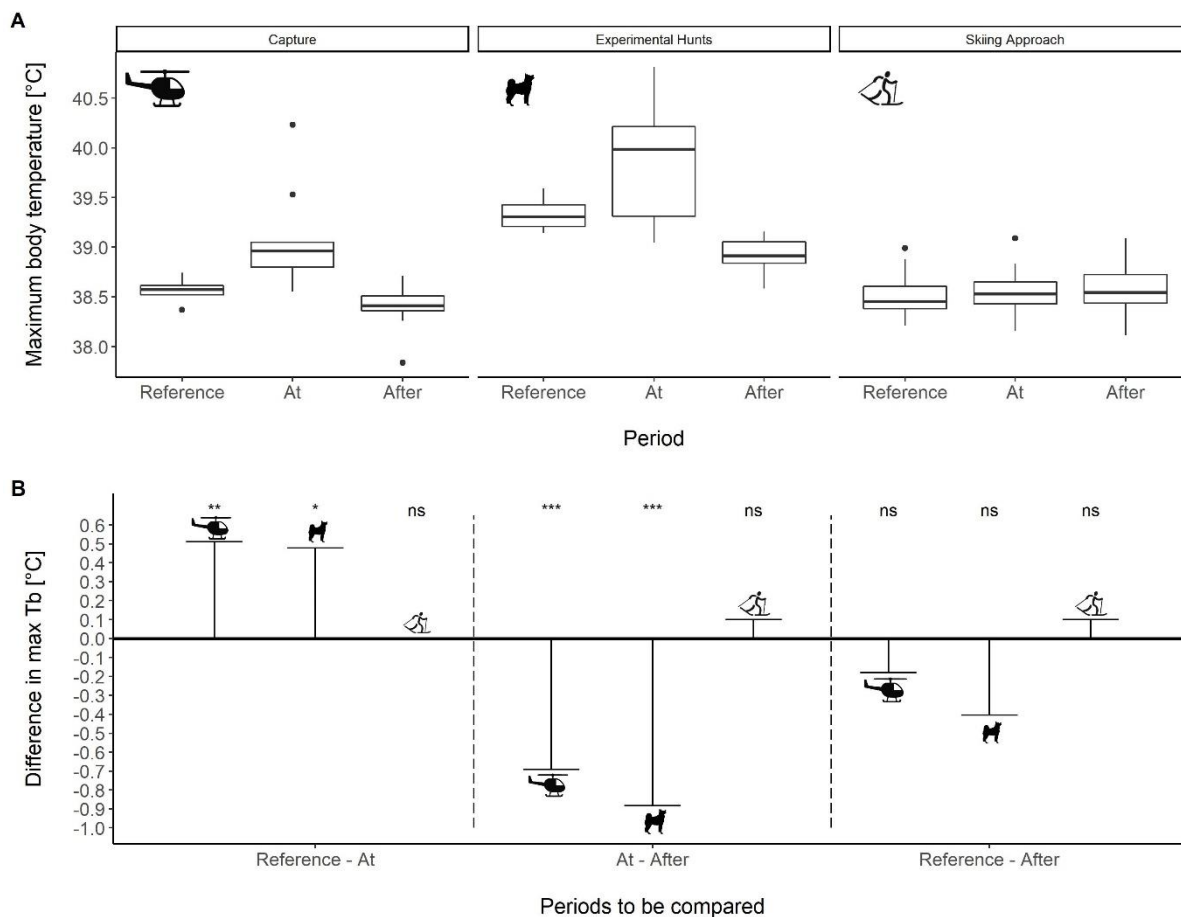
4. Discussion

4.1. Physiological and behavioural responses

Our results emphasize that both captures, and successful hunting approaches resulted in increased body temperature the day of the approach, while there was no significant increase in body temperature during ski approaches. Persisting high body temperatures could be life-threatening because of cytotoxicity. The damage of mammalian cells due to hyperthermia starts after a relatively short period with temperatures >40-41°C, and the degree of damage depends on the exposure time and other stress factors (Lepock 2003). Many of the successful hunting approaches resulted in body temperatures >40°C and we also saw some temperatures >40°C during captures. Although the maximum body temperature during the captures was lower than during hunting approaches, the daily mean body temperature during the period of captures is about 0.5°C lower than in the hunting period due to seasonal changes (Græsli et al., 2020a). The highest temperatures measured during captures might therefore also represent a potential danger for the moose, even if it's not above 40°C.

Heart rate response was only studied in hunting approaches, and we found increased heart rate values the day of the approach compared to the reference period and the day before. Heart rate is a good proxy for metabolic rate in several animals, including moose (Renecker and Hudson, 1985; Green, 2011). Increases in heart rate will therefor represent increased energy expenditure the day of the approach.

We demonstrated higher maximum speed and longer travel distance on the day of captures, hunting and ski approaches compared to the day after. Some of this might be due to increased resting time the day after an approach, as demonstrated in successful hunting approaches. We also saw that it took between 2-4 days after a capture before the movement was at the same level as before the capture. This could be due to recovery from the drug and/or disturbance effects. Previous research found a considerable shorter effect of immobilisation on movement speed in moose (Neumann et al., 2011b), suggesting different conclusions depending on the data resolution and effect assessment.

We detected behavioural responses based on changes in activity in most of the successful hunting approaches, all ski approaches, half of the calf checks, and in some of the on-leash approaches and disturbed hunting approaches. The differences might be because some of the disturbances are more stressful for the moose than others (e.g. moose judge to flight in some situations, while stay in others). In ungulates, features of an approacher (e.g. faster, more direct) as well as habitat settings (e.g. more open versus closed, wooded habitat) may affect animal response (Stankowich, 2008). Even if we detected changepoints (i.e. FIDs) in just half of the calf checks, this did not mean that the researcher was able to check just half of calves. It means that the approacher succeeded in performing the calf checks without the cow noticing/behaviourally reacting on the procedure. Changepoints in body temperature were detected in some of the successful approaches but not in any of the disturbed hunting approaches, calf checks or on leash approaches. The reason for that could be because of drinking events or that the moose was not affected so much physiologically that it resulted in detected changepoints.

4.2. Consequences for the moose

Increased heart rate, longer travel distance and higher maximum speed are all resulting in increased energy expenditure for the moose at the day of a successful hunting approach. In addition, the moose increased their resting time the day after a successful hunting approach, and the resting time was >90 minutes longer for moose after an successful approach compared to approaches classified as disturbed. Increased resting time could be a strategy to compensate for increased energy expenditure or to recover from physical exhaustion. Additionally, it can result in decreased time for foraging. If the disturbance by humans occur often, it thus could result in poorer moose body condition. Increased vigilance and habitat shift to safer habitats are examples of anti-predator behaviour (Brown et al.,

1999; Stankowich, 2008), suggesting that animals experience human disturbances similar to risk of predation (Frid and Dill, 2002). Anti-predator behaviour is the behavioural responses of a prey to stress caused by predators. If moose shift to habitats with poorer forage quality, and use less time to forage, this could result in lower fitness among the moose.

Our results indicate that moose, which are actively chased by a hunting dog are substantially disturbed and that those effects may last until the day after the chase, presented by increased resting time. In turn, moose, which have not been actively chased but have had a hunting dog in close vicinity showed less elevated responses in body temperature and movement. This might indicate that not the whole forest turns into a landscape of fear as soon as the hunting season starts but that moose can tolerate human activities in the forests to some extent with only limited disturbance effects. However, our sample size does not allow for generalization. We were currently unable to quantify energetic costs of human disturbance and hunting because we are lacking studies in captivity. One big question remains: Does moose hunting have long-term effects on the Scandinavian moose population? This is a question we were unable to address with our current study because of the lack of a control group, which is not hunted and our study was limited to study period of three years.

Another serious issue for moose is their poor heat tolerance (Renecker and Hudson, 1986; McCann et al., 2013; Thompson et al., 2019). In fact, moose are heat-sensitive year round with low threshold values in both summer and winter (Renecker and Hudson, 1986). Moose respond to increased ambient temperatures with increased heart rate, respiratory rate and body temperature (Renecker and Hudson, 1986). Also, they reduce their movement and change their habitat utilization (van Beest and Milner, 2013). Thompson et al. (2019) pointed out that moose accumulated a heat load during warmer days, resulting in moose reaching maximum T_b later in the day during the summer. Thus, increased body temperature due to human disturbances may enhance the thermal load for a given moose (e.g. at warmer days during the hunting season). Forecasts of climate change predict increasing ambient temperatures throughout the year in northern Europe (SMHI, 2019), suggesting higher ambient temperature during the annual moose hunt. In moose, thermoregulation (i.e. adjustments to reduce the thermal load) can therefore result in increased energy consumption, changes in food resources and increased infection risk (van Beest et al., 2012; McCann et al., 2013; van Beest and Milner, 2013). As a consequence, moose populations may experience lower survival and reproductive rates, which might be a reason for the population declines in the edges of the moose range (Lenarz et al., 2009; Ruprecht et al., 2016; Allen et al., 2017). The effect of climate change and increasing temperatures are most prone at the southern edges of moose distribution, and increased disturbance by human activity could strengthen this effect. We therefore recommend close monitoring of the edge populations.

Moose in our study area have had stable reproductive rates and slaughter weights for more than 20 years (Ericsson and Wallin, 1999; Svenska Jägareforbundet, 2019). Moose have lived close to humans and been hunted for thousands of years allowing for evolutionary adaption of moose to hunting disturbances. We therefore suggest that moose as a prey species, at least in our study area, are good at coping with the human disturbances at its current level.

5. Other studies with biologgers

5.1. Moose

Hypometabolism in female moose (Græsli et al. 2020a)

Animals living at higher latitudes are exposed to pronounced seasonal differences in both climate and in resource availability. Endotherms living in those environments can maintain a constant high body temperature (T_b), over a wide range of ambient temperatures (T_a). Nonetheless, many endotherms display seasonal shifts in metabolic rate (MR). Here, we studied the annual and circadian cycle of T_b and heart rate (HR) in female moose (*Alces alces*) in relation to activity and T_a. HR also can be used as a proxy of MR to calculate energy budgets. We deployed biologgers to 12 free-ranging female moose; a temperature sensor in the rumen, a HR logger subcutaneously, and a GPS collar equipped with acceleration and Ta sensors. We documented seasonal differences in T_b, HR and activity of moose, with lower levels during winter and higher values during summer (Figure 12). The highest daily mean T_b and HR were 38.64°C (10 July) and 71.9 beats per minute (bpm; 26 June), whereas the lowest daily mean T_b and HR were 38.03°C (17 March) and 40.5 bpm (6 March). High-resolution T_b and activity data allowed us to detect circadian and ultradian rhythmicity throughout the year. Based on previous calibration studies, MR decreased by 60 % from the highest to the lowest point. Our results demonstrate hypometabolism including lower T_b and HR during winter as a strategy to reduce energy expenditure during periods with colder climate and limited availability of resources.

