Norwegian University
of Life Sciences

Master's Thesis 2018   60 ECTS
Faculty of Environmental Sciences and Natural Resource Management
Dr. Ole-Gunnar Støen

The Behavioural and Physiological Response of Scandinavian Brown Bears to Dog Hunts and Human Encounters

Luc Le Grand
Master of Science in Ecology

Acknowledgments:

Thank you, Ole-Gunnar, for having me as a master's student and for allowing me to join the incredible Scandinavian Brown Bear Research Project (SBBRP). I am grateful for all the opportunities you gave me, for your trust and for your support throughout my master's degree. In our first email exchange, you proposed that I could scare bears to see how their heart rate reacted. You wrote "It can seem crazy and dangerous, but it is not." You were right to say it was not dangerous, but my whole adventure in Scandinavia has certainly been unbelievable!

My field work in Sweden was amazing and the people I had the chance to meet there made it even better. I would especially like to thank Alex, Andrea, Anne, Bastien, David, Elke, Essi, Gro, Gunther, Jack, Marte, Rasmus, Sven and Walter for all the great times we spent together in Tackåsen. The SBBRP gave me the opportunity to meet many other wonderful people that I also want to thank: Alina, Amanda, Andreas, Andrès, Boris, Hanna, Jon A., Jon S., Matej, Neri and Sam. The data used for my thesis was collected with the help of numerous volunteers, students, hunters and employees of the SBBRP. I would like to thank them all, as without this team effort this study would not have been possible.

An important thank you goes to Solve for his precious advice in statistics. I also want to thank Stig for his valuable IT advice and help. When my computer was not able to cope with my scripts, he built the computer that made my data processing possible. Many thanks to Juliana (J.) for allowing me to discover the world of scientific illustration and for the wonderful artwork she created for my thesis. I would like to thank Alex, Alina, Amanda, Boris, David, Jon A. and Sven once more for allowing me to join the captures. I have learnt a lot about physiology and biologgers during my thesis and your support helping me understand my data has been invaluable, especially when I had impossible values. Furthermore, you introduced me to a field of science that I find truly fascinating and that I hope to learn more about. Thank you, Alastair, Anne, Neri, Ole-Gunnar and Tali for proofreading my thesis and for all of your constructive comments.

I would like to express my deep gratitude to Dr. Anita Studer and the NORDESTA Reforestation & Education association she presides for their financial help throughout my master's course and for their general kindness.

There are many other people that have been important during my degree. I would like to thank the great class mates I had as well as Bastien, Einar, Essi, Jonas, Line, Matej and Sebastian for the amazing flatmates they have been. I extend my thanks to Einar, Jonas and Line for explaining how Norwegian culture works and for all the recipes we shared. A big thank you goes to Candice, Jonas and Silvia for being incredible friends and for all that we shared together. I also want to thank my family and friends from abroad for their support and for keeping in touch, my parents and Alastair, Geneviève, Martyna, Mehdi, Soline, Stacy and Sven, for coming to visit.

Finally, I would like to thank my partner Tali for joining me on this adventure, for her support and precious help throughout my entire master's and for being such a wonderful person.

Faculty of Environmental Sciences and Natural Resource Management
Norwegian University of Life Sciences
Ås 14th May 2018

Luc Le Grand

Abstract:

In Sweden, legal hunting is the primary cause of mortality in brown bears. The most common hunting method is based on the use of trained hunting dogs being let loose on the bears. The bear is then shot by hunters following their dogs. The popularity of bear hunting, the hunting quotas for bears, the use of dogs during the hunts and the number of hunters specialized in bear hunting is rising in Scandinavia. In addition to legally killed bears, the number of disturbed bears, i.e. when the bear is hunted and escapes, will thus increase. Bears also flee when encountering humans; events that are increasing in frequency with the current growth in human and bear populations.

To better understand the impact of human outdoor activities on bears, the behavioural and physiological responses of brown bears to hunts using dogs and human encounters were assessed using cardiac biologgers, body temperature biologgers, GPS and dual-axis activity data from 85 simulated hunts (a simulated real hunt on the bear using dogs with the bear allowed to flee at the end) and 96 human encounters (humans intentionally approaching the bear) on 46 GPS-collared brown bears in two study areas in Sweden.

The results showed that (1) Bears travelled longer distances, ran faster, had higher heart rates and body temperatures during the day of a simulated hunt compared to the day of a human encounter or a control period (3 previous days) without a known disturbance event. (2) Bears also travelled longer distances and ran faster during the day of a human encounter compared to the control period but did not show higher heart rates and higher body temperatures. (3) The amount of time bears rested after a simulated hunt increased linearly with the duration of the simulated hunts, implying a lasting behavioural impact relative to the intensity of the disturbance. (4) Heart rate variability rose during both human encounters and simulated hunts, and returned to the previous level two days later, suggesting lasting physiological change following these types of disturbance. (5) The travelled distances, speeds, heart rates and body temperatures of the bears used as energy consumption indexes indicated that both types of disturbance represent an increased energy use for brown bears, and that hunts using dogs induce greater energy use.

If experienced frequently, and the bears are unable to compensate for the energy use, human encounters and hunts using dogs could alter the body condition of the bears before denning. Adult female brown bears give birth during the winter at their den and their body condition is important for their reproductive success. Human encounters and hunts using dogs may thus lead to declines in the bears’ fitness and should be taken into account for the management of the species.

Table of Contents:

Introduction:

In Europe, brown bears (*Ursus arctos*) have suffered from previous extermination policies but are recovering from their near extirpation (Chapron et al. 2014). Thanks to a change in policies and favourable management, Scandinavian brown bears have recovered from a population bottleneck of about 130 individuals in 1930 (Swenson et al. 1995) to a population estimated at 2782 individuals in 2013 in Sweden (Kindberg & Swenson 2014). The carrying capacity of Sweden could allow for a larger population but is limited by policy goals that are driven by the public's attitude toward bears (Eriksson et al. 2015).

In Sweden, legal hunting is the primary cause of mortality in brown bears (Swenson et al. 2017). The most common hunting method is based on the use of trained hunting dogs (*Canis lupus familiaris*) that are let loose on the bears (hereafter dog hunts) (Bischof et al. 2008). The bear is then shot by the hunters who follow their dogs. Vaughan and Inman (2002) measured a 20 % harvesting success on chased black bears (*Ursus americanus*) in Virginia (USA). This means that for each bear that is shot, multiple bears may be chased but not killed. In Sweden, dog hunting is also practiced on other species such as the moose (*Alces alces*). As hunting dogs may chase species that are not specifically targeted by the hunters, moose-oriented hunters are able to hunt bears when their dogs follow one (Bischof et al. 2008). In other words, bear hunters are not the only hunters using dogs that may disturb bears. The popularity of bear hunting, the hunting quotas for bears, the use of dogs and the number of hunters specialized in bear hunting are rising in Scandinavia (Swenson et al. 2017). In addition to legally killed bears, the number of bears escaping a dog hunt will thus increase. Fredman et al. (2012) indicate that 70 to 80 % of the Swedish human population hike in the forest at least once in the year and that this ratio has not changed since the late '70s. Given that the Swedish human population (Statistics Sweden 2018) and the bear population (Swenson et al. 2017) are increasing, the interactions between bears and humans will most likely increase. It is therefore important to understand the impacts of human encounters and dog hunts on brown bears.

Bear hunting has known impacts beyond the initial offtake of direct mortality, such as altering life history traits (Bischof et al. 2017; Frank et al. 2017) or inducing an increase in sexually-selected infanticide through an increased male turnover (Gosselin et al. 2017; Swenson et al. 1997). Adult bears that would face naturally low mortality rates (Bischof et al. 2009; Bischof et al. 2017) adopt antipredator behaviours in response to human hunting pressure (Ordiz et al. 2013a). For example, when the hunting season starts, they decrease their foraging activity during the time of the day that has the highest risk of being shot (Hertel et al. 2016) and alter their circadian rhythm, favouring a more cryptic behaviour (Ordiz et al. 2012). Bateson and Bradshaw (1997) studied the impact of dog hunts on red deer (*Cervus elaphus*) and found that deer showed signs of muscle damage, low blood sugar, as well as high cortisol and endorphin concentrations. This indicated that the chase led to important psychological and physiological stress. Dog hunting has been criticised and apart from a part of Alaska, it is now illegal to carry out dog hunts on brown bears in North America (Miller et al. 2013). However, some parts of the USA and Canada still allow dog hunts on black bears (Hristienko & McDonald 2007; Treves et al. 2010). Another taboo is the use of Global Positioning System (GPS) technologies and other recent equipment advances whilst hunting (Von Essen 2018). The authors report that 1/3 of Swedish hunters distanced themselves from these technologies.

Hunting is not the only human outdoor activity that affects bears in Scandinavia. Ordiz et al. (2014) found that bears adopt movement patterns that are more nocturnal and less diurnal, a behaviour associated to a cryptical adaptation, in areas with higher road densities. Bears flee from encounters with humans that are on foot (Moen et al. 2012) and change their movement pattern for a minimum of 2 days after such events (Ordiz et al. 2013b). Bears also flee when encountering humans that have a dog on a leash (Hansen 2014). When denning, bears were found to avoid intermediate-sized roads that are associated with a potential source of human disturbance (Elfström et al. 2008) and when close to human infrastructures, to select for more concealed denning sites (Sahlén et al. 2011). All these studies confirm a general antipredator behaviour by the Scandinavian brown bear towards humans. A behaviour that is not only affected by hunting activities, but also by the year-round presence of humans.

When measuring the antipredator behaviour adopted by bears during the hunting season, Hertel et al. (2016) showed that bears forage less efficiently and in areas with poorer berry quality during the morning hours when hunting pressure is at its highest. The authors did not find similar effects in the afternoon when the hunting pressure decreases and interpret this as a proof that bears adopt an antipredator behaviour that has an important foraging cost. When measuring the alteration in the bears circadian rhythms, Ordiz et al. (2012) assumed a lower efficiency in foraging when bears foraged more during the night and, most likely, needed to see to search for food (MacHutchon et al. 1998). Hertel et al. (2016) and Ordiz et al. (2012) therefore suggest that this antipredator behaviour may have an energy cost. Rode et al. (2007) also showed that the presence of non-hunting humans could affect the distance travelled by bears and thus represent energy costs.

Ordiz et al. (2012) and Hertel et al. (2016) suggested that such energy costs could lead to a lower fitness if it prevents adult females from reaching an optimal body condition. Indeed, adult females give birth during the denning period and depend on their fat reserves for the gestation and lactation of their cubs (Lopez-Alfaro et al. 2013; Robbins et al. 2012). Robbins et al. (2012) observed that no captive adult female brown bears that had a body fat content lower than 20 % gave birth in their study even if they were observed mating. Lopez-Alfaro et al. (2013), using an energy consumption model describing the brown bears, estimated that with a body fat content below 19 % a female would not be able to reproduce during a hibernation period that lasts over 120 days. Maternal weight is affected by bilberry (*Vaccinium spp.*) abundance in Sweden (Hertel et al. 2018), with good bilberry years leading to heavier females and heavier yearlings. Hertel et al. (2018) also showed that poor bilberry years affected the reproductive success of the lightweight females. In addition, Zedrosser et al. (2013) showed that heavier yearling females subsequently had a better reproductive success and fitness throughout their lifetime.

To further understand the influence of human outdoor activities on brown bears the following hypotheses were explored: [H1] Dog hunts and human encounters are a source of physiological and behavioural disturbance for brown bears. [H2] The physiological and behavioural impacts of a dog hunt on brown bears are greater than the impact of a human encounter. [H3] Dog hunts that last longer in time have larger physiological and behavioural impacts on brown bears. [H4] Dog hunts and human encounters have lasting physiological and behavioural effects on brown bears. To test these hypotheses, the distance travelled by bears, their maximum speed, their maximum heart rate, their body temperature, their heart rate variability (HRV) and their resting behaviour were measured during a control period (over the three days prior to the experiment), during the day of the experiment and the two days after human encounters and experimental hunts using dogs (hereafter simulated hunts). The predictions are summarised and related to their corresponding hypothesis in Table 1.

Rode et al. (2007) used the daily distance travelled by brown bears to evaluate the impact of experimentally introduced tourists and considered it as an energy cost index. The authors associated longer travelled distances with higher energy costs and therefore a sign of disturbance. Following the same reasoning as Rode et al. (2007), bears were predicted to travel longer distances during the day of a human encounter or a simulated hunt than during the control period [P1 if H1 is correct]; to travel longer distances during the day of a simulated hunt than during the day of a human encounter [P2 if H2 is correct]; and to travel longer distances during the day of a simulated hunt if the simulated hunt lasts longer [P3 if H3 is correct].

Running faster has an energy cost (Taylor et al. 1982). The speed of the bear can thus be used as an indication of a disturbance and as an index for its cost. Bears were therefore predicted to have a higher maximum speed during the day of a human encounter or a simulated hunt than during the control period [P4 if H1 is correct]; to have a higher maximum speed during the day of a simulated hunt than during the day of a human encounter [P5 if H2 is correct]; and to have a higher maximum speed during the day of a simulated hunt if the simulated hunt lasts longer [P6 if H3 is correct].

Heart rate measurements have been used on different species to assess the physiological impact of a disturbance (as examples: ungulates (Weisenberger et al. 1996), birds (Culik et al. 1990) and black bears (Ditmer et al. 2015; Ditmer et al. 2018)). Heart rates can also be associated with energy consumption, with higher heart rates indicating higher energy consumption (Livingstone et al. 1992). Laske et al. (2011) measured a heart rate of 251 beats per minute (bpm) in a black bear that was legally shot during the hunting season. The authors also recorded heart rate peaks associated with their visits to the den. In all the mentioned studies, disturbances were always associated with higher heart rates. On this basis, bears were predicted to have a higher maximum heart rate during the day of a human encounter or a simulated hunt than during the control period [P7 if H1 is correct]; to have a higher maximum heart rate during the day of a simulated hunt than during the day of a human encounter [P8 if H2 is correct]; and to have a higher maximum heart rate during the day of a simulated hunt if the simulated hunt lasts longer [P9 if H3 is correct].

Changes in body temperature can be used to assess energy consumption (Evans et al. 2016b). The authors measured the area under the curve of daily mean body temperatures of brown bears to obtain a body temperature area value that they used as an energy consumption index, with a greater body temperature area indicating a higher energy consumption. They used this method to differentiate the energy consumption of bears woken up by humans during their hibernation and bears that were undisturbed. With a similar reasoning, bears were predicted to have a greater body temperature area during the day of a human encounter or a simulated hunt than during the control period [P10 if H1 is correct]; to have a greater body temperature area during the day of a simulated hunt than during the day of a human encounter [P11 if H2 is correct]; and to have a greater body temperature area during the day of a simulated hunt if the simulated hunt lasts longer [P12 if H3 is correct].

Bears typically rest in the middle of the day (Moe et al. 2007), when the experiments were carried out. Changes in resting behaviour can hence be used as clues to assess disturbances. Bears were thus predicted to rest less during the day of a human encounter or a simulated hunt than during the control period [P13 if H1 is correct]; to rest less the day of a simulated hunt than the day of a human encounter [P14 if H2 is correct]; and to rest less during the day of a simulated hunt if the simulated hunt lasts longer [P15 if H3 is correct].

HRV is a measure that gives an indication of the regularity of the heartbeats (Stein et al. 1994). The regularity of the beats can give indications about the balance between the parasympathetic and the sympathetic tone, with low HRV values being associated to an increase in the sympathetic or a decrease in the parasympathetic tone (Maros et al. 2008; Stein et al. 1994). Lower HRV values were found in humans (Taelman et al. 2009; Thayer et al. 2012), farm animals (Von Borell et al. 2007) and dogs (Gacsi et al. 2013) when individuals were psychologically stressed. Støen et al. (2015) measured lower HRV values in brown bears in Sweden when they were closer to human settlements and interpreted it as proof of a human landscape of fear. On that basis, bears were predicted to have lower HRV during the day of a human encounter or a simulated hunt than during the control period [P16 if H1 is correct]; to have lower HRV during the day of a simulated hunt than during the day of a human encounter [P17 if H2 is correct]; and to have lower HRV during the day of a simulated hunt if the simulated hunt lasts longer [P18 if H3 is correct].

From the hypothesis that dog hunts and human encounters have lasting physiological and behavioural effects on brown bears [H4], bears were expected to travel different distances [P19 if H4 is correct]; to have a different maximum speed [P20 if H4 is correct]; to have a different maximum heart rate [P21 if H4 is correct]; to have a different body temperature area [P22 if H4 is correct]; and to have different HRV during the first and second days following a human encounter or a simulated hunt compared to the control period [P23 if H4 is correct].

Finally, resting allows to recover from physical activities, and longer resting periods have been measured after greater physical performances (Davenne 2009). Bears were therefore predicted to rest more during the first and second days following a human encounter or a simulated hunt compared to the control period [P24 if H4 is correct]; to rest more during the first and second days following a simulated hunt than following a human encounter [P25 if H2 is correct]; and to rest more during the first and second days following a simulated hunt if the simulated hunt lasts longer [P26 if H3 is correct]

Table 1: Summary of the predictions with their corresponding hypothesis.

	Prediction	Hypotheses
1.	Bears travel longer distances during the day of a human encounter or a simulated hunt than during the control period.	1
2.	Bears travel longer distances during the day of a simulated hunt than during the day of a human encounter.	2
3.	Bears travel longer distances during the day of a simulated hunt if the simulated hunt lasts longer.	3
4.	Bears have a higher speed during the day of a human encounter or a simulated hunt than during the control period.	1
5.	Bears have a higher speed during the day of a simulated hunt than during the day of a human encounter.	2
6.	Bears have a higher speed during the day of a simulated hunt if the simulated hunt lasts longer.	3
7.	Bears have a higher maximum heart rate during the day of a human encounter or a simulated hunt than during the control period.	1
8.	Bears have a higher maximum heart rate during the day of a simulated hunt than during the day of a human encounter.	2
9.	Bears have a higher maximum heart rate during the day of a simulated hunt if the simulated hunt lasts longer.	3
10.	Bears have a greater body temperature area during the day of a human encounter or a simulated hunt than during the control period.	1
11.	Bears have a greater body temperature area during the day of a simulated hunt than during the day of a human encounter.	2
12.	Bears have a greater body temperature area during the day of a simulated hunt if the simulated hunt lasts longer.	3
13.	Bears rest less during the day of a human encounter or a simulated hunt than during the control period.	1
14.	Bears rest less the day of a simulated hunt than the day of a human encounter.	2
15.	Bears rest less during the day of a simulated hunt if the simulated hunt lasts longer.	3
16.	Bears have lower HRV during the day of a human encounter or a simulated hunt than during the control period.	1
17.	Bears have lower HRV during the day of a simulated hunt than during the day of a human encounter.	2
18.	Bears have lower HRV during the day of a simulated hunt if the simulated hunt lasts longer.	3
19.	Bears travel different distances during the first and second days following a human encounter or a simulated hunt compared to the control period.	4
20.	Bears have a different speed during the first and second days following a human encounter or a simulated hunt compared to the control period.	4
21.	Bears have a different maximum heart rate during the first and second days following a human encounter or a simulated hunt compared to the control period.	4
22.	Bears have different body temperature area during the first and second days following a human encounter or a simulated hunt compared to the control period.	4
23.	Bears have a different HRV during the first and second days following a human encounter or a simulated hunt compared to the control period.	4
24.	Bears rest more during the first and second days following a human encounter or a simulated hunt compared to the control period.	4
25.	Bears rest more during the first and second days following a simulated hunt than following a human encounter.	2
26.	Bears rest more during the first and second days following a simulated hunt if the simulated hunt lasts longer.	3

Materials and Methods:

Study Area and Study Species:

Scandinavian brown bears are distributed into three main populations (Norman 2016). The present study was carried out from 2014 to 2016 in 2 different areas covering the southernmost and northernmost bear subpopulations (61.50°N; 15.06°E & 66.76°N; 21.02°E; Figure 1). In both areas the landscape is hilly and mostly covered by managed productive forest, mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula spp.*). A dense network of roads is found in both areas (Ordiz et al. 2014) despite the low human density (2.6 - 16.7 habitants / km^2 in 2016) (Statistics Sweden 2017).

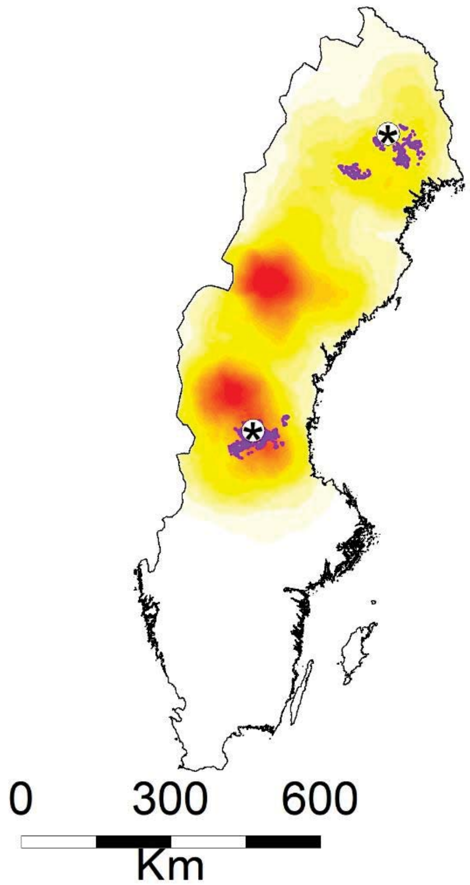


Figure 1: Sweden with its bear population distribution (heatmap based on scat distribution). The two stars indicate the positions of both field stations used from 2014 to 2016. The purple dots are GPS tracks from humans and dogs during the experiments.

Brown bears are a game species in Sweden since 1943 (Swenson et al. 2017) with a hunting season starting on the 21st of August and ending at the latest on the 15th of October unless the quotas set by the County board are filled before. No specific bear hunting licences exist or are required in Sweden (Bischof et al. 2008). There is also no limit in how many bears one hunter is allowed to harvest (Hertel et al. 2016), as long as the quota for the area is not filled. Hunters are required to use an appropriate weapon for big game hunting and can only hunt where they have a hunting right (Bischof et al. 2008). Legal hunting is also limited to a period from 1 hour after sunrise until 2 hours before sunset (Ordiz et al. 2011). Family groups (adult females with dependant cubs) are protected (Van de Walle et al. 2018), but there are no age or sex specifications applied to the hunting quotas (Bischof et al. 2008).

A brown bear's year can be divided into three main periods, two active and one inactive. The first active period starts in early spring (April) when they leave their den (Evans et al. 2016a). This period includes the mating season that can last until July (Dahle & Swenson 2003). The second active period is from July to den entry in October. During that time, the bears are in hyperphagia and mainly eat berries to gain weight (Dahle et al. 1998; Stenset et al. 2016; Swenson et al. 2007). Finally, the inactive period, which is characterised by the time of the year with snow cover, starts late October and ends when the bears come out of their den again after hibernation (Evans et al. 2016a). During this last period, bears use the fat reserves they accumulated during the hyperphagia period (Lopez-Alfaro et al. 2013). As winter is longer in the north of Sweden, the denning period is also longer (Manchi & Swenson 2005).

Brown bears' body temperature varies and depends on whether they are hibernating or active (Evans et al. 2016a). Evans et al. (2016a) measured an average body temperature of 37.2 ± 1.6°C in bears in summer and 33.2 ± 0.8°C in winter, with decreasing values 13 days before den entry. The heart rate of bears follow similar patterns as the body temperature, with higher values in summer, decreasing values about 25 days before the denning entry and low heart rates recorded during hibernation (Evans et al. 2016a). The authors also measured lower HRV during hibernation than during the active period, with HRV declining 5 days before den entry.

Data Collection:

Human encounters and simulated hunts were conducted on 46 free-ranging brown bears (18 males, 28 females). From those, 11 were subadults (< 4 years old), 31 were adults and 4 were studied when they were both subadults and adults. Bears were used for experiments, captured and equipped with the different devices presented below, as part of the ongoing research in the Scandinavian Brown Bear Research Project (SBBRP), who was granted all the necessary permissions from the appropriate authorities. For more details on how the bears were captured and immobilized please refer to Arnemo and Evans (2017).

GPS, VHF and Activity Data:

The 46 bears were equipped with GPS-Plus collars with GSM modems or Iridium modems with an included VHF transmitter (Vectronic Aerospace GmBh, Berlin, Germany). GPS coordinates recorded by the collars were estimated to have an accuracy of ± 10 meters (Moe et al. 2007). These collars were remotely programmed (via GSM or Iridium communication) to record 3 hours of positions every minute the day of the human encounter. GPS collars were either programmed in advance for simulated hunts or the dogs were equipped with Ultra High Frequency (UHF) transmitters (Vectronic Aerospace GmbH, Berlin, Germany) that emitted a signal every second triggering the recording of GPS coordinates every 70 seconds in the bears' GPS collars at 500 meters. The GPS collars on the brown bears scanned for UHF signals for 1.5 seconds every 8 seconds. As a default, the bear collars were set to record 1 GPS coordinate every 30 minutes or every hour. Each time 7 coordinates had been stored, the GPS collars sent the recorded coordinates by satellite or GSM depending on the model. This allowed, when the collar had a good reception, to know where the bear was in the hours preceding the experiments.

The activity of the bears was measured using a dual-axis motion sensor installed in the GPS collars. The true acceleration was measured in 2 orthogonal directions at a frequency of 6 to 8 times per second. The average activity values over 5 minutes for each orthogonal direction was then recorded in the GPS collar with its associated date and time (Friebe et al. 2014).

Humans (hereafter observers) were equipped with hand-held Garmin GPSMAP 60CSx or Astro 320 and the dogs were equipped with T 5 or DC40 Dog Devices, with all types of equipment being set to record a GPS coordinate every second (Garmin Ltd., USA). The dogs' GPS collars could be directly tracked by the observers who could monitor the dogs' tracks on their hand-held GPS.

In addition to the VHF transmitter in the bears' collars, a VHF transmitter implant (M1255B, Advanced Telemetry Systems, USA) was surgically implanted in each bear's abdomen (Arnemo & Evans 2017). The VHF implants as well as the VHF transmitters in the collars were used to locate bears prior to an experiment using triangulation.

Physiological Data:

Bears were equipped with a cardiac biologger (Reveal XT, Medtronic, Minnesota, USA) implemented with a modified software (BearWare) developed by Medtronic. Cardiac biologgers were surgically implanted on the left of the sternum between the muscles and subcutaneous fat (Arnemo & Evans 2017). The cardiac biologgers continuously recorded the bears' inter-beat intervals (R-R, in milliseconds) based on electrocardiogram (ECG) measurements. Every 2 minutes the mean R-R interval was converted into a heart rate in beats per minute (bpm) and stored in the cardiac biologger's memory with its associated date and time. The HRV of the bear was measured by the cardiac biologger simultaneously with the heart rate. The HRV was characterised as the standard deviation of intervals between heartbeats (SDANN). The median inter-beat intervals were calculated for every 5 minutes based on the ECG. The standard deviation of these medians was thereafter stored in the cardiac biologgers for every 24-hour period with its associated date and time. Thereby, every day was associated with a HRV value. The data stored in the cardiac biologger was retrieved during the next capture one year later by downloading the data through the skin of the bears using a device designed by Medtronic (CareLink, Medtronic, Minnesota, USA).

The body temperatures of the bears were measured every 4 minutes with an accuracy of ± 0.1°C using temperature biologgers (DST Centi-T, Star-Oddi, Gardabaer, Iceland). The temperature biologgers were surgically implanted in the abdomen of the bear during the capture (Arnemo & Evans 2017). Temperature biologgers were surgically extracted during a capture one or two years later and the data was downloaded at the field station (Mercury Application Software, Star-Oddi, Gardabaer, Iceland).

Every legally shot bear must immediately be reported to the county's administrative board. All carcases are controlled by officials from the county's administrative board, either directly on site or at an agreed checkpoint. There is no special protection for bears that are equipped with GPS collars. In the case of a shot bear, the GPS collar and the biologgers were first removed from the carcass by field personnel or the officials and the data was then retrieved.

Experimental Design:

Moen et al. (2012) found that bears that are inactive and most likely resting, have a flight initiation distance (FID) of 69 ± 47 meters, with a maximum FID measured at 309 meters. When the bears were active, the FID was longer (115 ± 94 meters), with a maximum FID measured at 324 meters. In the present study, the bears were considered as disturbed by the experiment if the minimum distance recorded during the experiment between the bear and observers or dogs was less than 200 meters. The 13 experiments where the minimum distance was longer than 200 meters were thus removed from the analyses (median 391 meters, minimum 229 meters, maximum 1818 meters, n = 13).