Figure 52: Daily mean body temperature, collar activity, heart rate, and ambient temperature for 12 female moose in Sweden. Solid line represents daily mean body temperature, collar activity, heart rate, and ambient temperature, respectively, dashed lines represents 95% confidence interval of the daily mean. Significantly increasing and decreasing periods are presented as red and blue, respectively, of the solid line.
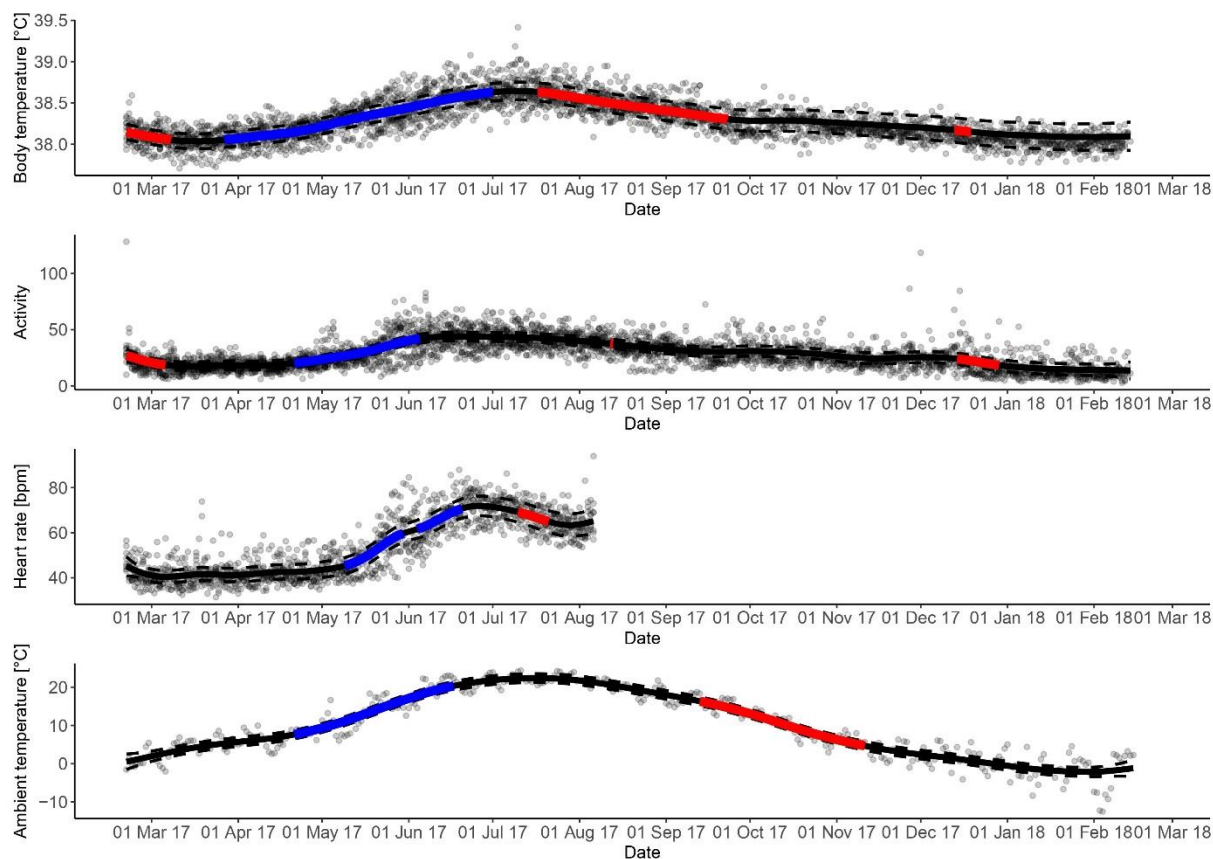
In addition to the experiments covered in chapters 2-4, moose were instrumented with MITs also in Norrbotten and Öland (Figure 13).

Summary [modified from Fohringer, 2021 (PhD thesis) and Singh et al., 2021 (manuscript)]

Understanding the physiological and behavioural responses of animals to rising global temperatures is vital for their future conservation. Cold-adapted migratory species are especially vulnerable to climate change due to coupling of their key life history events with seasonal changes in temperature and plant phenology. In this study, we investigated the ecophysiology of free-ranging moose (*Alces alces*) using MITs and GPS collars across three study areas covering a large latitudinal gradient from 56°N to 67°N in Sweden. The loggers measured simultaneous changes in T_b, T_c and activity, which allowed us to link physiological changes to thermal exposure and seasonal habitat selection patterns.

We showed the extent of spatial and temporal variation in moose T_b patterns (Figure 14, upper frame). We also showed that males had a significantly lower average T_b (38.06 °C) than females (38.29 °C), which is likely due to their sexual size dimorphism (Figure 14 lower frame). Ambient temperature experienced by moose in its microclimate drove changes in T_b and behaviour, specifically through changes in activity patterns to cope with thermal stress. The proportion of time during which moose exceeded their upper critical ambient temperature was variable across a latitudinal gradient. The longest period of thermal stress was encountered in the southern study area, where moose never experience thermal neutrality during winter and where moose are known to be suffering from low recruitment. The strategies to cope with thermal exposure were primarily reflected in the selection for wetland type habitats over other habitat types during stressful periods. This, however, occurred in parallel with the selection for foraging habitats, which may provide thermal shelter simultaneously.

We demonstrated the intricate linkages between external environment and internal state of wild endotherms and the trade-offs made between selecting forage and thermoregulation. The on-going increase in ambient temperature may affect physiology and behaviour of animals, and these effects may differ across areas and sexes, ultimately impacting population dynamics and long-term fitness.

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Figure 13: Map showing the study areas where 44 moose were instrumented with MITs. Norrbotten (blue, 15 males and 10 females), Västerbotten (green, 12 females) and Öland (red, 7 females).
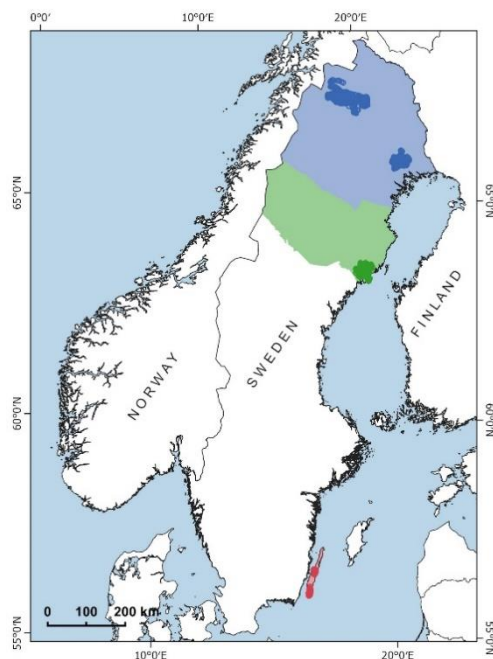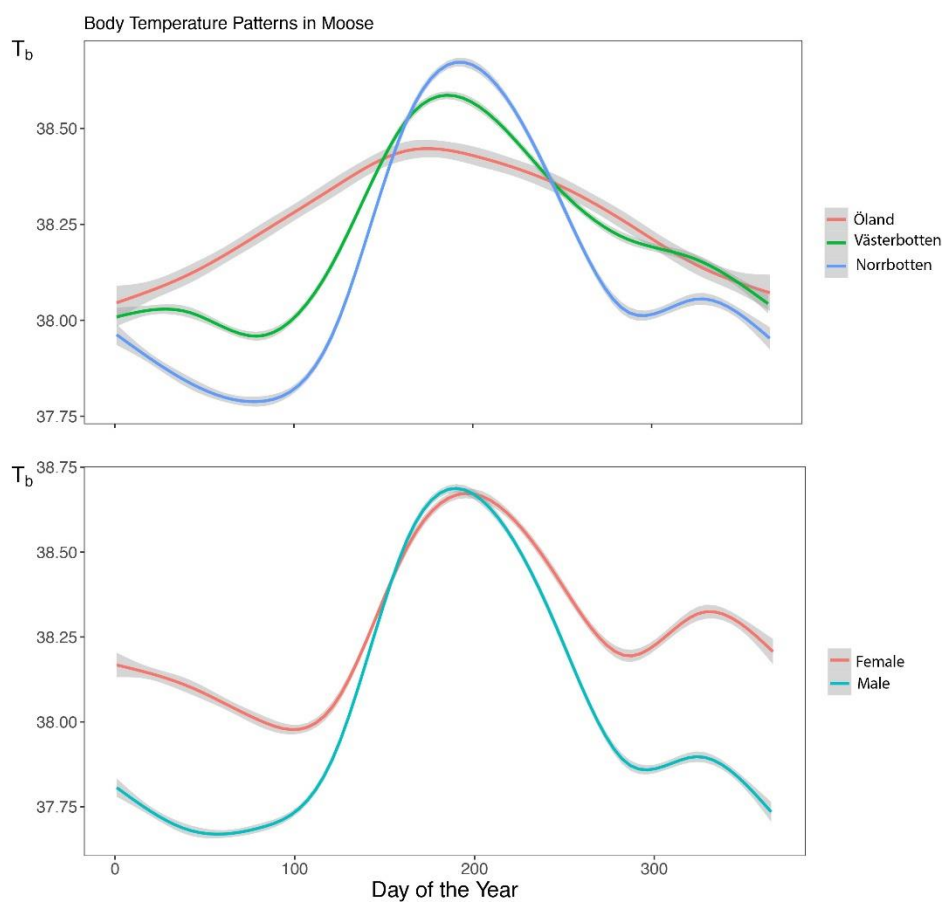

Figure 14: Spatial, temporal and gender T_b patterns in moose.