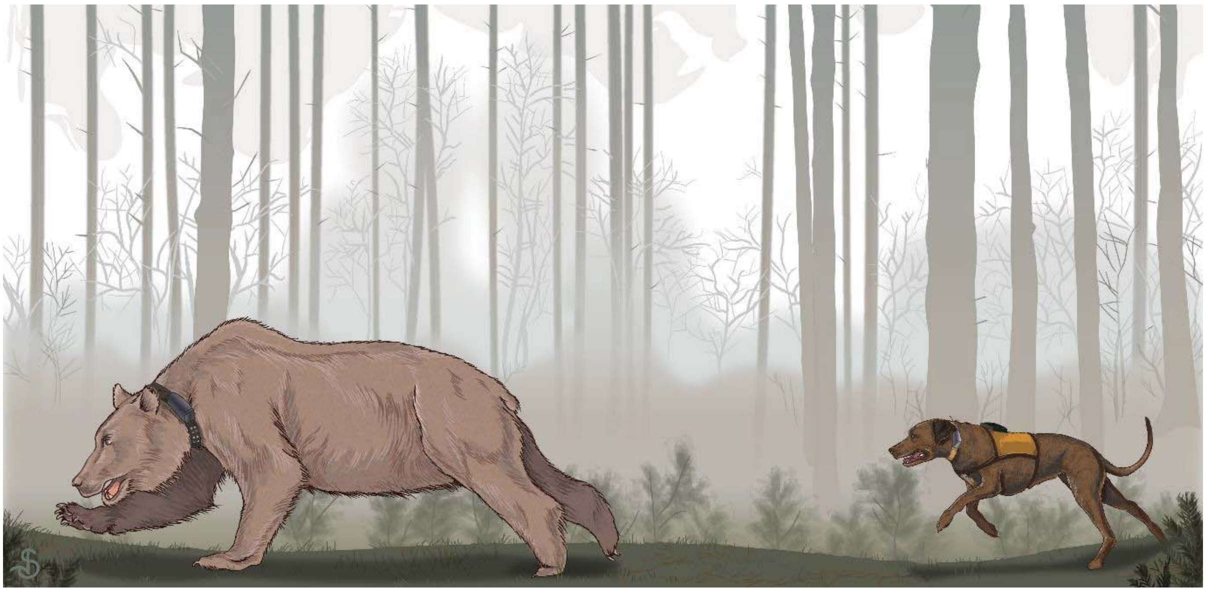
To obtain the minimum distance between the bear and the observers and dogs during an experiment, all the GPS tracks were temporally aligned, with each row corresponding to a second and each column corresponding to a GPS track. If some seconds did not have GPS coordinates for the observers' or dogs' GPS tracks, the missing values were linearly interpolated using the na.approx function from the zoo package, version 1.8-0 (Zeileis & Grothendieck 2005). The distance (shortest distance between two points on the WGS84 ellipsoid) between the bear's GPS coordinates and the human or dog tracks at the same time was then measured with the distGeo function from the geosphere package, version 1.5-7 (Hijmans et al. 2017). The minimum distance for each human approach or simulated hunt was extracted.

Following the same methods presented by Moen et al. (2012), the human encounters were started between 8:30 and 16:30 local time (GMT+2). This period of the day was preferred as bears are typically resting (Moe et al. 2007) and thus are easier to locate by triangulation. This is also the time of the day when most people are active and may disturb the bears. Before starting an experiment, the bear was located by triangulation using VHF signals transmitted by its collar and / or its VHF implant. If recent, the last transmitted GPS coordinates were used as a clue for the bear's location. Whilst searching for its position, not disturbing the bear was a priority. Once the bear was found, the observer(s) walked towards the bear, starting approximately half a kilometre away, intending to pass the bear at an approximate distance of 50 meters. To undertake a human encounter, observers, by groups of 1 to 6 (median = 2) mimicked hikers walking in the forest and talked to each other or to themselves if alone. The approach continued until the VHF signals indicated that the bear had been passed or that the bear was running away. At that point, the observer(s) returned to the car and made sure not to encounter the bear a second time. To do so, the position of the bear was continuously monitored along the way back. If the bear stayed at its initial position, the observer(s) carried on in the same direction and did a loop back to the car. The wind was monitored and if the wind direction was possible to determine the human encounters were carried out with the wind blowing at 90° from the observer(s) towards the bear when passing it.

To undertake a simulated hunt, the bear was first found using the same method as during the human encounters. Once the bear was found, at least two observers and one experienced hunting dog kept on a leash walked closer to the bear until the dog showed interest in the scent of the bear, either in the wind or from its tracks. At that point, the dog was released and allowed to pursue the bear. During the simulated hunt the movements of the bear and the dog(s) were monitored using VHF signals from the bear and GPS coordinates from the dog(s). The simulated hunt was stopped if the dog(s) came back to the hunter by itself / themselves or by the hunter calling in or intercepting the path of the dog(s). Simulated hunts were started between 7:30 and 19:30 local time (GMT+2). During the same simulated hunt, 1 to 6 different dogs were used. However, only a maximum of two dogs were let loose simultaneously to hunt the bear. Two main types of dogs are used for hunting in Sweden: pursuing dogs that chase game species whilst barking (e.g. plott hounds, Figure 2) and baying dogs that chase an animal and attempt to stop it (e.g. Elkhounds, Figure 3) (Ericsson et al. 2015). Both baying and pursuing breeds were used during the simulated hunts, but all simulated hunts were considered as one unique treatment to be compared to the human encounter treatment.

The 96 human encounters were carried out in 2014 (1st June – 7th August; n = 30), in 2015 (5th June – 28th July; n = 36) and in 2016 (2nd June – 20th August, n = 30). The minimum distance recorded between the observers and the bear was on average 55 ± 28 meters (median 49 meters, minimum 18 meters, maximum 137 meters, n = 96). In total 40 bears were used (15 males, 25 females). During the human encounters 11 bears were subadults, 25 were adults and 4 were used when they were both subadults and adults. Out of these 96 human encounters, 70 took place in the southernmost brown bear subpopulation and 26 in the northernmost subpopulation.

The 85 simulated hunts were carried out in 2014 (4th August – 15th August; n = 15), in 2015 (11th June – 2nd October; n = 33) and in 2016 (18th June – 7th October, n = 37). The minimum distance recorded between the observers and / or the dogs and the bear was on average 22 ± 36 meters (median 4 meters, minimum 0 meters, maximum 168 meters, n = 85). The length of a simulated hunt was defined as the time between when the hunter and dog(s) started heading from the car towards the bear until when they were back at the car. Simulated hunts lasted on average 229 ± 108 minutes (median 194 minutes, minimum 67 minutes, maximum 556 minutes, n = 85). In total, 31 bears were used (14 males, 17 females). During the simulated hunts, 6 bears were subadults, 24 were adults and 1 was used when it was both a subadult and an adult. Out of these 85 simulated hunts, 60 took place in the southernmost brown bear subpopulation and 25 in the northernmost subpopulation.



Scientific Illustration by Juliana D. Spahr Contact: Juliana.D.Spahr@gmail.com

Figure 2: Plott hound pursuing a bear during a simulated hunt. The dog is equipped with a collar (DC40 Dog Device) used to collect GPS coordinates, as well as a dog harness equipped with a UHF transmitter that triggers the recording of coordinates every 70 seconds in the GPS-Plus collar fitted on the bear.

Scientific Illustration by Juliana D. Spahr Contact: Juliana.D.Spahr@gmail.com

Figure 3: Elkhound baying a bear during a simulated hunt. The dog is equipped with a collar (DC40 Dog Device) used to collect GPS coordinates, as well as a dog harness equipped with a UHF transmitter that triggers the recording of coordinates every 70 seconds in the GPS-Plus collar fitted on the bear.

Data Processing and Statistical Analyses:

All the data analyses and data processing were carried out using the statistical programming language and environment, R 3.4.2 (R Core Team 2017).

Response Variables:

TRAVEL: As bears do not walk in a straight line, more GPS coordinates within a same day leads to a better estimation of their movements, and thus longer distances. To account for this bias, the distance travelled by the bears was based on 1 coordinate every hour. In this way, days with GPS coordinates taken with a different frequency were directly comparable. The distances (shortest distance between two points on the WGS84 ellipsoid) between the hourly positions were measured using the distGeo function from the geosphere package, version 1.5-7 (Hijmans et al. 2017). The variable TRAVEL is the sum of all hourly displacements for each day.

MAXSPEED: More GPS coordinates also give a better precision for the speed of the bears, with more GPS coordinates giving higher speeds. The MAXSPEED variable was thus also based on hourly positions. The distances and differences in time between each coordinate were then used to calculate the speed of the bear. The variable MAXSPEED is the highest speed recorded within the 24 hours.

HEARTRATE30: When processing the heart rate data, a mismatch between the heart rate and the corresponding time was observed. The origin of this problem has not been found but is most likely due to a problem in the software installed in each cardiac biologger. The mismatch was corrected following a method based on the correlation between the activity of the bear and its heart rate (see Appendix 1). Heart rate data was not used in the analysis if the activity data was not available or if the method led to a suggested time shift that was not consistent during the year, i.e. difference in suggested time shifts > 5 minutes during a year. The cardiac biologgers saved some ECG samples in their memory. Carrying out quality control tests using the software Pdd EGM waveform tool (Medtronic, Minnesota, USA) allowed to realise that the software installed in the cardiac biologger was sometimes making mistakes when recognizing the R-R peaks (see Appendix 2). In 2016, one bear was equipped with 2 cardiac biologgers recording heart rates simultaneously to check the reliability of the measurements. The differences in bpm between the simultaneously recorded values by the 2 cardiac biologgers increased with higher heart rates (see Appendix 2). This indicated a decreasing reliability of the measurements at higher heart rates. As higher heart rate values were associated with lower reliability, the strict maximum values were not compared directly. Instead, a mean heart rate over 30 minutes was computed every second minute of the day. This was done by using the rollmean function from the zoo package, version 1.8-0 (Zeileis & Grothendieck 2005). The variable HEARTRATE30 is the maximum mean heart rate recorded within the 24 hours.

T_bAREA: To obtain the variable T_bAREA, the median body temperature from 1st June to 30th September for each bear-year was first computed. Days when the bears were involved in research activities (human encounters, simulated hunts or captures) were not included in this data set. Secondly, the area over a 24-hour period situated above the median and under the measured body temperature values was computed. The area was calculated using a trapezoidal approximation (all points are connected by a direct line forming multiple trapezoids) by using the AUC function from the DescTools package, version 0.99.23 (Signorell 2017) (example in Appendix 3). A T_bAREA equal to 0 means that no body temperatures higher than the median were recorded during the 24 hours. The higher the values recorded during the day, the greater the T_bAREA. Some of the body temperature biologgers could move freely in the abdominal cavity and the temperature values were different depending on whether the temperature biologger was closer to the skin or if it was situated in the middle of the bear's abdominal cavity. For this reason, some bears had cooler temperatures than others. The mean body temperature of 3 bears was lower than 35°C and thus considered abnormal and removed from the dataset. The median body temperature of the bears remained variable (average 37.3 ± 0.5°C, minimum 35.3°C, maximum 37.8°C). However, by using a median temperature calculated for each bear-year, the T_bAREA provided a method that limited biases due to this problem.

REST: After extracting the activity data from the collars, the two values for each orthogonal direction were summed resulting in a variable ranging from 0 to 510. Gervasi et al (2006) were able to predict if bears were active or passive using the same type of dual-axis motion sensors. Based on their work, bears were considered to have a 5-minute rest when the activity variable had a value ranging from 0 to 23. The REST variable is the number of activity points with a value lower than 23 during a day (24 hours) multiplied by 5 to give a time in minutes.

HRV: Each day was associated with a HRV value in milliseconds. The variables could thus be directly used in the models.

Explanatory Variables:

TYPE: Human encounters and simulated hunts were considered as two different treatments in a binary variable hereafter named TYPE.

PERIOD: The variable PERIOD consisted of 4 unique levels. The 1st level represents the control period defined as the mean values recorded during the 3 days prior to the human encounter day or simulated hunt day. The 2nd level represents the day of the experiment. The 3rd and 4th levels represent the following and the second day after the experiment respectively. Some bears were used in multiple human encounters or / and simulated hunts during a same year. To be able to have a control period of 3 days, no research activities that could have affected the bear were carried out for at least 5 days before the experiment. This allowed for a 2-day buffer period if any experiments were carried out during the 6th day before the experiment and for the 3-day control period. The 2 days after an experiment were also free of any research activities, allowing for the assessment of potential lasting physiological and behavioural effects on brown bears.

The length of the simulated hunts was used as an explanatory variable. However, the sex and the age of the bears as well as the study areas were not considered as explanatory variables due to relatively low sample sizes. The human encounters and simulated hunts nevertheless had similar proportions of experiments carried out in the 2 study areas and on bears that were subadult / adult, male / female. No differences were found when carrying out a Pearson's Chi-squared test (Chisq = 5.9, df = 5, p-value = 0.32). In addition, 134 out of the 181 experiments (74 %) were carried out with bears that were used for both human encounters and simulated hunts. When it comes to comparing human encounters to simulated hunts, no bias due to different ratios or the use of different individuals should thus be expected. However, both human encounters and simulated hunts were mainly carried out in the southernmost bear population on adult female individuals (Table 2). Results presented in this study may thus be more representative of how adult females from the southernmost population are impacted.

Table 2: Chi-squared tests of the different ratios of experiments carried out on bears depending on their sex, age and population.

Sex:	Male	Female	Chisq	df	p-value
Human encounters	26	70	20.2	1	< 0.0001
Simulated hunts	33	52	4.25	1	0.039

Age:	Subadult	Adult	Chisq	df	p-value
Human encounters	26	70	20.2	1	< 0.0001
Simulated hunts	14	71	38.2	1	< 0.0001

Area:	South	North	Chisq	df	p-value
Human encounters	70	26	20.2	1	< 0.0001
Simulated hunts	60	25	14.4	1	0.00015

Random Factors:

The ID of the bears as well as the ID of the experiments were considered as random factors. As multiple experiments were carried out on the same bears, the experiments' ID was nested in the bears' ID. The random factors were used to acknowledge that some values were not independent as they were linked to the same bears and / or to the same experiment. The random factors were thus necessary to avoid any pseudo-replication and were included in the model by default. The random intercept on the bear's ID also recognised that individuals may have different traits. The random intercept on the experiment's ID acknowledged that experiments were carried out in different situations.

Model Construction:

The variables TRAVEL, MAXSPEED, HEARTRATE30 and T_bAREA had an over-dispersed Poisson distribution. A Generalized Linear Mixed Model with Penalized Quasi-Likelihood (glmmPQL) can be a typical type of model to use in this case (Bolker et al. 2009). When random factors have large standard deviations, glmmPQL are nevertheless known to compute biased parameter estimates (Bolker et al. 2009) that can lead to wrong low p-values. In addition, glmmPQL are inaccurate with small sample sizes (Bolker et al. 2009). Linear models are considered to be resistant to non-normality as a result of the Central Limit Theorem (Zuur et al. 2009). A square root transformation of the response variables largely improved the normality of the residuals. Residuals were close to normality with a heavier tail than normal. Heavier tails will result in larger error estimates leading to slightly too conservative tests. All in all, LME models with a square root transformation of the response variables were preferred to glmmPQL for their conservative aspect.

The variables TRAVEL, MAXSPEED, HEARTRATE30, TbAREA, REST and HRV were thus all used as response variables in linear mixed effect (LME) models. The models were created using the lmer function from the lme4 package, version 1.1-14 (Bates et al. 2014) and fitted using the restricted maximum likelihood (REML) method as the models were composed of small sample sizes. The homogeneity of variance was visually checked by plotting the predicted values against the residuals. The homogeneity of variance across groups was visually inspected by comparing boxplots of the residuals for each group. The normality of the residuals was inspected using a quantile-comparison plot as well as a histogram of the residuals. Not all the 96 human encounters and 85 simulated hunts had data for all the explanatory variables. For this reason, n varied between the different LME models (Table 3).

The variables TYPE and PERIOD as well as the interaction were first all considered as explanatory variables in a full model. The final model was obtained by removing the least significant interaction or variables following the backward selection method. The significance of the variables and the interaction were computed using the Anova function from the car package, version 2.1-6 (Fox & Weisberg 2011). The Anova function was used with the type-III method that computes a p-value for each variable or interaction as if they were added as the last variable in the model with all other variables and interactions present. A pairwise analysis of the estimated marginal means (EMMs) was then performed to interpret the final models using the emmeans package, version 1.1. (Lenth 2018). This method was used as the models had an unbalanced number of human encounters and simulated hunts. The EMMs were based on a 0.95 confidence level with the Tukey correction method.