5.2. Brown bears

Abstract

Over ten years (2010-2020), we used biologgers in brown bears (*Ursus arctos*) for body temperature (T_b) heart rate, heart rate variability (as proxy for autonomic nervous system levels) and activity to assess the timing and duration of pregnancy, the interplay between physiological and ecological drivers of den entry and den exit, the interplay between heart rate and movement, metabolism during the hyperphagic period and the effects of body mass on hibernation depth and duration. The mean gestation period was 56 days, with pregnant bears having higher T_b during the gestation and lactation periods. Non-pregnant bears entered the den when the snow arrived and when the ambient temperature neared 0°C. Activity, heart rate and T_b started to drop slowly several weeks before den entry. Denning appeared to be tightly coupled with metabolic suppression. During arousal, T_b unexpectedly rose two months before den exit and was driven by ambient temperature (T_A), independently of autonomic nervous system activity which only became active three weeks before den exit. The difference between T_b and T_A decreased gradually. Although the sympathetic nervous system began to restore euthermic metabolism three weeks before den exit, it was not until T_A reached the bear's lower critical temperature that bears exited the den. We further evaluated T_b throughout the year in 34 bears and found consistently lower T_b in sequentially smaller bears in winter (Jan-Mar) with the opposite pattern in summer. During summer, heart rate increases with long distances travelled, but varies with day-of-year and reproductive status, depending on the metabolic rate. During autumn, we compared brown bears to Asiatic black bears (*Ursus thibetanus*), which had decreased heart rates during summer but had doubled heart rate values throughout the hyperphagic period compared to brown bears.

The use of heart rate and T_b data has allowed us to fill in important knowledge gaps in the basic ecology and physiology of free-ranging brown bears while also providing a solid foundation for exploring further details on conservation, management, and implicates of climate variability on bear biology.

Drivers of hibernation in the brown bear (Evans et al., 2016a)

Hibernation has been a key area of research for several decades, essentially in small mammals in the laboratory, yet we know very little about what triggers or ends it in the wild. Do climatic factors, an internal biological clock, or physiological processes dominate? Using state-of-the-art tracking and monitoring technology on fourteen free-ranging brown bears over three winters, we recorded movement, heart rate (HR), heart rate variability (HRV), body temperature (T_b), physical activity, ambient temperature (T_a), and snow depth to identify the drivers of the start and end of hibernation. We used behavioural change point analyses to estimate the start and end of hibernation and convergent cross mapping to identify the causal interactions between the ecological and physiological variables over time. To our knowledge, we have built the first chronology of both ecological and physiological events from before the start to the end of hibernation in the field (Figure 15). Activity, HR, and T_b started to drop slowly several weeks before den entry (Figure 16, Figure 17). Bears entered the den when snow arrived and when T_a reached 0 °C. HRV, taken as a proxy of sympathetic nervous system activity, dropped dramatically once the bear entered the den. This indirectly suggests that denning is tightly coupled to metabolic suppression. During arousal, the unexpected early rise in T_b (two months before den exit) was driven by T_a, but was independent of HRV. The difference between T_b and T_a decreased gradually suggesting that bears were not thermoconforming. HRV increased only three weeks before exit, indicating that late activation of the sympathetic nervous system likely finalized restoration of euthermic metabolism. Interestingly, it was not until T_a reached the presumed lower critical temperature, likely indicating that the bears were seeking thermoneutrality, that they exited the den. We conclude that brown bear hibernation was initiated primarily by environmental cues, but terminated by physiological cues.

Figure 15: Sequence of environmental and physiological events in the entry and exit into hibernation (Evans et al., 2016a).
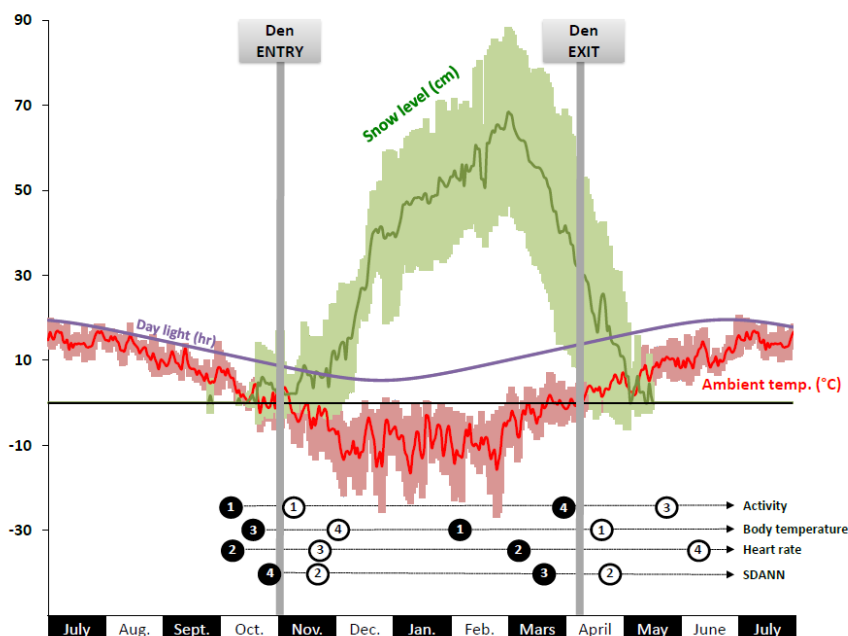
*Figure 16: The relationship between physiological parameters of brown bears in Sweden and the dates of den entry and exit indicated by time zero. The data have been aligned to the date of den entry and exit (blue vertical line) to determine the sequence of physiological changes **a**: body temperature; **b**: Activity; **c**: heart rate; **d**: SDANN, and environmental **e**: Ambient temperature; **f**: Snow levels events. The red lines indicate when the variable began to decrease during den entry and increase during den exit, with the number of days from the entry/exit indicated. This is based on generalized additive mixed models (GAMMs). The gray points indicate the daily average value for each of the 14 individuals (Evans et al., 2016a).*
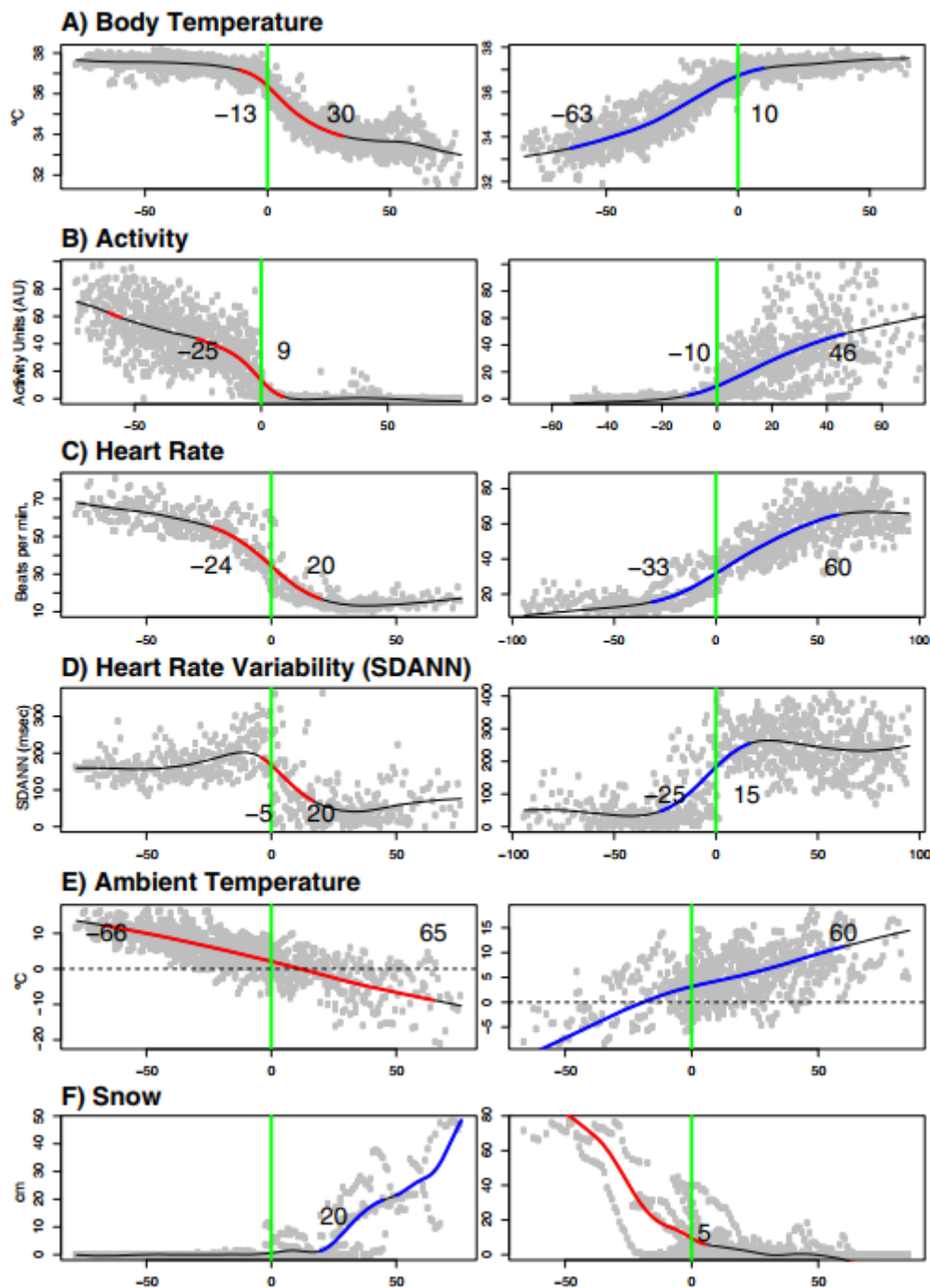
Figure 17: Average of the daily mean values for ambient temperature (a) bear body temperature (b), heart rate (c) and activity level in accelerometry units (d) for 14 individual free-ranging brown bears in central Sweden collected over 3 years. The X-axis indicates the time of year. Green vertical bars indicate the den entry and exit periods. The width of the green bars denotes the range of den entry and exit dates across all individuals. Trend lines were calculated using GAMMs (Evans et al., 2016a).
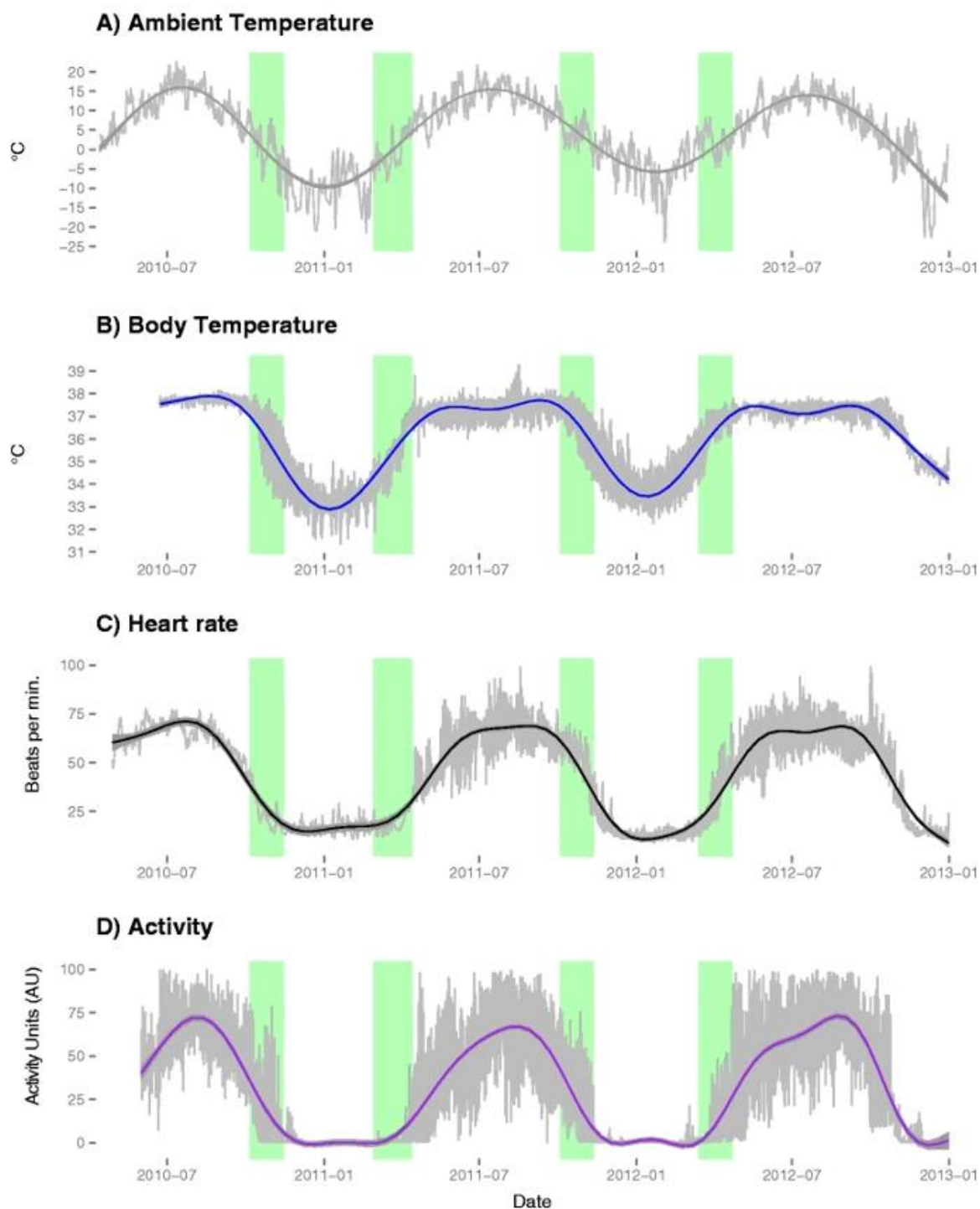
Physiological reactions to capture in hibernating bears (Evans et al., 2016b)

Human disturbance can affect animal life history and even population dynamics. However, the consequences of these disturbances are difficult to measure. This is especially true for hibernating animals, which are highly vulnerable to disturbance, because hibernation is a process of major physiological changes, involving conservation of energy during a resource-depleted time of year. During the winters of 2011–15, we captured 15 subadult brown bears (and recorded their body temperatures (n = 11, Figure18: Plots of body temperature of four of the captured bears in this study. The highlight shows the day of capture (Evans et al 2016b).) and heart rates (n = 10) before, during and after capture using biologgers. We estimated the time for body temperature and heart rate to normalize after the capture event. We then evaluated the effect of the captures on the pattern and depth of hibernation and the day of den emergence by comparing the body temperature of captured bears with that of undisturbed subadult bears (n = 11). Both body temperature and heart rate increased during capture and returned to hibernation levels after 15–20 days (Figure 19). We showed that bears required 2–3 weeks to return to hibernation levels after winter captures, suggesting high metabolic costs during this period. There were also indications that the winter captures resulted in delayed den emergence (Evans et al., 2016b).

Figure18: Plots of body temperature of four of the captured bears in this study. The highlight shows the day of capture (Evans et al 2016b).
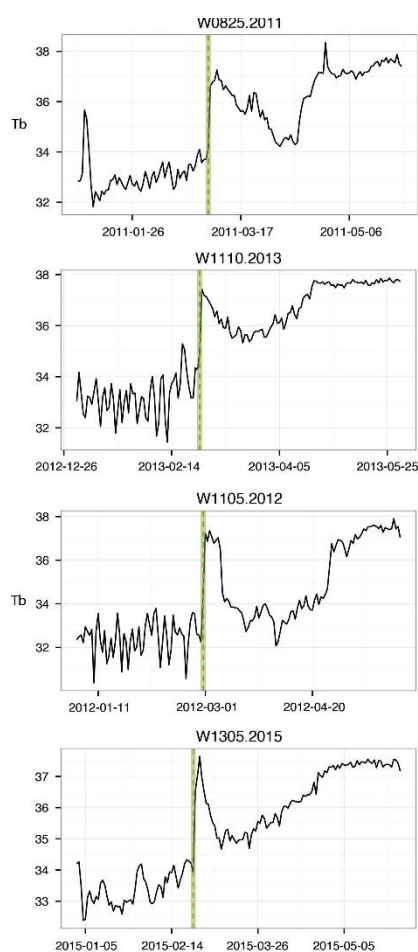
Figure 19: Comparison of physiological variables in captured and undisturbed hibernating brown bears in Sweden. (A) Mean daily body temperature of captured (n = 11) and undisturbed bears (n = 11). (B) Mean daytime heart rates of captured (n = 7) and undisturbed bears (N=11). The continuous lines show the daily means for individual captured bears with standard errors as shaded areas (Evans et al., 2016b).
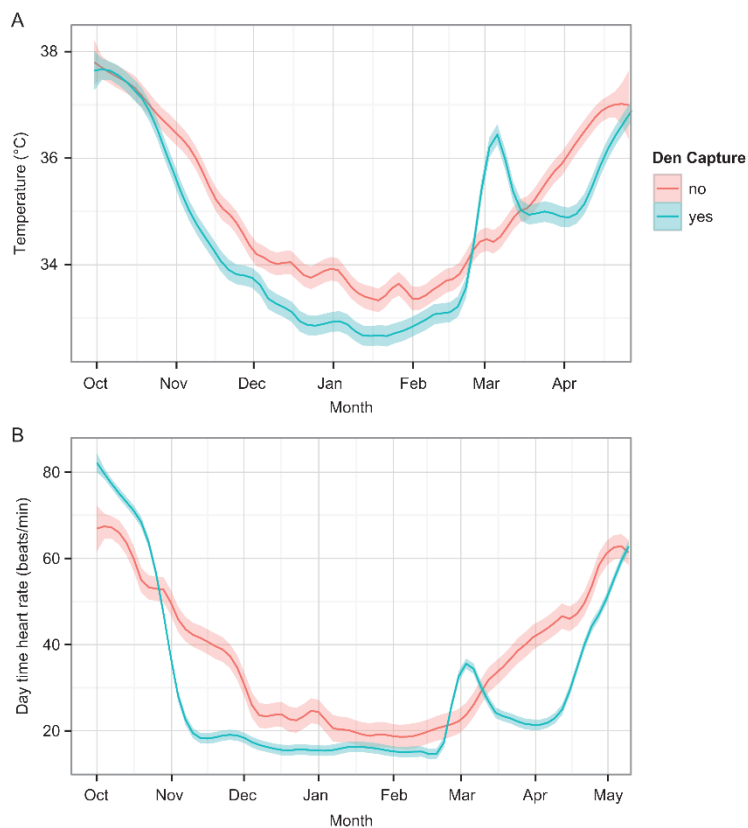
Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears (Friebe et al., 2014)

Knowledge of factors influencing the timing of reproduction is important for animal conservation and management. Brown bears are able to vary the birth date of their cubs in response to their fat stores, but little information is available about the timing of implantation and parturition in free-ranging brown bears. Body temperature and activity of pregnant brown bears is higher during the gestation period than during the rest of hibernation and drops at parturition. We compared mean daily body temperature and activity levels of pregnant and non-pregnant females during preimplantation, gestation, and lactation. Additionally we tested whether age, litter size, primiparity, environmental conditions, and the start of hibernation influence the timing of parturition. The mean date of implantation was 1 December (SD = 12), the mean date of parturition was 26 January (SD = 12), and the mean duration of the gestation period was 56 days (SD = 2). The body temperature of pregnant females was higher during the gestation (>35.9°C) and lactation periods than that of non-pregnant bears (**Error! Reference source not found.**20). Activity recordings were also used to determine the date of parturition. The parturition dates calculated with activity and body temperature data did not differ significantly and were the same in 50% of the females. Older females started hibernation earlier. The start of hibernation was earlier during years with favorable environmental conditions. Dates of parturition were later during years with good environmental conditions which was unexpected. We suggest that free-ranging pregnant brown bears in areas with high levels of human activities at the beginning of the denning period, as in our study area, might prioritize investing energy in early denning than in early parturition during years with favorable environmental conditions, as a strategy to prevent disturbances caused by humans. Six adult female bears became pregnant after instrumentation with temperature loggers. Using the spike in T_b as the primary indicator for the start of pregnancy, the mean date of implantation was 1 December (SD = 12), the mean date of parturition was 26 January (SD = 12), and the mean duration of the gestation period was 56±2 days. The T_b of pregnant bears rose to euthermia for the gestation period and dropped after parturition. We found that parturition could also be detected from activity recordings; however start and length of gestation was less accurate with activity recordings (Friebe et al., 2014)

Figure 20: Body temperature (°C) for pregnant (N=6, colored lines) and the mean body temperature and standard deviation of non-pregnant bears (N=9, black dots; Friebe et al., 2014).
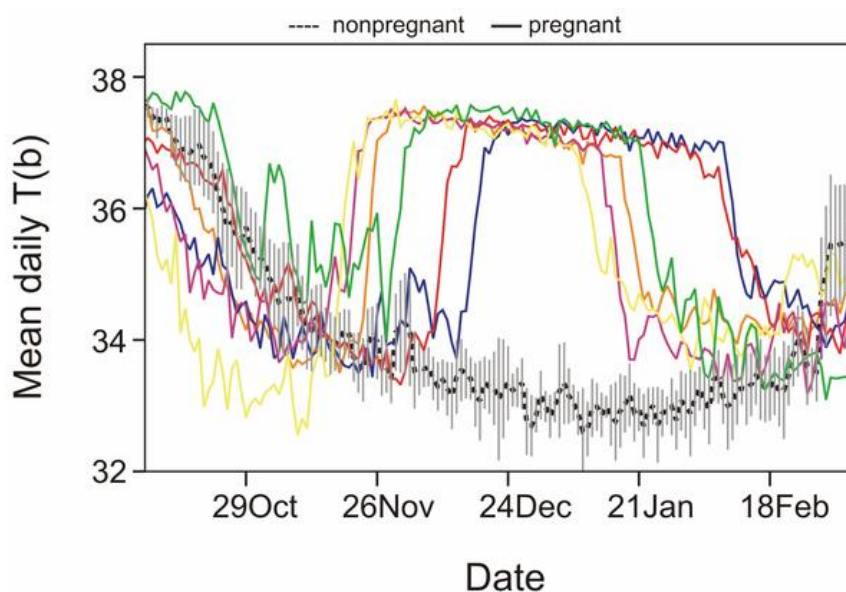
Movement and heart rate (Blanchet et al., 2019)