When only considering the simulated hunts, the variables TRAVEL, MAXSPEED, HEARTRATE30, T_bAREA, REST and HRV were also used as response variables in LME models with the length of the simulated hunts as explanatory variable. The models were created following the same method as the method presented for the previous LME models but were created using the lme function from the nlme package, version 3.1-131 (Pinheiro et al. 2017). The model included the ID of the bears as a random factor, as some simulated hunts were carried out on the same bears. The experiment ID was however not used as a random factor as only one value was available for each experiment ID. The variables TRAVEL, MAXSPEED and T_bAREA were square root transformed to improve the normality of the residuals.

Table 3: Number of human encounters and simulated hunts that had data for the different response variables and could thus be included in the corresponding models.

Variable:	N human encounters	N simulated hunts	N bears
TRAVEL	96	83	45
MAXSPEED	96	83	45
HEARTRATE30	29	40	21
T_bAREA	47	45	24
REST	82	78	41
HRV	51	51	27

Results:

The distances travelled by the bears (TRAVEL) were longer during the day of a simulated hunt than during the control period (post hoc test: estimated difference = 773 ± 10 meters, p < 0.0001, 32 % longer) and longer than during the day of human encounter (post hoc test: estimated difference = 219 ± 16 meters, p = 0.006, 15 % longer) (Figure 4). Bears also travelled longer distances the day of a human encounter than during the control period (post hoc test: estimated difference = 89 ± 9 meters, p = 0.034, 11 % longer). There were no differences in distance travelled the first and second days following a human encounter or a simulated hunt compared to the corresponding control period (all p > 0.16). However, bears travelled less during the first and second days following a simulated hunt than during the first and second days following a human encounter (first day: post hoc test: estimated difference = -209 ± 16 meters, p = 0.009, 19 % less; second day: post hoc test: estimated difference = -252 ± 16 meters, p = 0.002, 20 % less). There was no difference between the control periods of the human encounters and the control periods of the simulated hunts (p > 0.90). The length of the simulated hunts had no effect on the distance travelled by the bears the day of the simulated hunt (Table 4).

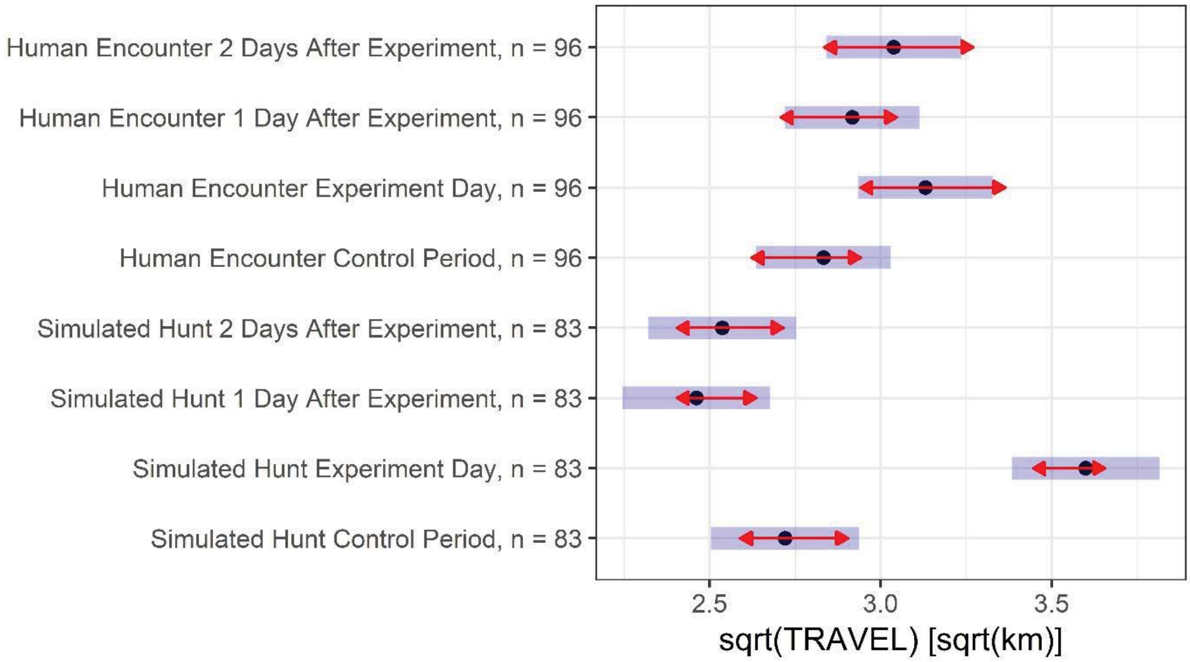


Figure 4: EMMs of the distances travelled by the bears for 24 hours (TRAVEL square root transformed) depending on the explanatory variables PERIOD and TYPE. The EMMs presented here are based on a 0.95 confidence level with the Tukey correction method. Blue bars are the confidence intervals of the EMMs and the red arrows are displayed for intergroup comparison purposes. If two red arrows overlap, there is no significant difference between the two groups. The ANOVA table of the LME model (Table A.4.1) as well as the numerical values of all the EMMs (Table A.4.7) and of each contrast (Table A.4.13) associated to the figure are displayed in the Appendix 4.

Table 4: LME model for the effect of the length of the simulated hunts on the distance (TRAVEL) travelled by the bears the day of the simulated hunt. The values are in square root kilometres. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model TRAVEL ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	3.5677	0.2143	52	16.6498	< 0.0001
Length Simulated Hunt	0.0376	0.0499	52	0.7544	0.454

The bears ran faster (MAXSPEED) during the day of a simulated hunt than during the control period (post hoc test: estimated difference = 346 ± 2 meters / hour, $p < 0.0001$, 48 % faster) and faster than during the day of a human encounter (post hoc test: estimated difference = 167 ± 3 meters / hour, $p < 0.0001$, 29 % faster) (Figure 5). Bears also ran faster the day of a human encounter than during the control period (post hoc test: estimated difference = 26 ± 2 meters / hour, $p = 0.028$, 13 % faster). There were no differences in maximum speeds the first and second days following a human encounter or a simulated hunt compared to the corresponding control period (all $p > 0.89$). There was no difference between the control periods of the human encounters and the control periods of the simulated hunts ($p > 0.90$). The length of the simulated hunts had no effect on the maximum speeds of the bears the day of the simulated hunt (Table 5).

Table 5: LME model for the effect of the length of the simulated hunts on the running speed (MAXSPEED) of the bears the day of the simulated hunt. The values are in square root kilometres / hour. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model MAXSPEED ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	1.8542	0.1210	52	15.3191	< 0.0001
Length Simulated Hunt	-0.0087	0.0281	52	-0.3101	0.758

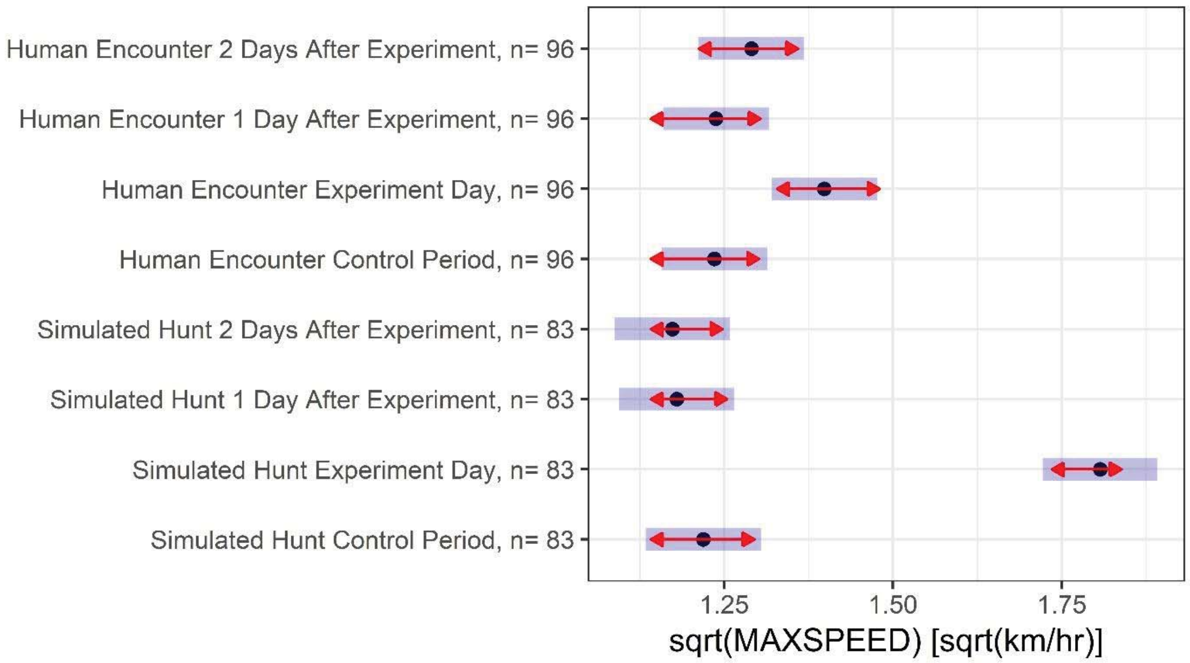


Figure 5: EMMs of the maximum running speed of the bears (MAXSPEED square root transformed) depending on the explanatory variables PERIOD and TYPE. The EMMs presented here are based on a 0.95 confidence level with the Tukey correction method. Blue bars are the confidence intervals of the EMMs and the red arrows are displayed for intergroup comparison purposes. If two red arrows overlap, there is no significant difference between the two groups. The ANOVA table of the LME model (Table A.4.2) as well as the numerical values of all the EMMs (Table A.4.8) and of each contrast (Table A.4.14) associated to the figure are displayed in the Appendix 4.

The maximum heart rates (HEARTRATE30) were higher during the day of a simulated hunt than during the control period (post hoc test: estimated difference = 7 ± 0.04 bpm, $p < 0.0001$, 26 % higher) and higher than during the day of human encounter (post hoc test: estimated difference = 3 ± 0.07 bpm, $p < 0.0001$, 17 % higher) (Figure 6). Bears did not have a different maximum heart rate the day of a human encounter than during the control period ($p = 0.065$). There were no differences in maximum heart rates the first and second days following a human encounter or a simulated hunt compared to the corresponding control periods (all $p > 0.85$). There was no difference between the control periods of the human encounters and the control periods of the simulated hunts ($p > 0.90$). The length of the simulated hunts had no effect on the maximum heart rate the day of the simulated hunt (Table 6).

Table 6: LME model for the effect of the length of the simulated hunts on the maximum heart rate (HEARTRATE30) of the bears the day of the simulated hunt. The values are in bpm. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model HEARTRATE30 ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	162.6755	12.5001	22	13.0139	< 0.0001
Length Simulated Hunt	0.8050	3.0144	22	0.2670	0.792

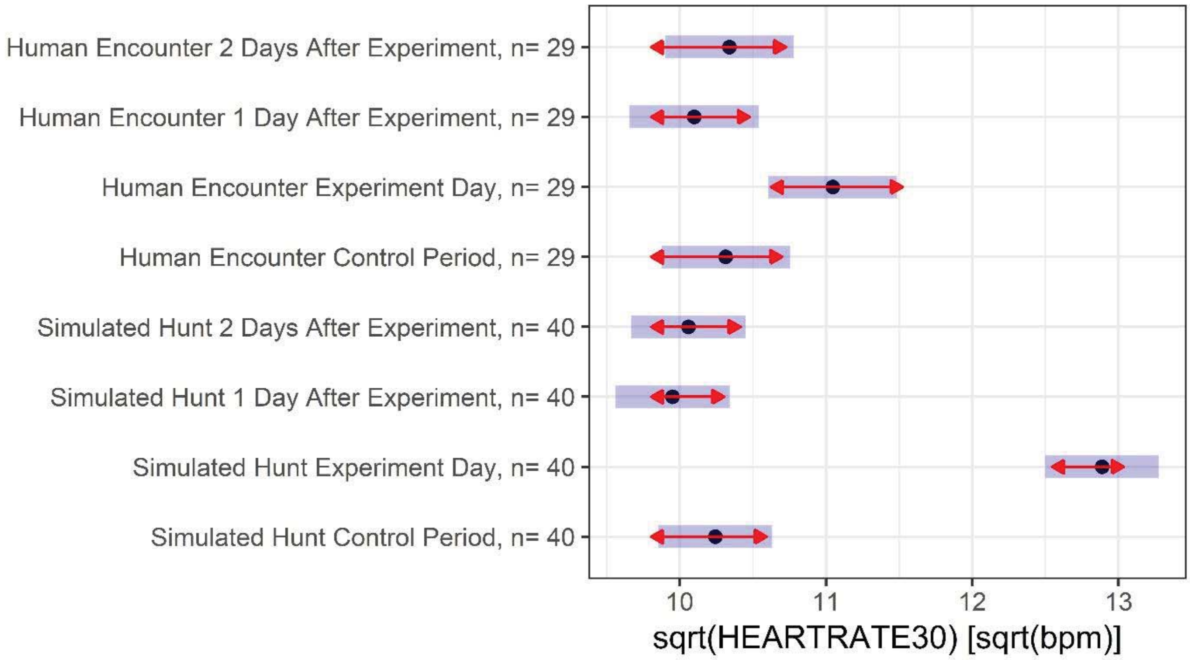


Figure 6: EMMs of the maximum heart rates (HEARTRATE30 square root transformed) depending on the explanatory variables PERIOD and TYPE. The EMMs presented here are based on a 0.95 confidence level with the Tukey correction method. Blue bars are the confidence intervals of the EMMs and the red arrows are displayed for intergroup comparison purposes. If two red arrows overlap, there is no significant difference between the two groups. The ANOVA table of the LME model (Table A.4.3) as well as the numerical values of all the EMMs (Table A.4.9) and of each contrast (Table A.4.15) associated to the figure are displayed in the Appendix 4.

The body temperature areas (T_bAREA) were greater during the day of a simulated hunt than during the control period (post hoc test: estimated difference = 1648 ± 45 T_bAREA, $p < 0.0001$, 39 % greater) and greater than during the day of human encounter (post hoc test: estimated difference = 1164 ± 76, $p = 0.0029$ T_bAREA, 31 % greater) (Figure 7). The body temperature area was not different the day of a human encounter than during the control period ($p > 0.90$). There were no differences in body temperature areas the first and second days following a human encounter or a simulated hunt compared to the corresponding control periods (all $p > 0.19$). There was no difference between the control periods of the human encounters and the control periods of the simulated hunts ($p > 0.90$). The length of the simulated hunts had no effect on the body temperature area the day of the simulated hunt (Table 7).