The link between movement and physiology holds clues to the basic drivers of animal behaviours. In bears, heart rate increases with the metabolic rate during the active phase. Their movement and heart rate change at seasonal and daily scales and can also depend on environmental factors. Their behaviour is, therefore, flexible in activity patterns with high individual variations. The aim of this study was to establish the relationship between heart rate and distance travelled, and test whether this relationship was influenced by environmental (e.g., time of year and time of day) and biological (e.g., reproductive status, sex, body mass and age of the bears) factors. We analysed data of distance travelled and heart rate of 15 GPS-collared brown bears, both males and females, equipped with cardiac loggers in the south of Sweden in 2014–2017. Heart rate increased with distances travelled exceeding 50 m in an hour, but this correlation depended on the day-of-year with higher heart rate in August than in May (Figure 21). Bears accompanied by cubs had lower heart rate than solitary bears especially in May (Figure 21). When movement was minimum (< 50 m in an hour), heart rate was not related to distance travelled and was very variable, regardless of the months (Figure 22). Our findings suggest that heart rate increases with long distances travelled, but varies with day-of-year and reproductive status, depending on the metabolic rate. Studying the change in heart rate in bears can help to evaluate their seasonal rhythms and how different factors affect them. This study illustrates the usefulness of combined bio-logging proxies, i.e., movement and heart rates in our case, in animal ecology (Blanchet et al., 2019).

Figure 21: Scatter plot of day-of-year (x-axis) against heart rate (bpm) (y-axis) grouped by reproductive status (accompanied bears (A, n = 5) in green and solitary bears (S, n = 18) in orange), in brown bears in southcentral Sweden (P < 0.001). The values are re Scatter plot of day-of-year (x-axis) against heart rate (bpm) (y-axis) grouped by reproductive status (accompanied bears (A, n = 5) in green and solitary bears (S, n = 18) in orange), in brown bears in southcentral Sweden (P < 0.001). The values are represented by dots and the lines represent the smoothed regression lines (mean ± se) with degree of smoothing α = 0.4. The grey vertical lines separate the different months: [121–151] for May, [152–181] for June, [182–212] for July and [213–243] for August except in 2016 which is bissextile (shift of 1 day for each month; Blanchet et al., 2019).
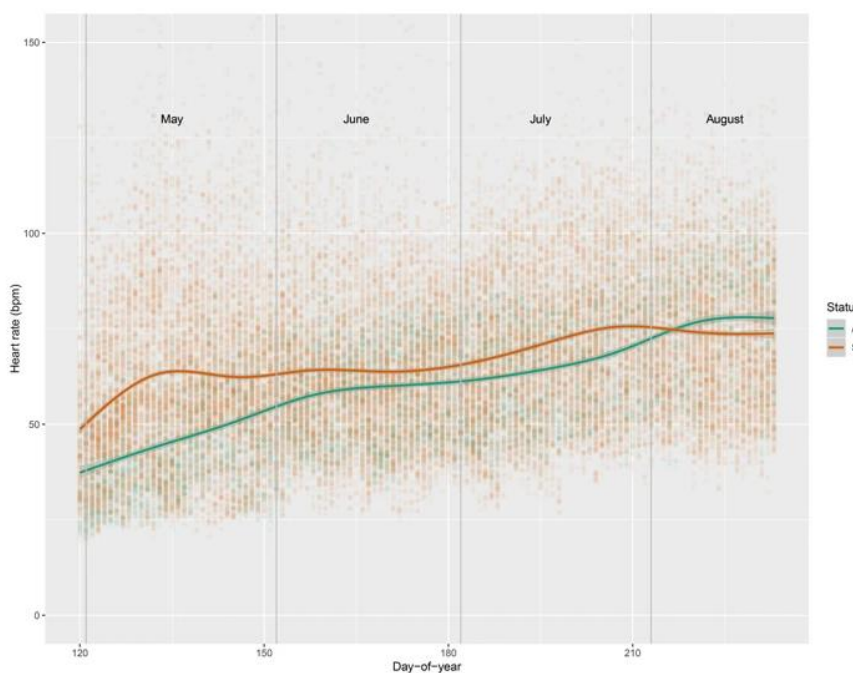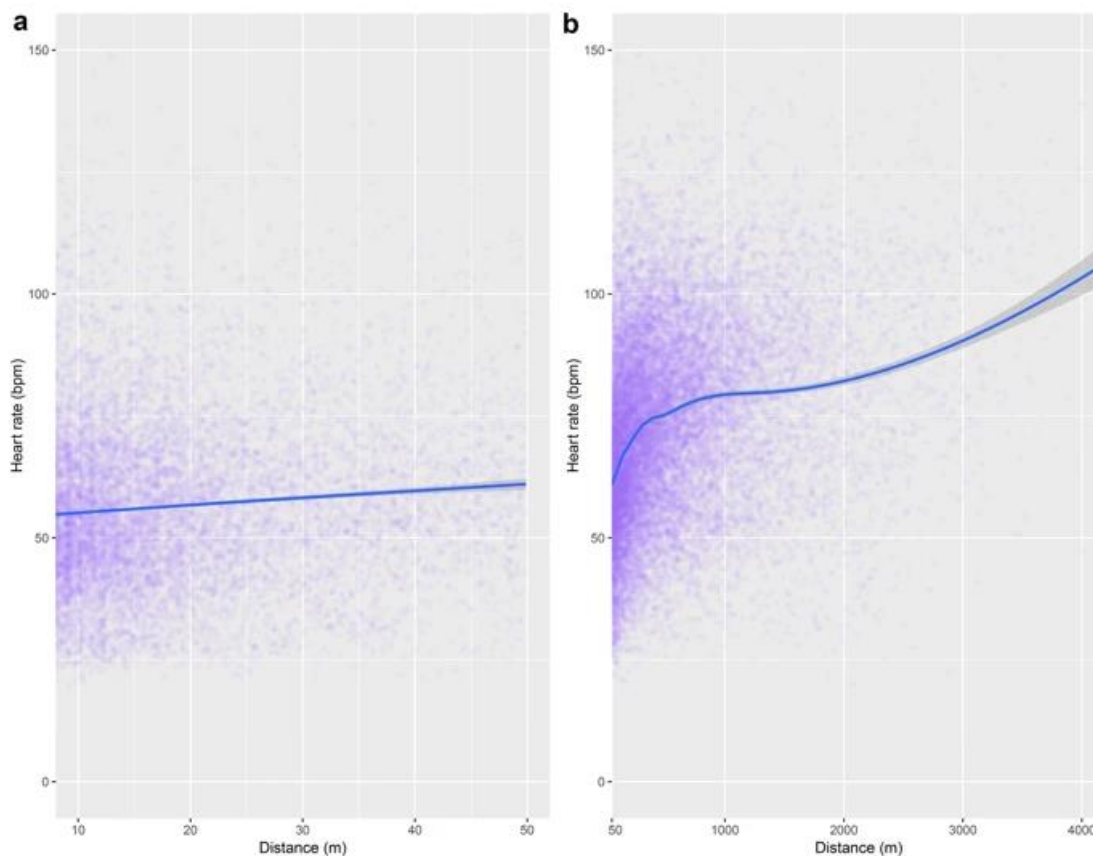
Figure 22: Scatter plots of distance travelled (m) (x-axis) against heart rate (bpm) (y-axis) during a short distances and b long distances in brown bears in southcentral Sweden (n = 15) (P < 0.001). The values are represented by dots and the lines represent the s represent the smoothed regression lines (mean ± se) with degree of smoothing α = 0.4 (Blanchet et al., 2019).

Body mass and hibernation

The amplitude of metabolic rate reduction in hibernators is dependent on body mass. Small hibernators have a body-size adjusted high metabolic rate when euthermic, but make a drastic decrease in core temperature during torpor, which is necessary to reach a very low metabolic rate. Conversely, as a large hibernator, the brown bear shows a moderate decrease in core temperature during hibernation, which is thought to be related to the bear's large size. Interestingly, bears vary considerably in mass, which offers a unique opportunity to study the intraspecific effects of body mass on body temperature during hibernation. Such data are lacking for most mammalian species. We studied body mass, body temperature, heart rate, and accelerometer-derived activity data from 63 free-ranging brown bears (1-15 years old, 15-233 kg, Figure 23). We tested for relationships between body mass and body temperature as well as heart rate in winter and summer, in addition to hibernation duration, and den exit date. The smallest individuals reached lower body temperatures during hibernation, hibernated longer, and exited their dens later than large bears (Figure 24, Figure 25). Unlike body temperature, winter heart rates were not associated with body mass (Figure 24, Figure 25). These relationships were consistent across a range of masses. In summer, the opposite pattern was found, with smaller individuals having higher body temperature and daytime heart rates (Figure 25, Figure 26, and Figure 27). Body mass, even in a large hibernating mammal, is associated with body temperature in the winter hypometabolic state. Smaller bears, which have higher thermal conductance, reached lower body temperatures during hibernation. During summer, smaller bears

had higher body temperatures and daytime heart rates, a phenomenon not previously documented in mammals.

*Figure 23: **Sample sizes for each analysis (body size).** Some brown bears had only body temperature (T_b) or heart rate (HR) logging, and not both, and some were excluded from HR or T_b, due to failure of a specific logger or from one season, due to pregnancy, or in one case, killed by another bear. Some bears from summer were not available in winter, because they were killed during the autumn bear hunt.*
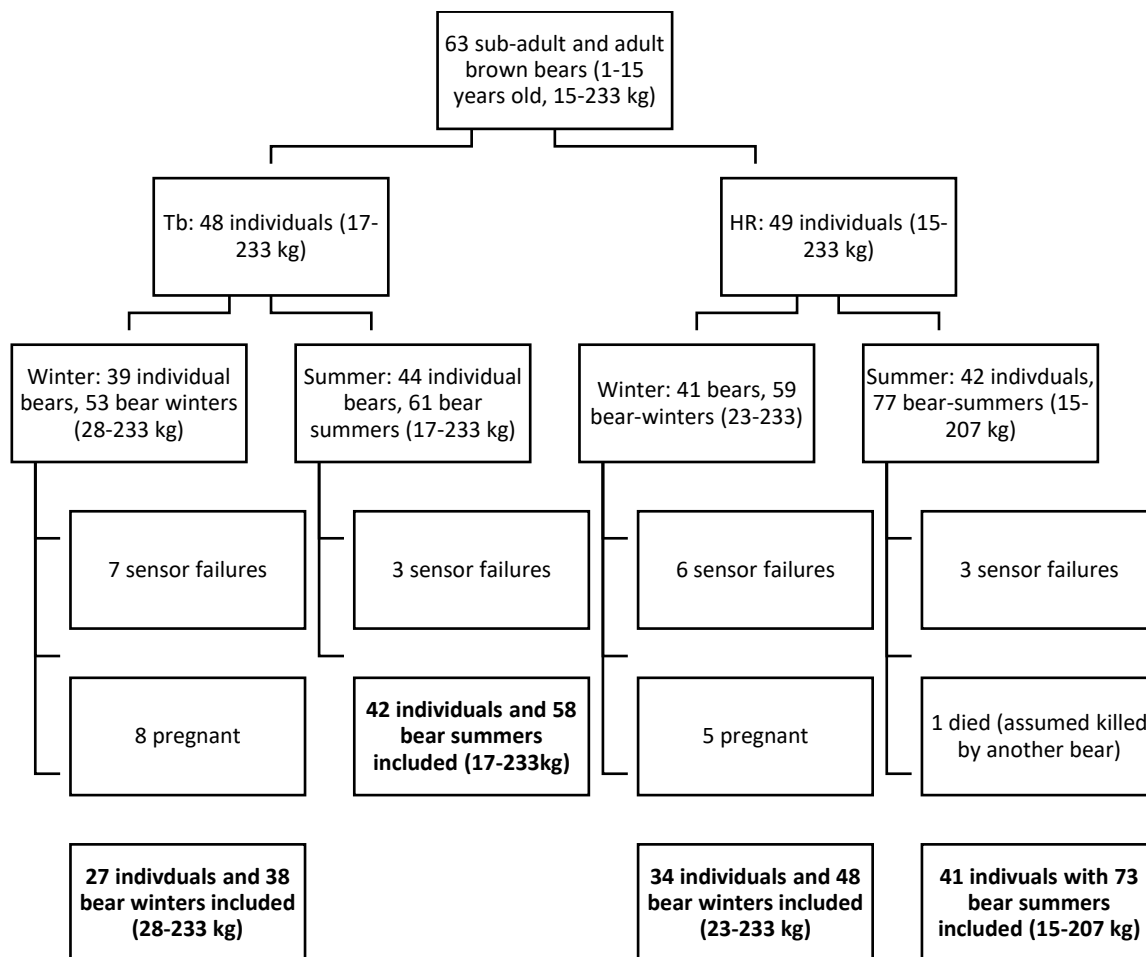
Figure 24: Annual variation in body temperature and heart rate across size groups; a). The analyzed daily mean body temperature data of brown bears in Sweden pooled in to three body mass groups: "Small" (orange) was defined as < 60 kg, "medium" (blues) as 60-120 kg, and "large" (black) as 120-240 kg. To illustrate all phases, the same data is partly shown twice (February to June), b). Mean daytime heart rate for the same size groups.
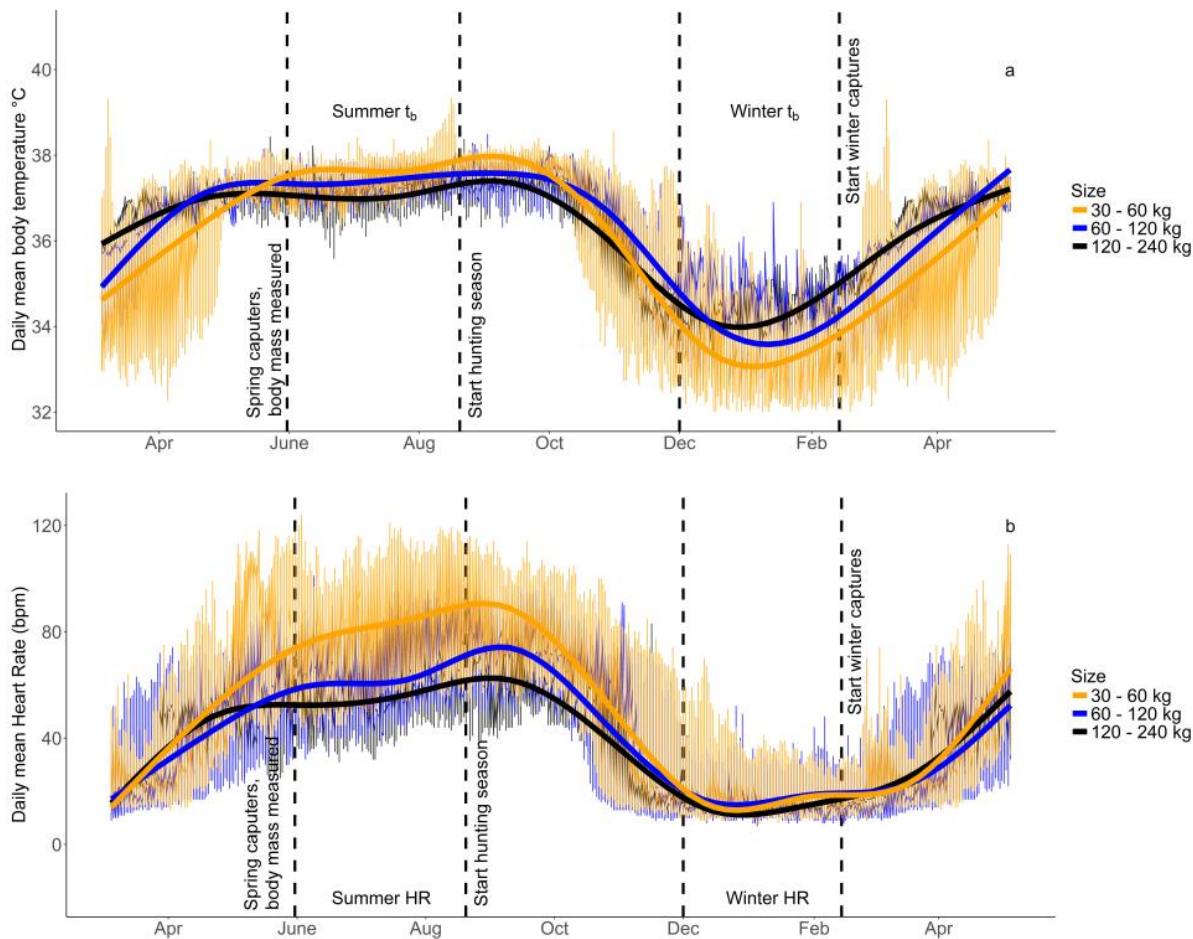

Figure 25: Heart rate and body temperature in winter: Predicted daily mean heart rate (left) and body temperature (right) for hibernating brown bears with body mass of 40 kg (orange solid line), bears with body mass of 120 kg (blue dashed line), and fitted values for each bear winter (gray solid line). Shaded areas display 95% confidence intervals. The data is from 1 December to 23 February.
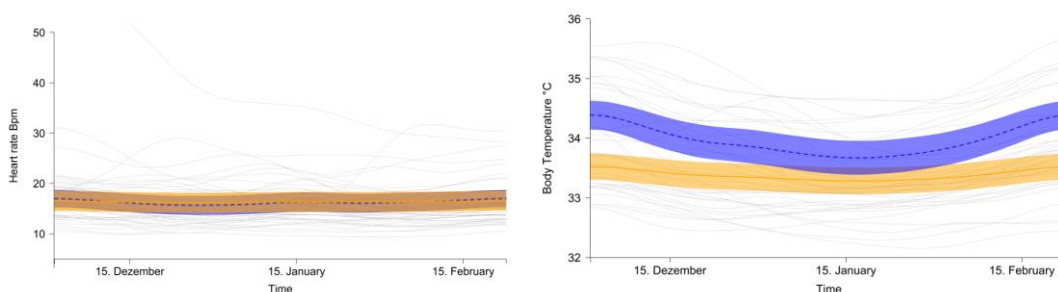
Figure 26: Heart rate during daytime and nighttime in summer. Predicted mean heart rate (HR) for brown bears during summer and during day time (left) and at night (right) with body mass of 40 kg (orange solid line), and bears with body mass of 120 kg (blue dashed line) and fitted values for each bear summer 8 gray solid lines). Shaded areas display 95% confidence intervals. HR data from 1 June to 21 August measured between 10:00 and 22:00 for daytime (left) and 02:00 and 06:00 (right).
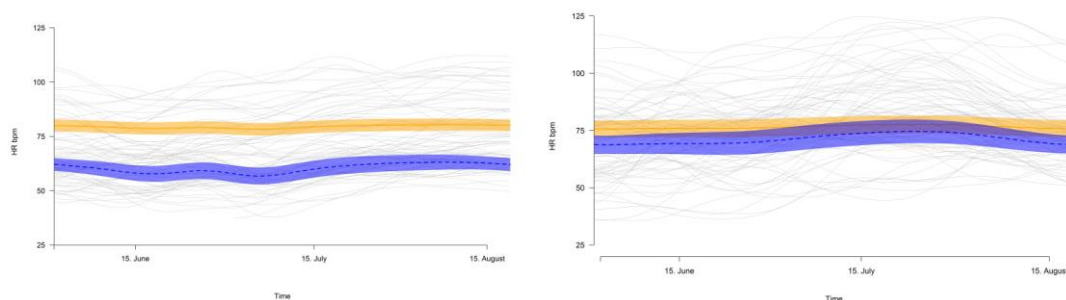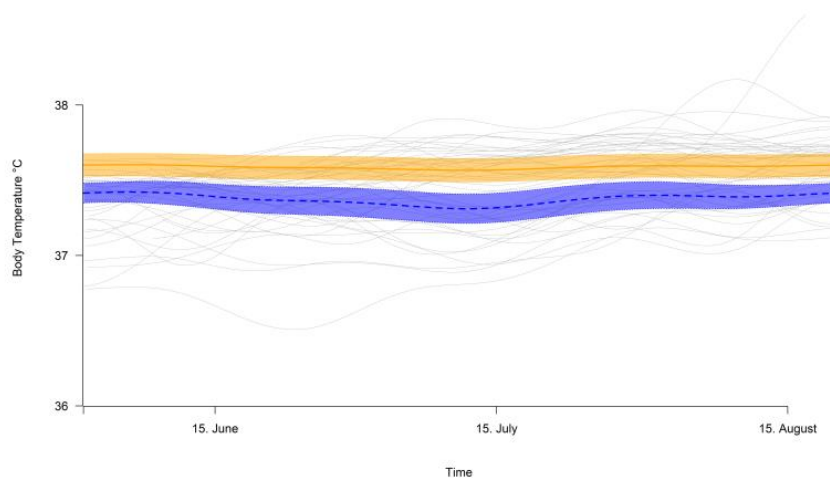

Figure 27: Passive summer body temperature: Predicted daily mean body temperature (T_b) for brown bears during inactivity in summer with body mass of 40 kg (orange solid line), and bears with body mass of 120 kg (blue dashed line) and fitted values for each bear summer (gray solid line). Shaded areas display 95% confidence intervals. T_b data from 1 June to 21 August.