Table 7: LME model for the effect of the length of the simulated hunts on the bear's body temperature area (T_bAREA) the day of the simulated hunt. The values are in square root T_bAREA. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model T_bAREA ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	132.9025	14.8193	26	8.9682	< 0.0001
Length Simulated Hunt	3.2392	3.6275	26	0.8930	0.380

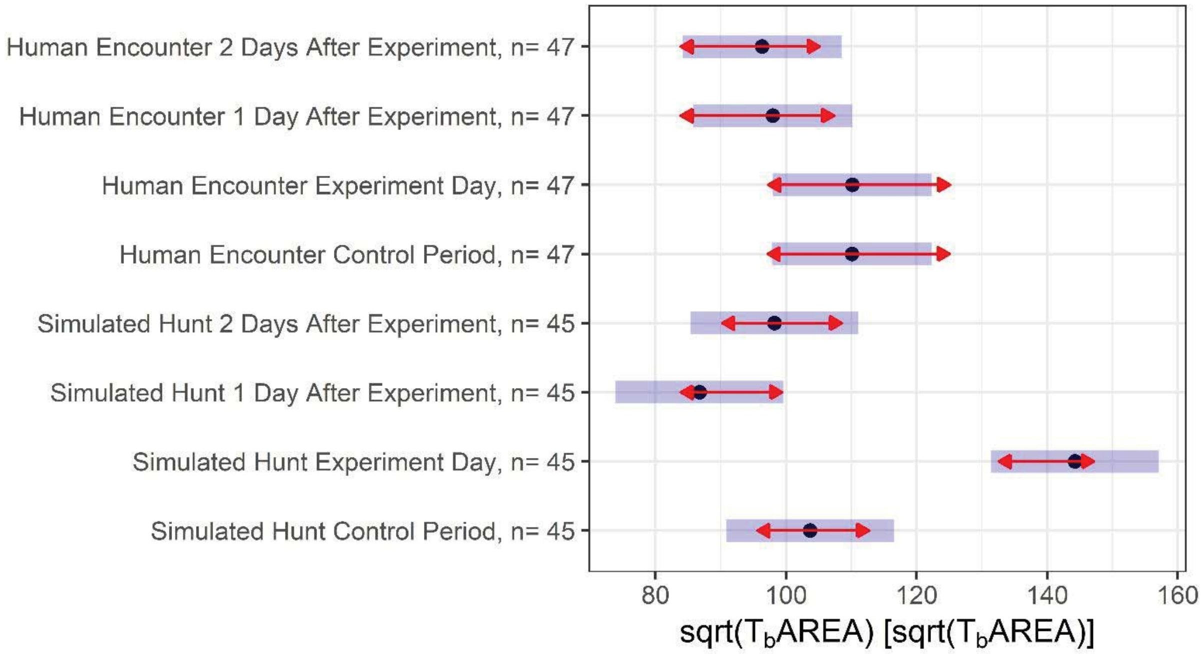


Figure 7: EMMs of the body temperature areas (T_bAREA square root transformed) depending on the explanatory variables PERIOD and TYPE. The EMMs presented here are based on a 0.95 confidence level with the Tukey correction method. Blue bars are the confidence intervals of the EMMs and the red arrows are displayed for intergroup comparison purposes. If two red arrows overlap, there is no significant difference between the two groups. The ANOVA table of the LME model (Table A.4.4) as well as the numerical values of all the EMMs (Table A.4.10) and of each contrast (Table A.4.16) associated to the figure are displayed in the Appendix 4.

During the control period before a simulated hunt, which was not different from the control period before a human encounter ($p = 0.51$), bears rested (REST) on average 10 hours and 18 ± 17 minutes each day (Figure 8). The day after a simulated hunt, bears rested more than the control period (post hoc test: estimated difference = 77 ± 16 minutes, $p < 0.0001$, 12 % more) and more than the day after a human encounter (post hoc test: estimated difference = 65 ± 20 minutes, $p < 0.036$, 10 % more) (Figure 8). No similar effect was measured after a human encounter. The amount of time bears rested the day after a simulated hunt increased linearly with the duration of the simulated hunt (Table 8, Figure 9). Bears rested about 36 minutes more after a simulated hunt that was 1 hour longer. Bears did not rest less during the day of a human encounter or a simulated hunt than during the control period (both $p > 0.90$).

Bears did not rest less during the day of a simulated hunt than the day of a human encounter (p = 0.35). The length of the simulated hunt did not affect the bear's rest during the day of the simulated hunt (Table 9).

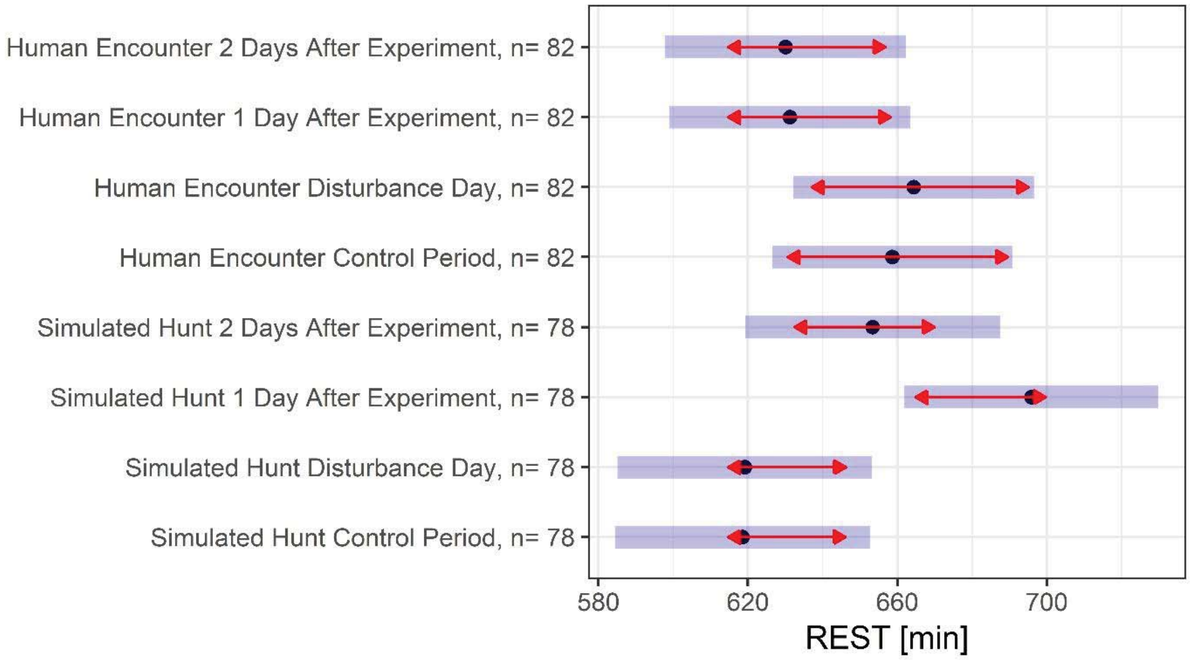


Figure 8: EMMs of the amount of time bears rested in 24 hours (REST) depending on the explanatory variables PERIOD and TYPE. The EMMs presented here are based on a 0.95 confidence level with the Tukey correction method. Blue bars are the confidence intervals of the EMMs and the red arrows are displayed for intergroup comparison purposes. If two red arrows overlap, there is no significant difference between the two groups. The ANOVA table of the LME model (Table A.4.5) as well as the numerical values of all the EMMs (Table A.4.11) and of each contrast (Table A.4.17) associated to the figure are displayed in the Appendix 4.

Table 8: LME model for the effect of the length of the simulated hunts on the amount of time bears rested (REST) the day following the simulated hunt. The values are in minutes. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model REST following day ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	561.40	37.65	48	14.91	< 0.0001
Length Simulated Hunt	0.61	0.15	48	4.11	0.0002

Table 9: LME model for the effect of the length of the simulated hunts on the amount of time bears rested (REST) the day of the simulated hunt. The values are in minutes. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model REST day of the simulated hunt ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	614.61	35.56	48	17.28	< 0.0001
Length Simulated Hunt	0.04	0.14	48	0.27	0.788

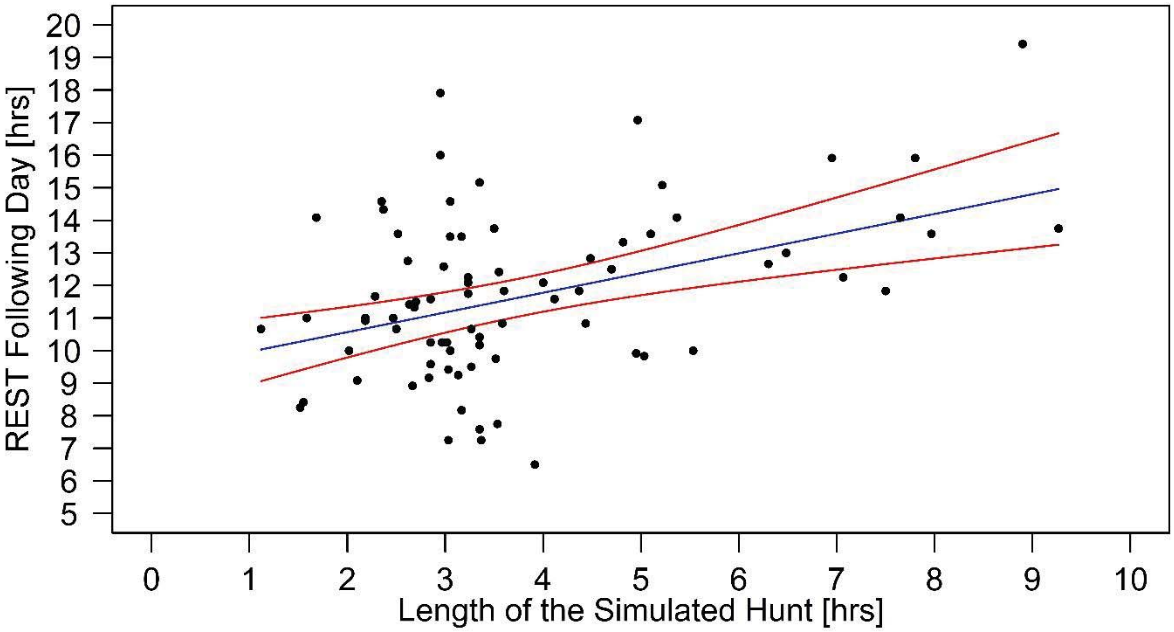


Figure 9: The day after a simulated hunt, bears rested more if the simulated hunt was longer (intercept: 561 ± 38 minutes, slope: 0.61 ± 0.15, p = 0.0002). The regression line is in blue with the lower and upper 95% confidence interval in red. The 78 simulated hunts are represented by the black points.

Human encounters and simulated hunts induced similar changes in HRV in bears (Figure 10). The HRV was significantly higher during the day of the experiment than during the control period (post hoc test: estimated difference = 29 ± 5 milliseconds, p < 0.0001, 15 % higher). The day following the experiments, the HRV was still higher than the control period (post hoc test: estimated difference = 22 ± 5 milliseconds, p = 0.0002, 11 % higher). There was no difference in HRV when comparing the second day after the experiment and the control period (p = 0.13). The length of the simulated hunt did not affect the HRV during the day of the simulated hunt (Table 10).

Table 10: LME model for the effect of the length of the simulated hunts on the HRV measured in bears the day of the simulated hunt. The values are in milliseconds. In the model, the ID of the bears was considered as a random factor as some simulated hunts were carried out on the same bears.

Model HRV ~ Length Simulated Hunt

	Value	**SD**	**DF**	**t-value**	**p-value**
Intercept	205.9927	17.5647	32	11.7277	< 0.0001
Length Simulated Hunt	2.5990	3.5384	32	0.7345	0.468

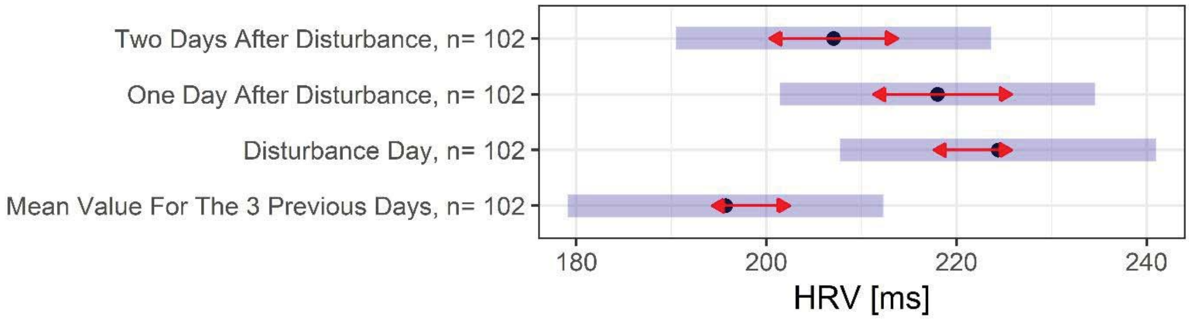


Figure 10: EMMs of the HRV depending on the explanatory variable PERIOD. The EMMs presented here are based on a 0.95 confidence level with the Tukey correction method. Blue bars are the confidence intervals of the EMMs and the red arrows are displayed for intergroup comparison purposes. If two red arrows overlap, there is no significant difference between the two groups. The ANOVA table of the LME model (Table A.4.6) as well as the numerical values of all the EMMs (Table A.4.12) and of each contrast (Table A.4.18) associated to the figure are displayed in the Appendix 4.

Discussion:

As predicted, during the day of a human encounter and during the day of a simulated hunt, bears travelled longer distances [P1] and ran faster [P4] than during the control period, supporting the hypothesis that both events are a source of behavioural disturbance for brown bears [H1] (Table 11). During the day of a simulated hunt, bears also had higher heart rates [P7] and greater body temperature areas [P10] than during the control period. This confirms that dog hunts are also a physiological disturbance [H1]. Contrary to what was predicted, human encounters did not induce similar physiological stress [P7, P10]. Dog hunts therefore have an impact on both the behaviour and the physiology of the bears, whereas human encounters may only represent a behavioural impact.

As the heart rates and the body temperature areas were not affected the day of a human encounter, bears were most likely running away from observers without having to behave physiologically differently from their normal behaviour (control period). This could be because bears were not followed when fleeing and could thus flee at their own rhythm. When carrying out human encounters using the same method as the present study, Moen et al. (2012) found that 20 % of the bears did not run away but remained hidden. This behaviour could explain in part why no difference in heart rates and body temperature areas were found between the control period and the day of the human encounter. Nonetheless, Ditmer et al. (2015) found higher heart rates in black bears that did not increase their movement rates when experimentally disturbing them with drones.

The exposure to simulated hunts, compared to human encounters, led to longer travelled distances [P2], higher speeds [P5], higher heart rates [P8] and greater body temperature areas [P11], strongly supporting the hypothesis that dog hunts have a greater physiological and behavioural impacts on brown bears than human encounters [H2]. During simulated hunts, bears were pursued by dogs and may have been forced to flee in a more dramatic way than when running away from encountered humans. This is most likely one of the main reasons why simulated hunts had a greater impact.

Bears typically rest during the middle of the day (Moe et al. 2007), when the experiments were carried out. Disturbing bears during their resting period could thus have prevented them from doing so. However, contrary to the predictions, bears did not rest less during the experiment days than during the control period [P13], bears did not rest less during simulated hunts than during human encounters [P14] and bears did not rest less during days with longer hunts [P15]. This suggests that these types of disturbance do not lead to rest deprivation. Moen et al. (2012) showed that some bears went back to a resting behaviour about half an hour after being disturbed by a human encounter. The resting time over a 24-hour period may thus not have been affected because bears rested just after the experiments.

Although there was no effect on the resting period the day of the experiments, bears, as predicted, rested more the day after a simulated hunt than during the control period [P24] and rested more the day after a simulated hunt than the day after a human encounter [P25]. This suggests that bears were fatigued by the simulated hunts and further supports that dog hunts are a greater source of disturbance than human encounters [H2]. This also indicates that simulated hunts had a lasting behavioural effect on brown bears [H4]. This prediction was not verified for human encounters [P24] as the amount of rest after human encounters was not different from the control period. Human encounters may thus not fatigue the bears like dog hunts do.

Table 11: Summary of all predictions related to their hypotheses and results. Predictions that are in bold were predicted correctly. The predictions that are not in bold were not supported by the results found in this study.

Variable	Disturbance	H1	H2	H3	H4
TRAVEL	Human encounters:	**P1**	**P2**	-	P19
	Simulated hunts:	**P1**		P3	P19
MAXSPEED	Human encounters:	**P4**	**P5**	-	P20
	Simulated hunts:	**P4**		P6	P20
HEARTRATE30	Human encounters:	P7	**P8**	-	P21
	Simulated hunts:	**P7**		P9	P21
TbAREA	Human encounters:	P10	**P11**	-	P22
	Simulated hunts:	**P10**		P12	P22
REST	Human encounters:	P13	P14, **P25**	-	P24
	Simulated hunts:	P13		P15, **P26**	**P24**
HRV	Human encounters:	P16	P17	-	**P23**
	Simulated hunts:	P16		P18	**P23**

The day after a simulated hunt, bears rested more if the simulated hunt was longer [P26]. This supports the hypothesis that longer dog hunts have a greater behavioural impact on brown bears [H3]. Some bears rested for a surprisingly long time. Gervasi et al. (2006), when predicting the behaviour of bears using the activity data measured by their collars, could correctly predict a passive behaviour versus an active behaviour in 94.3 % of the cases. This precision may nonetheless be variable depending on each individual and how the collar is fitted on the neck of the bear. However, when studying the impact of the simulated hunts the focus was not to get an accurate estimation of how much bears rest, but rather to assess the relative change in rest. The relative change should not present any bias linked to precision as the bears had the same collar before, during and after the experiments.

The fact that bears rested more after simulated hunts than human encounters may be explained by the greater energy cost of the simulated hunts. However, longer hunts did not seem to lead to additional energy costs. Indeed, the distance travelled [P3], the speed [P6], the maximum heart rate of the day [P9] or the body temperature area [P12], all indexes of energy consumptions, were not affected by the simulated hunts' length. This suggests that the energy cost is not what leads bears to rest more after longer simulated hunts. As bears did not rest less the day of longer simulated hunts, a lack of rest does not seem to be a good explanation either. When Bateson and Bradshaw (1997) studied the physiological effects of dog hunting on deer, they noted that longer hunts had greater impacts. For example, they found that longer dog hunts were associated with a higher concentration in enzymes related to muscle tissue disruption. Bears may suffer from similar physiological impacts as the ones found in deer and increase their rest to recover from it. Bateson and Bradshaw (1997) concluded from their results that red deer were not well adapted to fleeing dogs. Bears are large carnivores and may be less adapted to dog hunts than red deer that have been predated throughout their evolutionary history.

There was no difference in distance travelled between the control period and the day after the experiments. However, the distance travelled the 2 days after simulated hunts was significantly lower than the distance travelled the 2 days after human encounters. This may be due to the longer rest after the simulated hunts and could further support that dog hunts have lasting behavioural impact [H4].

Low HRV values can be due to higher psychological stress levels (Bassett 2016; Lennartsson et al. 2016). Human encounters and simulated hunts are most likely psychologically stressful for brown bears. However, bears had higher HRV values during the experiment days contrary to the predictions [P16,17 and 18]. The method used to obtain the HRV values is sensitive to the variability of the heart rates over the 24-hour period. A bear with some very high heart rates or some very low heart rates during a same day will for example have a higher HRV than a bear with more constant mean heart rates. Higher heart rates were recorded the day of simulated hunts and could have explained the higher HRV values observed. However, human encounters did not lead to significantly higher heart rates, but did lead to higher HRV values. Støen et al. (2015) found higher HRV values in bears that had travelled longer distances. The longer distances travelled the day of the human encounters and simulated hunts could have explained the higher HRV values found the day of the experiments, but bears did not travel longer distances the day after the experiments, and still had higher HRV values. Little research has been carried out on the impact of overtraining and physical overreach on the HRV in humans (Urhausen & Kindermann 2002). When Urhausen and Kindermann (2002) reviewed the present findings, they concluded that results have differed in several studies making it difficult to establish an overtraining diagnosis based on HRV. The high HRV measured in bears the day following the experiments could be due to a physical overreaching but no clear support for this theory is established.

Nevertheless, as predicted, a different HRV was measured after the experiments [P23]. Supporting the hypothesis that dog hunts and human encounters have lasting physiological effects on brown bears [H4]. Ordiz et al. (2013b) showed that bears altered their daily movement patterns after having been disturbed by human encounters. Bears travelled longer distances during the night and shorter distances during the day than they did during the previous week (Ordiz et al. 2013b). The effect was mainly observed the two first days after the disturbance. The high HRV values recorded the day after the disturbance could thus be due to a change in behaviour that lasted after the event. Both human encounters and simulated hunts led to the same change in HRV, suggesting that in both situations bears may have changed their behaviour in a similar way. However, no further support was found for the hypothesis that human encounters and dog hunts have a lasting physiological and behavioural effect [H4] as the predictions to find different values in distance travelled [P19], in speed [P20], in maximum heart rate [P21] and in body temperature area [P22] were not verified when comparing the control periods to the 2 days following the experiments.

Since travelling longer distances (Rode et al. 2007) and running faster (Taylor et al. 1982) can be associated with higher energy costs, human encounters and dog hunts can be considered as disturbances that have a direct cost in energy, with dog hunts that have an even higher energy cost. Simulated hunts also led to higher heart rates and greater body temperature areas, implying a clear energy cost due to the disturbance. Gervasi et al. (2006), when predicting the passive or active behaviour of the bears, could not differentiate specific active behaviours, such as eating or walking. The time spent foraging could thus not be quantitively measured. Nevertheless, human encounters and simulated hunts represented time during which bears were potentially prevented from foraging implying an additional energy cost. When Ordiz et al. (2013b) discussed the lasting behavioural impact of human encounters on bears, they mentioned that changes in the bears' time allocation could have an impact on their fitness. Human encounters and simulated hunts may thus have a direct cost in energy associated to the energy needed during the fleeing behaviour and an indirect energy cost due to the change in behaviour during the days following the disturbance.

If a bear is frequently disturbed by human encounters and dog hunts, its body condition may be affected by the energy cost they represent. It has been shown that the food conditions of the year influenced the size (Zedrosser et al. 2006) and the weight (Hertel et al. 2018) of the adult females. Bears do not always reach their needs, as poor berry seasons affect the reproductive success of the lightweight females in Sweden (Hertel et al. 2018). Additional energy costs due to human encounters and dog hunts may have similar effects as poor berry seasons by lowering the weight and body fat content of the bears and affect their fitness by preventing their reproduction. Dahle et al. (2006) found that bigger females gave birth to bigger yearlings with a better survival. If these disturbances have a comparable effect to unfavourable berry years and they occur every year, the size of the females could be affected as well as the survival of their cubs. Massopust and Anderson (1984) carried out 8 dog hunts on 5 black bears with a maximum of 2 dog hunts per individual. The authors did not observe any injuries or important loss in weight on the bears when they captured them again at their den. More than 2 dog hunts are thus probably needed to affect the weight of the bears. Rode et al. (2007) did not find any loss in weight either, nor any changes in body condition when experimentally introducing tourism (bear viewing) for 1 summer in an undisturbed bear area in Alaska. However, the studied bear population could feed on salmon (*Oncorhynchus kisutch and O. nerk*) a more nutrient-rich alimentation than the berries eaten by the Scandinavian brown bears (Welch et al. 1997).

Several aspects with regards to the design of this study's experiments need to be discussed. First, the simulated hunts were carried out later in the season than the human encounters. The bears' behaviour and physiology could thus have been different due to seasonal changes. However, no differences were found between the control period before the human encounters and the control period before the simulated hunts for any of the tested response variables. Furthermore, decreasing heart rates, body temperatures and HRVs were measured before den entry (Evans et al. 2016a). A seasonal effect may have led to an incorrect underestimation of the effects of simulated hunts. The results presented in this study should, for this reason, be conservative when saying that dog hunts have an impact. Secondly, the results may be more representative of the impact on adult females, as adult female individuals were used more often throughout the experiments. Moen et al. (2012) found that younger bears had a longer FID, suggesting that younger bears may be impacted more by human encounters and simulated hunts. However, the authors found no effect of age and sex when looking at the distance travelled by bears after a human encounter. Thirdly, simulated hunts may have been different from real dog hunts as the bear could be tracked. The bears' collars were however mainly used to find the individual and make sure the experiment was carried out on the right bear. Hunters hired for this study mimicked their normal hunts once the bear was found. The simulated hunts should thus be very close to dog hunts. Fourthly, the 3-day control periods could only be assumed to be control periods, as it was not possible to know what happened to the bear during this time. However, if any non-experimental disturbances had occurred, the differences between the values recorded during the experimental days and the control period would have been smaller. Higher p-values would have been found and interpreted as being not significant. As the main interest of the pairwise analyses was to find differences, the method used is robust to non-experimental disturbances in the control periods. Lastly, no human encounters or simulated hunts were experimentally carried out on an adult female with its cubs. This is because family groups may get separated when fleeing. It is thus not possible to know what would have happened if this precaution would not have been taken. However, Elowe (1990) never recorded a dog hunt carried out on black bears that separated the family group for longer than the hunt. Dog hunts should thus not lead to family group separations in brown bears either. It has also recently been shown that Scandinavian brown bear female adults tend to provide maternal care for a longer period at higher hunting pressures (Van de Walle et al. 2018). One could have expected shorter periods if dog hunts typically lead to family separations. As dog hunts have more dramatic impacts than human encounters, one should not expect family separations after human encounters.

After reviewing all known indirect effects of hunting on the Scandinavian brown bear, Frank et al. (2017) conclude that those effects should be accounted for by managers as population growth rates can also be affected by them. Further research is needed to assess if bears that are repeatedly disturbed by dog hunts have lower fitness levels. Nonetheless, if it is the case, this effect should be added to the list of indirect effects presented by Frank et al. (2017) and considered by managers. Other hunters using dogs, such as moose hunters, should also be considered as they can also affect bears.

Human encounters have a lower impact than dog hunts on the bears. Human encounters are however not restricted in time like dog hunts are. There is no season when humans are not allowed to go in the forest for instance. Dog hunt events also most likely happen less often than human encounters. Human encounters may thus have a lower impact per se but may still have an important impact due to their higher frequency. Bears situated in high human density areas, in popular touristic areas or where more dog hunts occur may be disturbed more often and be subsequently be impacted more.

Conclusion:

Dog hunts represent a greater physiological and behavioural source of disturbance for brown bears than human encounters. Bears were behaviourally disturbed by human encounters but did not have different heart rates and body temperatures. Dog hunts are disturbances that have lasting behavioural effects on bears by inducing longer resting periods the day following the actual dog hunt. The higher HRV found the day after human encounters and simulated hunts indicates that both types of disturbance have lasting physiological impacts. Longer resting periods found after longer simulated hunts suggested that the impact of dog hunts increases with their length. By representing an energy cost, human encounters and dog hunts could lower the bears' fitness if experienced frequently. As both disturbance types will most likely increase in frequency in the future, their impact may increase in importance and should be considered by managers.

References:

Arnemo, J. M. & Evans, A. (2017). Biomedical protocols for free-ranging brown bears, wolves, wolverines and lynx. Inland Norway University of Applied Sciences, Campus Evenstad.

Bassett, D. (2016). A literature review of heart rate variability in depressive and bipolar disorders. *Australian & New Zealand Journal of Psychiatry*, 50 (6): 511-519.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014). *Fitting linear mixed-effects models using lme4*. arXiv preprint arXiv:1406.5823. pp. version 1.1-14.

Bateson, P. & Bradshaw, E. L. (1997). Physiological effects of hunting red deer (Cervus elaphus). In vol. 264 *Proceedings of the Royal Society of London B: Biological Sciences*, pp. 1707-1714: The Royal Society.

Bischof, R., Fujita, R., Zedrosser, A., Söderberg, A. & Swenson, J. E. (2008). Hunting patterns, ban on baiting, and harvest demographics of brown bears in Sweden. *Journal of Wildlife Management*, 72 (1): 79-88.

Bischof, R., Swenson, J. E., Yoccoz, N. G., Mysterud, A. & Gimenez, O. (2009). The magnitude and selectivity of natural and multiple anthropogenic mortality causes in hunted brown bears. *Journal of Animal Ecology*, 78 (3): 656-665.

Bischof, R., Bonenfant, C., Rivrud, I. M., Zedrosser, A., Friebe, A., Coulson, T., Mysterud, A. & Swenson, J. E. (2017). Regulated hunting re-shapes the life history of brown bears. *Nature ecology & evolution*, 2 (1): 116-123.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in ecology & evolution*, 24 (3): 127-135.

Chapron, G., Kaczensky, P., Linnell, J. D., Von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F. & Anders, O. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *science*, 346 (6216): 1517-1519.

Culik, B., Adelung, D. & Woakes, A. (1990). The effect of disturbance on the heart rate and behaviour of Adélie penguins (Pygoscelis adeliae) during the breeding season. In Kerry, K. R. & Hempel, G. (eds) *Antarctic ecosystems*, pp. 177-182: Springer.

Dahle, B., Sørensen, O. J., Wedul, E. H., Swenson, J. E. & Sandegren, F. (1998). The diet of brown bears Ursus arctos in central Scandinavia: effect of access to free-ranging domestic sheep Ovis aries. *Wildlife biology*, 4 (3): 147-158.

Dahle, B. & Swenson, J. E. (2003). Family breakup in brown bears: are young forced to leave? *Journal of Mammalogy*, 84 (2): 536-540.

Dahle, B., Zedrosser, A. & Swenson, J. E. (2006). Correlates with body size and mass in yearling brown bears (Ursus arctos). *Journal of Zoology*, 269 (3): 273-283.

Davenne, D. (2009). Sleep of athletes–problems and possible solutions. *Biological Rhythm Research*, 40 (1): 45-52.

Ditmer, M. A., Vincent, J. B., Werden, L. K., Tanner, J. C., Laske, T. G., Iaizzo, P. A., Garshelis, D. L. & Fieberg, J. R. (2015). Bears show a physiological but limited behavioral response to unmanned aerial vehicles. *Current Biology*, 25 (17): 2278-2283.