Hyperphagia (Fuchs et al., 2019)

Hyperphagia is a critical part of the yearly cycle of bears when they gain fat reserves before entering hibernation. We used heart rate as a proxy to compare the metabolic rate between the Asian black bear in Japan and the Eurasian brown bear in Sweden from summer into hibernation. In the hyperphagic period, black bears feed on fat- and carbohydrate-rich hard masts whereas brown bears feed on sugar-rich berries. Availability of hard masts has quantitative and spatial annual fluctuations, which might require increased activity and result in intraspecific stress. Using generalized additive mixed models we analysed the differences in heart rate between the two species. Black bears had decreased heart rates during summer but had doubled heart rate values throughout the hyperphagic period compared to brown bears (Figure 28). This illustrates the different physiological consequences

of seasonal differences in food availability in two species of the same genus dealing with the same phenological challenge.

Figure 28: Daily mean heart rate of three Asian black bears (black, open triangles) and four Eurasian brown bears (brown triangles) from June to the end of the year. At time zero bears entered denning period (mean date November 5th). The fitted difference between the species is shown as solid black lines with the 95% c.i. and is considered significant when it did not overlap 0 (red, horizontal solid line).
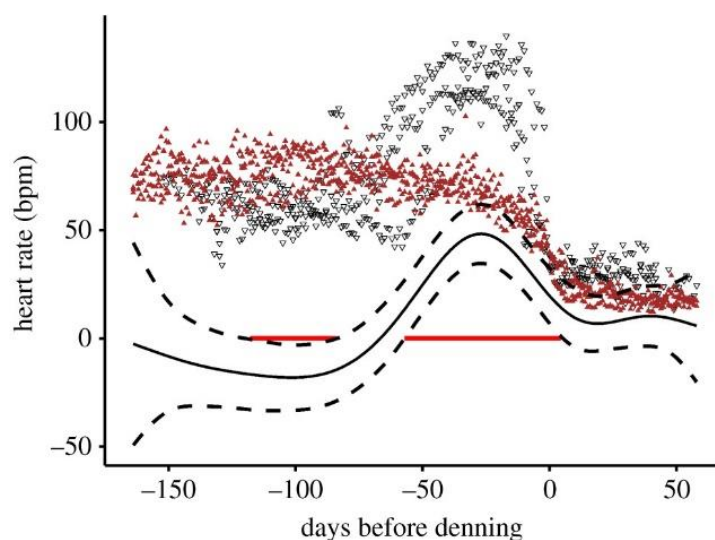
Summary

To our knowledge, we have built the first chronology of both ecological and physiological events from before the start to the end of hibernation in the field, examining the interplay between environmental, behavioural, and physiological time-keeping mechanisms and applying statistical techniques to determine den entry and exit dates and to assess causation between factors.

We further used biologging techniques to describe the pregnancy of the brown bear, including implantation, parturition, and gestation, by comparing body temperature in pregnant and non-pregnant females and determined that activity data can be used to establish parturition date, and to give an estimate for the implantation date based on the gestation length. During years with better environmental conditions, pregnant females began hibernating earlier, but did not implant earlier. During years with poor conditions, there was a shorter period of hibernation before implantation.

We found that the differences in body mass between individual brown bears had a dramatic effect on depth of hibernation, with the smallest bears hibernating at T_b approximately 1.5 C lower than the largest bears. We found consistent relationships between body size and T_b during December-March (with smallest bears coldest) and from July-September (with smallest bears warmest). During the other months, there was overlap between the groups, as they transitioned between these two patterns. During summer, heart rate increases with long distances travelled, but varies with day-of-year and reproductive status, depending on the metabolic rate. During autumn, we compared brown bears to Asiatic black bears, which had decreased heart rates during summer but had doubled heart rate values throughout the hyperphagic period compared to brown bears.

5.3. Beavers

In Norway, beavers *(Castor fiber)* are hunted from 1 October to 30 April and the hunting season might be extended to 15 May in areas with late ice cover on rivers and lakes. This late hunting season raised concerns that it potentially overlaps with parturition and that reproducing females are shot from their new-born offspring. Body temperature (T_b) can be an exact proxy for parturition. In a report to the Norwegian environmental agency, Mayer et al. (2017) provided a detailed analysis on parturition dates in beavers with the contribution of T_b data, concluding that beavers give birth after the hunting season.

Beavers, especially in areas with long ice cover, are trapped in their lodge with access only to the waterbody below the ice. In this situation they could pose an interesting case for hypometabolism. In addition to T_b, we also measured heart rate (HR) and extended the study area from around Bø in Telemark, with mostly ice-free beaver home ranges, to Stor-Elvdal where ice hinders the beaver's access to land for up to 5 months.

An unexpected challenge was the beaver's ability to expel both subcutaneous and abdominal biologgers. In 36 beavers, we implanted temperature loggers into the abdominal cavity. Of 22 recaptured beavers, nine (41%) beavers had lost the abdominal temperature logger after two years and for seven of those we confirmed the loss by x-ray one year later. In five loggers, no measurements were taken, the measurements were not realistic or the memory could not be accessed upon retrieval. Additionally, two temperature loggers failed after ca. four months of measurements. Similar problems were encountered with the HR loggers: Of 14 recaptured beavers, nine (64%) beavers had lost the HR logger within three years. Only three (21%) beavers kept the HR logger for more than one year, one of them with poor data quality. In total, 18 HR loggers were initially implanted subcutaneously in beavers that also carried a temperature logger. Due to the loss of loggers, we have not been able to compare the two study areas.

Figure 29: Box plot for each month of the body temperature from five female and three male beavers combined.
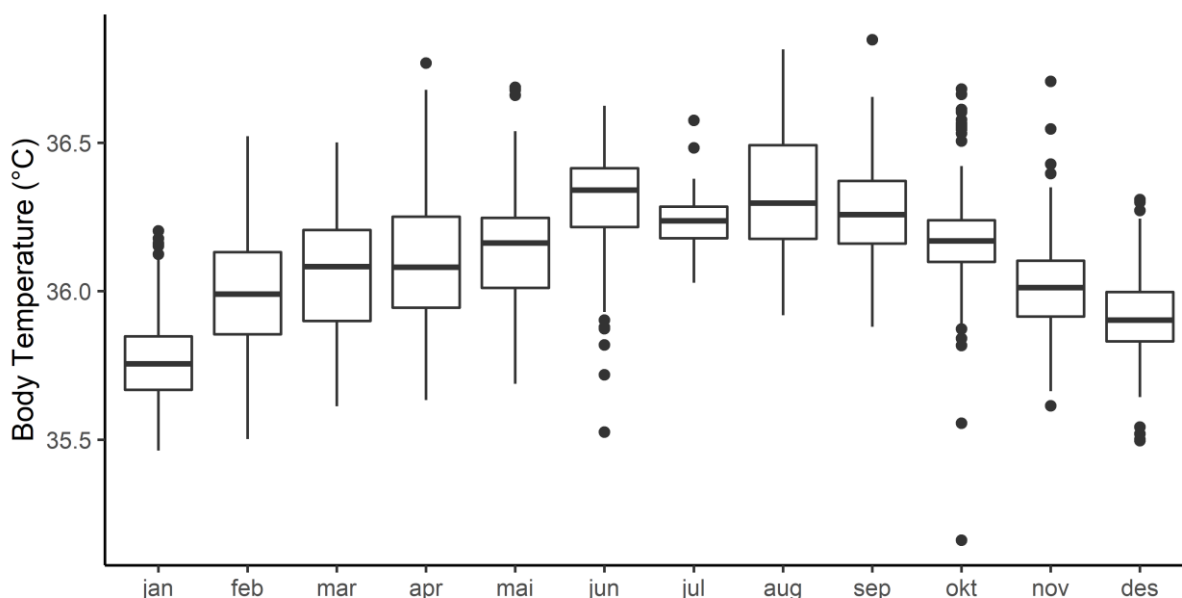
The retrieved data has not yet been analysed in detail. Descriptive analyses reveal a seasonal pattern with a lower daily mean T_b in winter than in summer (Figure 29).

The mean (SD) T_b (males and females combined) was 35.8 (0.15) °C in January and 36.3 (0.20) °C in June, August and September. Heart rate data from the two successful loggers indicate a similar pattern, with lower HR in winter compared to summer. The mean (SD) nightly HR (22:00 to 04:00 GMT) in January was 78 (10) beats per minute (bpm) and 101 (5) bpm in June and July (Figure 30). Based on the available data, we found sexual difference in the seasonal T_b patterns, particularly in late winter and spring. Females have a wigglier curve than males, with high individual differences (Figure 30). The cycling T_b pattern in female beavers is likely influenced by gestation and parturition and the high individual differences suggests individual variation in parturition date.

Figure 30: Mean heart rate during night (22:00 to 04:00 GMT) in a male (orange triangles, dashed line) and a female (yellow points and solid line) beaver.
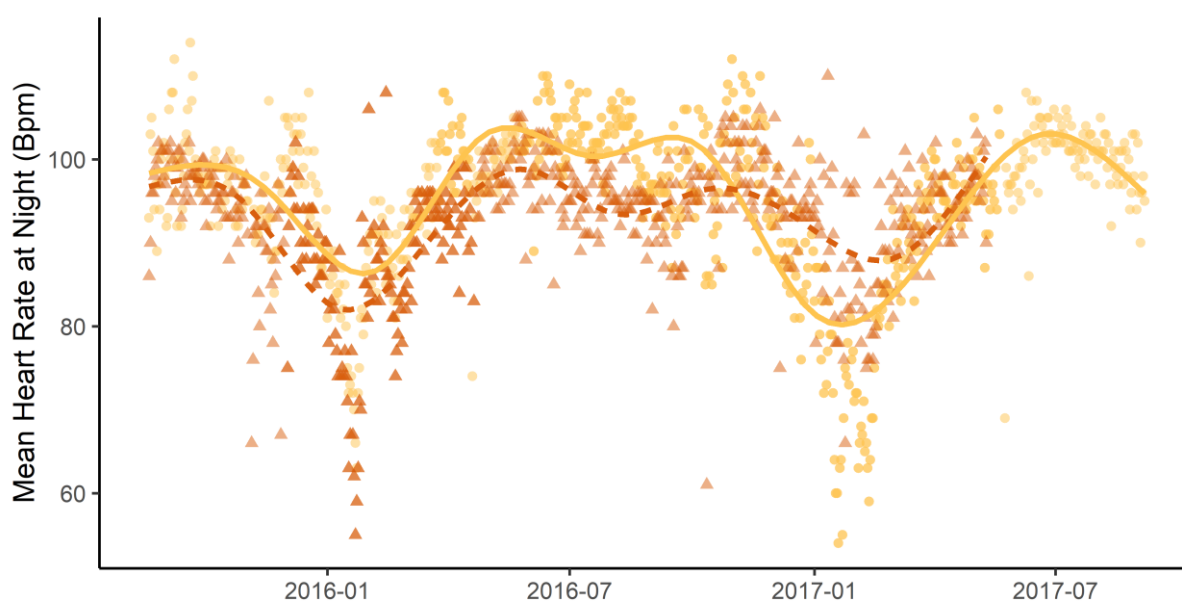
5.4. Wolverines

Summary of Thiel et al. (2019). Mammals in the far north are exposed to extreme seasonal changes in environmental conditions, such as temperature and photoperiod, which have notable effects on animal physiology and behaviour. The wolverine (*Gulo gulo*) is a carnivore with a circumpolar distribution and well-adapted to extreme environmental conditions. Still, ecophysiological studies on free-ranging wolverines are lacking. In this study, we used abdominally implanted body temperature loggers in combination with GPS collars with acceleration sensors on 14 free-ranging wolverines (Figure 31) in northern Sweden to study daily and seasonal variation in body temperature and activity patterns.

We used generalized additive mixed modelling to investigate body temperature patterns over time and Lomb-Scargle periodogram analysis to analyze circadian rhythms. We found that wolverines have an average core body temperature of 38.5 ± 0.2 °C with a daily variation of up to 6°C. Body temperature patterns varied between reproductive states. Pregnant females showed a distinct decrease in body temperature during gestation (Figure 32).

Wolverines were active during both day and night, but displayed distinct activity peaks during crepuscular hours. However, body temperature and activity patterns changed seasonally, with a gradual change from a unimodal pattern in winter with concentrated activity during the short period of day light to a bimodal pattern in autumn with activity peaks around dusk and dawn. Wolverines were less likely to display 24-h rhythms in winter, when hours of day light are limited. The combination of different biologging techniques gave novel insight into the ecophysiology, activity patterns and reproductive biology of free-ranging wolverines, adding important knowledge to our understanding of animals adapted to cold environments at northern latitudes.

Figure 31: Scientific illustration of a wolverine equipped with body temperature logger, surgically implanted in the abdomen, and a GPS collar. Illustration by Juliana Spahr, SciVisuals.com.

Figure 32: Daily averaged (a) body temperature (T$_b$, [°C]) and (b) activity of each individual wolverine (grey line) and all individuals together (pregnant individuals: black dots, non-pregnant individuals: hollow circles) and daily averaged ambient temperature from 2011 to 2014 [°C] (black lines) and day length [hours] (orange line)
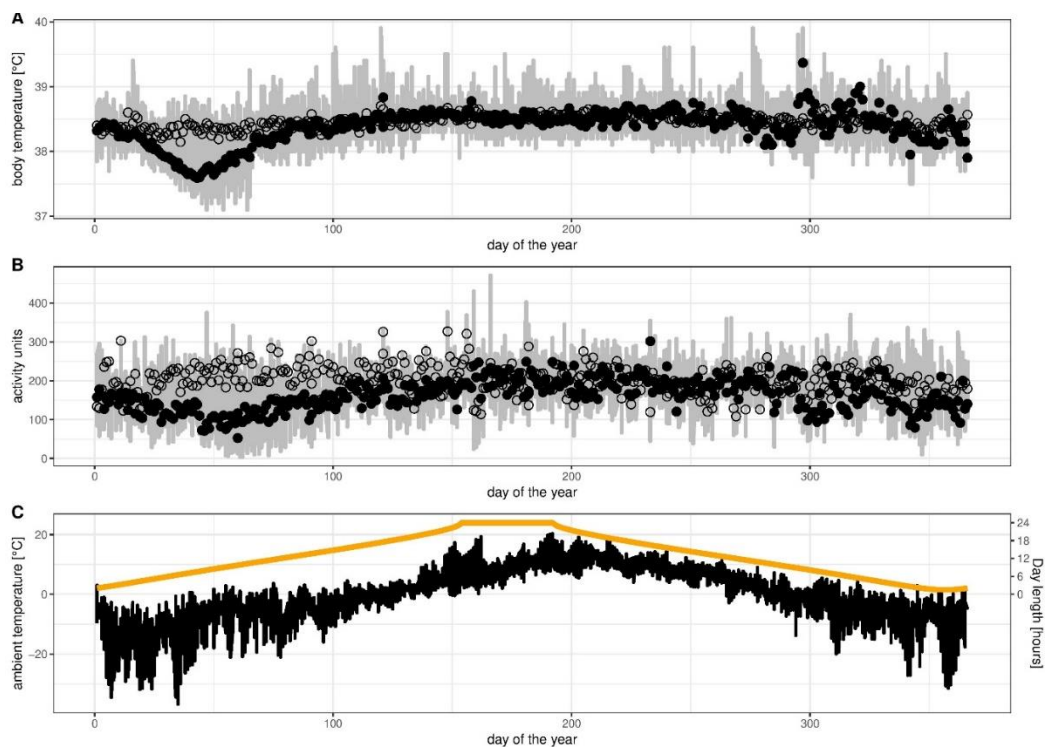
6. Learning outcomes of studies with biologgers

Our results highlighted the relevance of using biologgers in wildlife in their natural setting to understand animal responses to human activity in anthropogenic landscapes. A stress response might not be necessarily visible in the behaviour. After having performed several studies with biologgers on wildlife, we want to emphasize that pilot studies are crucial in order to adjust materials and methods applied to a given species and system.

Besides the general scientific interest, the quantification of stress has increasing practical and economic implications for wildlife such as deer species in human-modified landscapes. It is therefore important to apply methods for evaluation of disturbance and stress conditions that are relevant to free-ranging large-bodied animals like deer species and to test their usefulness in different contexts.

In order to assess and quantify stress and behavioural responses due to both natural and anthropengic disturbances and challenges, reference ("normal") ranges for physiological variables need to be established. For most wildlife species, such values do not exist. At best, data have been collected from captive animals that may not be representative for free-living individuals or information is only available from studies carried out in completely different environmental conditions.

We encountered many different challenges with biologgers that did not work properly because they are not designed for each animal species individually – some are even designed for use in humans. Some species were more prone to lose the loggers, e.g. beavers. The Reveal XT worked fine in bears, but when we applied the same algorithm used for detection for R peaks in the ECG in moose, it did not work properly. Sometimes it did not detect the heart beat and sometimes the heart beat was double counted. Therefore, calibration is important when applying a logger on a new species to ensure that the results are reliable. Therefore, we highly recommend validation studies in captivity before carrying out experiments in the field.

We also experienced that a high sample size is needed to get as reliable results as possible. This is especially needed in studies where the data comes from more than one biologger, like the hunting approach studies in moose and bears.

As in other wildlife studies, a general limitation is the lack of a control group, i.e. animals that are not 'treated' (e.g. captured, tagged and handled). This is especially evident for assessment of possible long-term effects.

7. Conclusion

Our main goal in this project was to test the suitability of certain biologgers in order to study movement and physiology for the application of questions relevant to wildlife management. We conclude that future studies should be carried out in a step-wise manner: 1) Testing and validation of the biologgers on captive animals in a controlled environment; 2) Establishing reference ranges for physiological variables in free-living animals in their natural environment: 3) Instrumenting enough animals to enable statistical interpretation of the results from experimental studies; 4) Establishing control groups to enable both assessment of potential side-effects of instrumentation and possible long-term effects of environmental challenges.

8. Acknowledgements

9. Publications from the project

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Et nøkkelspørsmål innen økologi er hvordan menneskelig aktivitet påvirker atferd og fysiologi hos viltlevende dyr. Utvikling av biologgere har muliggjort studier av ville dyr i deres naturlige miljø. Biologgere er sensorer som festes til dyret og som registrerer data om fysiologi, atferd, bevegelser og miljø. Ved å kombinere ulike biologgere, kan man øke kunnskapen og forståelsen av biologi, økologi og fysiologi hos viltlevende dyr og hvordan de tilpasser seg omgivelsene.

Fra 2010 har vi brukt biologgere i flere studier på ulike viltarter, inkludert bever (*Castor fiber*), brunbjørn (*Ursus arctos*), elg (*Alces alces*) og jerv (*Gulo gulo*). Vi har anvendt biologgere både i basal og anvendt forskning, inkludert å etablere normalverdier for kroppstemperatur, hjerte- frekvens, bevegelser og aktivitet, avdekke sesongmessige variasjoner i disse parameterne og studere hvilken effekt menneskelig aktivitet har på dyrenes fysiologi og atferd.

Hovedfokus i denne rapporten var å vurdere hvordan jakt og andre menneskelige forstyrrelser påvirker fysiologi og atferd hos elg. Elgene ble instrumentert med GPS-halsbånd og biologgere for å registrere bevegelser, aktivitet, hjertefrekvens og/eller kroppstemperatur. Vi studerte effekten av eksperimentelle og reelle jaktsituasjoner med løshund, hvordan elgene reagerte på en skiløper, en person med hund i bånd, en person som sjekket kalvingsstatus og bedøvelse fra helikopter.

Vi fant at vellykkete eksperimentelle jaktsituasjoner med løshund (avstand elg-hund mindre enn 240 meter i mer enn 10 minutter) resulterte i høyere maksimal kroppstemperatur (0,88 °C høyere) og en gjennomsnittlig økning i hjertefrekvens på 24 slag per minutt sammenlignet med dagen etter jaktsituasjonen. Elgene hvilte i gjennomsnitt mer enn 90 minutter lengre dagen etter jakten. Resultatene viser at jakt med løshund øker individets energiforbruk og hviletid (og reduserer dermed også tilgjengelig tid for beiting). Helikopterfangst resulterte også i økt kroppstemperatur samme dag, mens det ikke ble registrert noen økning i kroppstemperaturen når elgen ble forstyrret av en skiløper. Vi fant at elgen beveget seg raskere og lenger den dagen de ble bedøvet fra helikopter og etter forstyrrelser av løshund og skiløper, sammen- lignet med dagen etter. Noe av denne forskjellen skyldes økt hviletid dagen etter forstyrrelsen.