Ditmer, M. A., Rettler, S. J., Fieberg, J. R., Iaizzo, P. A., Laske, T. G., Noyce, K. V. & Garshelis, D. L. (2018). American black bears perceive the risks of crossing roads. *Behavioral Ecology*, 00 (00): 1-9.

Elfström, M., Swenson, J. E. & Ball, J. P. (2008). Selection of denning habitats by Scandinavian brown bears Ursus arctos. *Wildlife Biology*, 14 (2): 176-187.

Elowe, K. (ed.) (1990). *Bear hunting with hounds: techniques and effects on bears and the public*. Proceedings of the Eastern Black Bear Workshop, vol. 10. 101-109 pp.

Ericsson, G., Neumann, W. & Dettki, H. (2015). Moose anti-predator behaviour towards baying dogs in a wolf-free area. *European journal of wildlife research*, 61 (4): 575-582.

Eriksson, M., Sandström, C. & Ericsson, G. (2015). Direct experience and attitude change towards bears and wolves. *Wildlife Biology*, 21 (3): 131-137.

Evans, A. L., Singh, N. J., Friebe, A., Arnemo, J. M., Laske, T., Fröbert, O., Swenson, J. E. & Blanc, S. (2016a). Drivers of hibernation in the brown bear. *Frontiers in zoology*, 13 (1): 7.

Evans, A. L., Singh, N. J., Fuchs, B., Blanc, S., Friebe, A., Laske, T. G., Frobert, O., Swenson, J. E. & Arnemo, J. M. (2016b). Physiological reactions to capture in hibernating brown bears. *Conservation physiology*, 4 (1): 1-11.

Fox, J. & Weisberg, S. (2011). *An R companion to applied regression*: Sage Publications.

Frank, S. C., Ordiz, A., Gosselin, J., Hertel, A., Kindberg, J., Leclerc, M., Pelletier, F., Steyaert, S. M., Støen, O.-G. & Van de Walle, J. (2017). Indirect effects of bear hunting: a review from Scandinavia. *Ursus*, 28 (2): 150-164.

Fredman, P., Lindhagen, A. & Nordström, G. (2012). Monitoring outdoor recreation trends in Sweden. MMV6; Stockholm.

Friebe, A., Evans, A. L., Arnemo, J. M., Blanc, S., Brunberg, S., Fleissner, G., Swenson, J. E. & Zedrosser, A. (2014). Factors affecting date of implantation, parturition, and den entry estimated from activity and body temperature in free-ranging brown bears. *PLoS One*, 9 (7): e101410.

Gacsi, M., Maros, K., Sernkvist, S., Farago, T. & Miklosi, A. (2013). Human analogue safe haven effect of the owner: behavioural and heart rate response to stressful social stimuli in dogs. *PLoS One*, 8 (3): e58475.

Gervasi, V., Brunberg, S. & Swenson, J. E. (2006). An individual-based method to measure animal activity levels: a test on brown bears. *Wildlife Society Bulletin*, 34 (5): 1314-1319.

Gosselin, J., Leclerc, M., Zedrosser, A., Steyaert, S. M., Swenson, J. E. & Pelletier, F. (2017). Hunting promotes sexual conflict in brown bears. *Journal of Animal Ecology*, 86 (1): 35-42.

Hansen, S. E. N. (2014). *Behavior of Scandinavian brown bears when encountered by dogs and humans*: Norwegian University of Life Sciences, Ås.

Hertel, A. G., Zedrosser, A., Mysterud, A., Støen, O.-G., Steyaert, S. M. & Swenson, J. E. (2016). Temporal effects of hunting on foraging behavior of an apex predator: Do bears forego foraging when risk is high? *Oecologia*, 182 (4): 1019-1029.

Hertel, A. G., Bischof, R., Langval, O., Mysterud, A., Kindberg, J., Swenson, J. E. & Zedrosser, A. (2018). Berry production drives bottom–up effects on body mass and reproductive success in an omnivore. *Oikos*, 127 (2): 197-207.

Hijmans, R. J., Williams, E., Vennes, C. & Hijmans, M. R. J. (2017). *Package 'geosphere'*. pp. version 1.5-7.

Hristienko, H. & McDonald, J. E. (2007). Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus*, 18 (1): 72-88.

Kindberg, J. & Swenson, J. (2014). Björnstammens storlek i Sverige 2013 — länsvisa skattningar och trender — Report no. 2014–2 from the Scandinavian Brown Bear Research Project.

Laske, T. G., Garshelis, D. L. & Iaizzo, P. A. (2011). Monitoring the wild black bear's reaction to human and environmental stressors. *BMC physiology*, 11 (1): 1-14.

Lennartsson, A.-K., Jonsdottir, I. & Sjörs, A. (2016). Low heart rate variability in patients with clinical burnout. *International Journal of Psychophysiology*, 110: 171-178.

Lenth, R. (2018). *emmeans: Estimated Marginal Means, aka Least-Squares Means. R package* p. version 1.1.

Livingstone, M., Coward, W., Prentice, A. M., Davies, P., Strain, J. J., McKenna, P. G., Mahoney, C. A., White, J. A., Stewart, C. M. & Kerr, M. (1992). Daily energy expenditure in free-living children: comparison of heart-rate monitoring with the doubly labeled water (2H218O) method. *The American journal of clinical nutrition*, 56 (2): 343-352.

Lopez-Alfaro, C., Robbins, C. T., Zedrosser, A. & Nielsen, S. E. (2013). Energetics of hibernation and reproductive trade-offs in brown bears. *Ecological Modelling*, 270: 1-10.

MacHutchon, A. G., Himmer, S., Davis, H. & Gallagher, M. (1998). Temporal and spatial activity patterns among coastal bear populations. In *Ursus*, pp. 539-546: International Association for Bear Research and Management.

Manchi, S. & Swenson, J. E. (2005). Denning behaviour of Scandinavian brown bears Ursus arctos. *Wildlife Biology*, 11 (2): 123-132.

Maros, K., Dóka, A. & Miklósi, Á. (2008). Behavioural correlation of heart rate changes in family dogs. *Applied Animal Behaviour Science*, 109 (2): 329-341.

Massopust, J. L. & Anderson, R. K. (1984). The response of black bears to being chased by hunting dogs. In vol. 7 *Proc. East. Workshop Black Bear Manage. and Res*, pp. 59-65.

Miller, S. D., McLellan, B. N. & Derocher, A. E. (2013). Conservation and management of large carnivores in North America. *International journal of environmental studies*, 70 (3): 383-398.

Moe, T., Kindberg, J., Jansson, I. & Swenson, J. (2007). Importance of diel behaviour when studying habitat selection: examples from female Scandinavian brown bears (Ursus arctos). *Canadian Journal of zoology*, 85 (4): 518-525.

Moen, G. K., Stoen, O. G., Sahlen, V. & Swenson, J. E. (2012). Behaviour of solitary adult Scandinavian brown bears (Ursus arctos) when approached by humans on foot. *PLoS One*, 7 (2): e31699.

Norman, A. J. (2016). *Genomic studies of contemporary processes in wild populations*. Umeå Swedish University of Agricultural Sciences, Department of Wildlife, Fish and Environmental Studies. 49 pp.

Ordiz, A., Støen, O.-G., Delibes, M. & Swenson, J. E. (2011). Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia*, 166 (1): 59-67.

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M. & Swenson, J. E. (2012). Do bears know they are being hunted? *Biological Conservation*, 152: 21-28.

Ordiz, A., Bischof, R. & Swenson, J. E. (2013a). Saving large carnivores, but losing the apex predator? *Biological Conservation*, 168: 128-133.

Ordiz, A., Støen, O. G., Sæbø, S., Sahlen, V., Pedersen, B. E., Kindberg, J. & Swenson, J. E. (2013b). Lasting behavioural responses of brown bears to experimental encounters with humans. *Journal of Applied Ecology*, 50 (2): 306-314.

Ordiz, A., Kindberg, J., Sæbø, S., Swenson, J. E. & Støen, O.-G. (2014). Brown bear circadian behavior reveals human environmental encroachment. *Biological Conservation*, 173: 1-9.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2017). *nlme: Linear and Nonlinear Mixed Effects Models*. pp. version 3.1-131

R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Robbins, C. T., Ben-David, M., Fortin, J. K. & Nelson, O. L. (2012). Maternal condition determines birth date and growth of newborn bear cubs. *Journal of Mammalogy*, 93 (2): 540-546.

Rode, K. D., Farley, S. D., Fortin, J. & Robbins, C. T. (2007). Nutritional consequences of experimentally introduced tourism in brown bears. *Journal of Wildlife Management*, 71 (3): 929-939.

Sahlén, E., Støen, O.-G. & Swenson, J. E. (2011). Brown bear den site concealment in relation to human activity in Sweden. *Ursus*, 22 (2): 152-158.

Signorell, A. (2017). *DescTools: Tools for descriptive statistics*. p. version 0.99.23.

Statistics Sweden. (2017). *Population density per sq. km, population and land area by region and sex. Year 1991 – 2016*. Available at: http://www.scb.se/en/finding-statistics/ (accessed: 30/03/2017).

Statistics Sweden. (2018). *Population and Population Changes 1749–2017*. Available at: http://www.scb.se/en/finding-statistics/ (accessed: 14/04/2018).

Stein, P. K., Bosner, M. S., Kleiger, R. E. & Conger, B. M. (1994). Heart rate variability: a measure of cardiac autonomic tone. *American heart journal*, 127 (5): 1376-1381.

Stenset, N. E., Lutnæs, P. N., Bjarnadóttir, V., Dahle, B., Fossum, K. H., Jigsved, P., Johansen, T., Neumann, W., Opseth, O. & Rønning, O. (2016). Seasonal and annual variation in the diet of brown bears Ursus arctos in the boreal forest of southcentral Sweden. *Wildlife Biology*, 22 (3): 107-116.

Støen, O.-G., Ordiz, A., Evans, A. L., Laske, T. G., Kindberg, J., Fröbert, O., Swenson, J. E. & Arnemo, J. M. (2015). Physiological evidence for a human-induced landscape of fear in brown bears (Ursus arctos). *Physiology & behavior*, 152: 244-248.

Swenson, J. E., Wabakken, P., Sandegren, F., Bjärvall, A., Franzén, R. & Söderberg, A. (1995). The Near Extinction and Recovery of Brown Bears in Scandinavia-in Relation to the Bear Management Policies of Norway and Sweden. *Wildlife Biology*, 1 (1): 11-25.

Swenson, J. E., Sandegren, F., Söderberg, A., Bjärvall, A., Franzén, R. & Wabakken, P. (1997). Infanticide caused by hunting of male bears. *Nature*, 386 (6624): 450.

Swenson, J. E., Adamič, M., Huber, D. & Stokke, S. (2007). Brown bear body mass and growth in northern and southern Europe. *Oecologia*, 153 (1): 37-47.

Swenson, J. E., Schneider, M., Zedrosser, A., Söderberg, A., Franzén, R. & Kindberg, J. (2017). Challenges of managing a European brown bear population; lessons from Sweden, 1943–2013. *Wildlife Biology*, 2017 (4): wlb. 00251.

Taelman, J., Vandeput, S., Spaepen, A. & Van Huffel, S. (2009). *Influence of mental stress on heart rate and heart rate variability*. 4th European conference of the international federation for medical and biological engineering: Springer. 1366-1369 pp.

Taylor, C. R., Heglund, N. C. & Maloiy, G. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology*, 97 (1): 1-21.

Thayer, J. F., Åhs, F., Fredrikson, M., Sollers III, J. J. & Wager, T. D. (2012). A meta-analysis of heart rate variability and neuroimaging studies: implications for heart rate variability as a marker of stress and health. *Neuroscience & Biobehavioral Reviews*, 36 (2): 747-756.

Treves, A., Kapp, K. J. & MacFarland, D. M. (2010). American black bear nuisance complaints and hunter take. *Ursus*, 21 (1): 30-42.

Urhausen, A. & Kindermann, W. (2002). Diagnosis of overtraining. *Sports medicine*, 32 (2): 95-102.

Van de Walle, J., Pigeon, G., Zedrosser, A., Swenson, J. E. & Pelletier, F. (2018). Hunting regulation favors slow life histories in a large carnivore. *Nature communications*, 9 (1): 1100.

Vaughan, M. R. & Inman, K. L. H. (2002). Hunter effort and success rates of hunting bears with hounds in Virginia. In vol. 13 *Ursus*, pp. 223-230: International Association for Bear Research and Management.

Von Borell, E., Langbein, J., Després, G., Hansen, S., Leterrier, C., Marchant-Forde, J., Marchant-Forde, R., Minero, M., Mohr, E. & Prunier, A. (2007). Heart rate variability as a measure of autonomic regulation of cardiac activity for assessing stress and welfare in farm animals—a review. *Physiology & Behavior*, 92 (3): 293-316.

Von Essen, E. (2018). The impact of modernization on hunting ethics: Emerging taboos among contemporary Swedish hunters. *Human Dimensions of Wildlife*, 23 (1): 21-38.

Weisenberger, M. E., Krausman, P. R., Wallace, M. C., De Young, D. W. & Maughan, O. E. (1996). Effects of simulated jet aircraft noise on heart rate and behavior of desert ungulates. *The Journal of Wildlife Management*, 60 (1): 52-61.

Welch, C. A., Keay, J., Kendall, K. C. & Robbins, C. T. (1997). Constraints on frugivory by bears. *Ecology*, 78 (4): 1105-1119.

Zedrosser, A., Dahle, B. & Swenson, J. E. (2006). Population density and food conditions determine adult female body size in brown bears. *Journal of Mammalogy*, 87 (3): 510-518.

Zedrosser, A., Pelletier, F., Bischof, R., Festa-Bianchet, M. & Swenson, J. E. (2013). Determinants of lifetime reproduction in female brown bears: early body mass, longevity, and hunting regulations. *Ecology*, 94 (1): 231-240.

Zeileis, A. & Grothendieck, G. (2005). zoo: S3 infrastructure for regular and irregular time series. *arXiv preprint math/0505527*.

Zuur, A., Ieno, E., Walker, N., Saveliev, A. & Smith, G. (2009). *Mixed effects models and extensions in ecology with R. Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W, editors*. New York, NY: Spring Science and Business Media. New York: Spring Science and Business Media. 574 pp.

Appendices:

Appendix 1: Heart Rate Shift Correction Method

Gervasi et al. (2006) were able to predict if bears were passive or active using the same dual-axis motion sensors that were installed in the GPS collars used for this study. As increased activity levels were expected to give higher heart rates in the bears, the activity variable was expected to be correlated with the bears' heart rate variable. However, by plotting both variables together, a mismatch between peaks of activities and peaks of heart rates was found for some bears (Figure A.1.1). As the activity recorded by the dual-axis motion sensors is linked to the GPS collar, these sensors have a satellite time, which is correct. The time of the cardiac biologgers is set during the capture just before the implantation using a device designed by Medtronic. Thus, the problem was assumed to be an incorrect time in the cardiac biologgers data. The time problem could be one of 3 types: 1) a problem that lead to a fixed shift in time, i.e. the same device has the same shift throughout the year (e.g. the whole time data stored in the cardiac biologger got shifted by 5 hours and the heart rate values did not), 2) a problem that lead to a regular shift in time, i.e. the same device changes time consistently throughout the year (e.g. one extra minute per 24 hours), 3) a problem that leads to a random time shift throughout the year.

Time shifts of 60 seconds, continuously from – 10 hours to + 10 hours were applied to the heart rate data. The correlation between the heart rate variable and the activity variable was then computed for every time shift applied, and the best correlation was assumed to indicate the true time shift (Figure A.1.2). This was then repeated for each simulated hunt day and each human encounter day (Figure A.1.3). To get a perfect match between the two variables that were not recorded at the same time and frequencies (heart rate every 2 minutes and activity every 5 minutes), a linear interpolation of both variables was carried out using the function na.approx from the zoo package, version 1.8-0 (Zeileis & Grothendieck 2005).

This method gave a correction value for each bear, sensor and year. Most devices gave the same shift throughout the year (Figure A.1.3). For each bear, sensor and year, the time shift giving the best correlation was used to correct the time of the heart rate data. By plotting the corrected heart rate data with the activity data, the applied time shifts were visually inspected to check that the correction made sense (Figure A.1.4).

Heart rate data was not used in the analysis if the activity data was not available or if the method led to a suggested time shift that was not consistent during the year, i.e. difference in suggested time shifts > 5 minutes during a year.

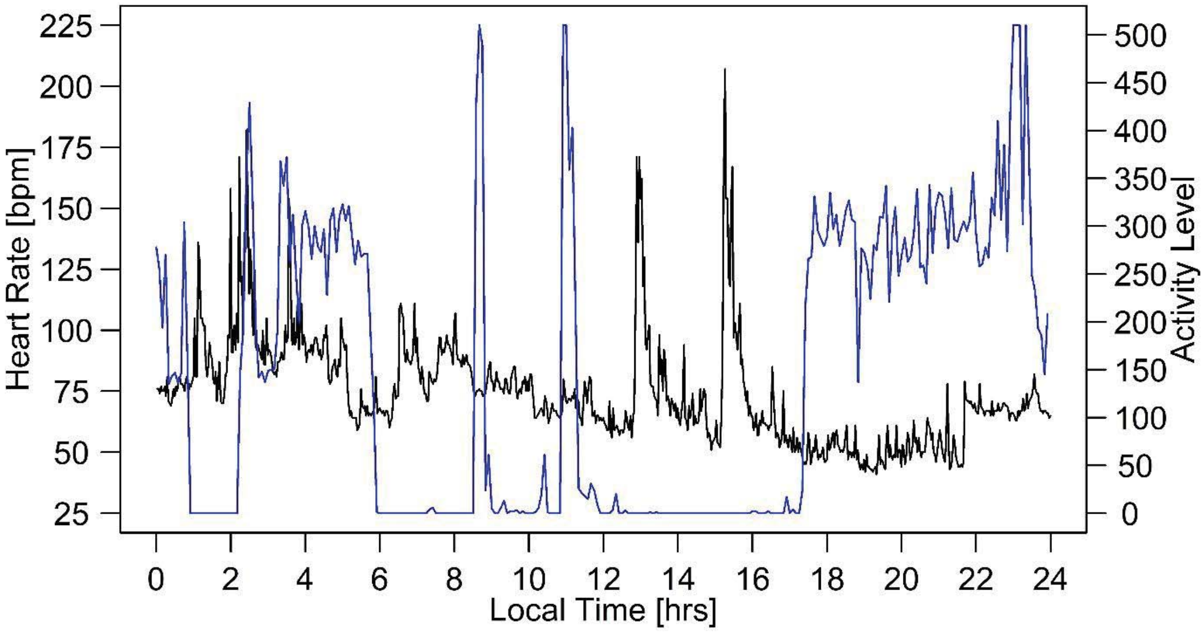


Figure A.1.1: Example of heart rate data not matching the activity data. In blue the activity of the bear, in black the heart rate of the bear. Here the peaks do not match.

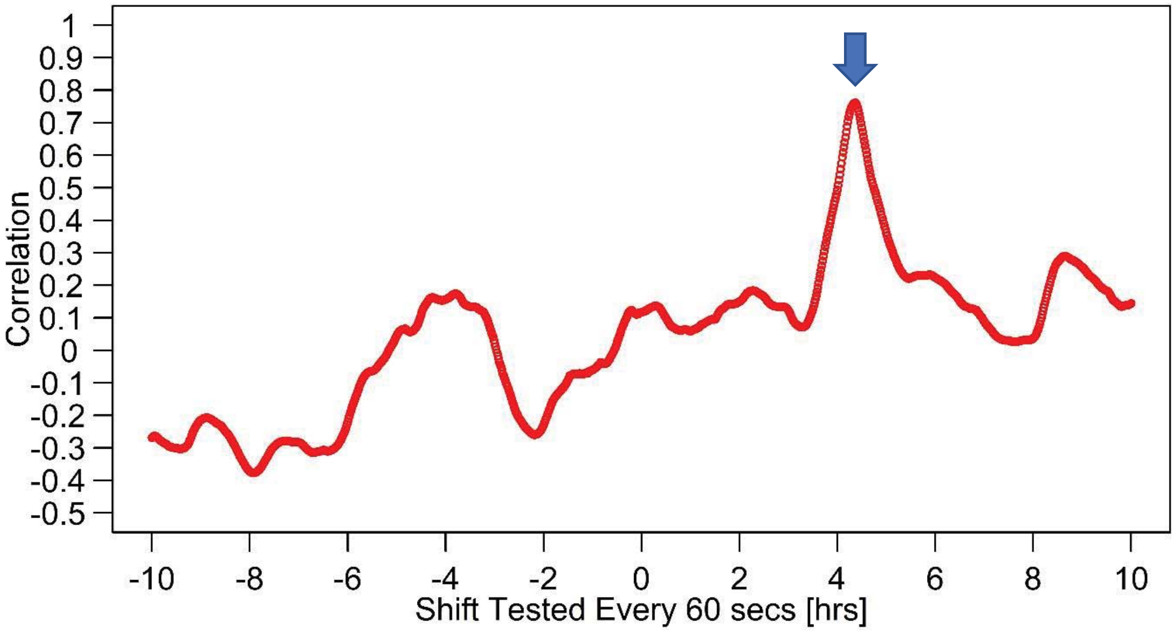


Figure A.1.2: Time shift tested every 60 seconds from -10 hours to +10 hours. The peak indicates the best correlation and the suggested time shift to be applied to the heart rate data.

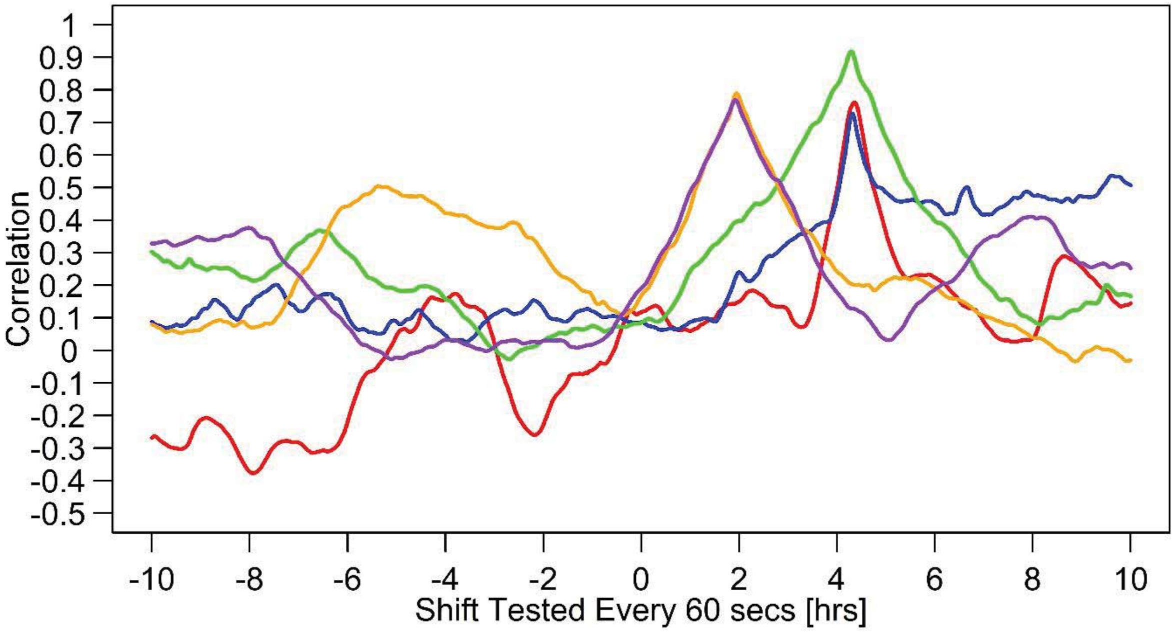


Figure A.1.3: Correlation between activity data and heart rate data tested in two different years for multiple days on the same bear with the same cardiac biologger. The purple and orange lines correspond to 2 simulated hunts in 2016 on the same bear with the same cardiac biologger. The red, green and blue lines correspond to 3 simulated hunts in 2015 on the same bear with the same cardiac biologger. Within the same bear, sensor and year, the suggested time shift was similar.

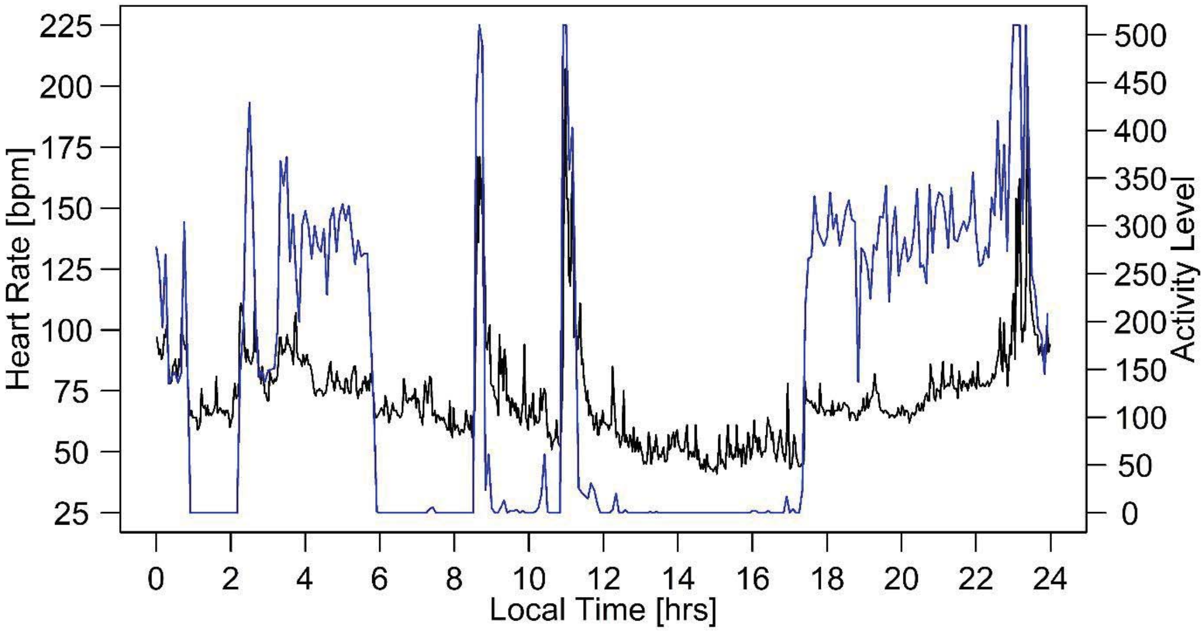


Figure A.1.4: Example plot with the time corrected for the heart rate data. In blue the activity of the bear, in black the heart rate of the bear. This is the same day, bear and cardiac biologger as in figure A.1.1.

Appendix 2: Quality of the Heart Rate Estimation

The cardiac biologgers stored some electrocardiogram (ECG) samples in addition to the heart rate data. Inspections of these ECGs showed that the software installed in the cardiac biologgers sometimes made mistakes when recognizing the R-R peaks (Figure A.2.1). In 2016, 1 bear was equipped with 2 cardiac biologgers simultaneously recording its heart rate to check the reliability of the measurements. The differences in the recorded beats per minute (bpm) between the 2 cardiac biologgers increased with increasing bpm (Figure A.2.2). This indicates a decreasing reliability of the bpm measurement at higher heart rates. A possible explanation is that higher activity of the muscles in the chest of the bear during high physical activity, e.g. when it is running, may affect the quality of the ECG (more noise). The decrease in ECG quality may make it more difficult for the software installed in the cardiac biologgers to correctly detect electric signals from the heart rate and thus may lead to more mistakes in the heart rate data.

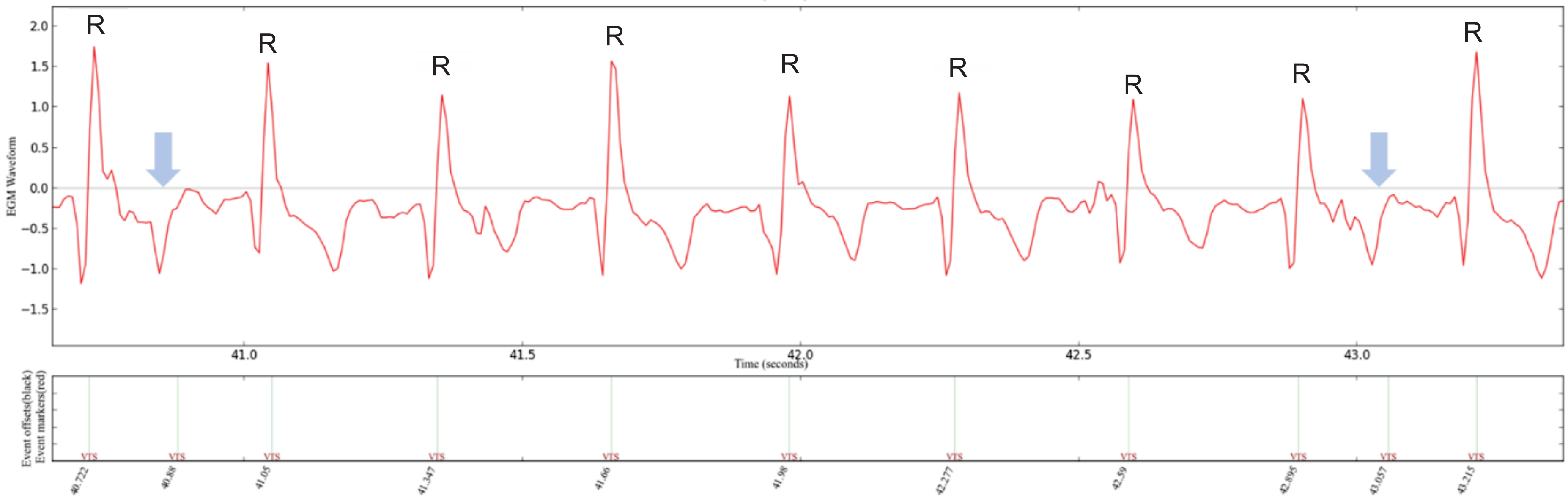
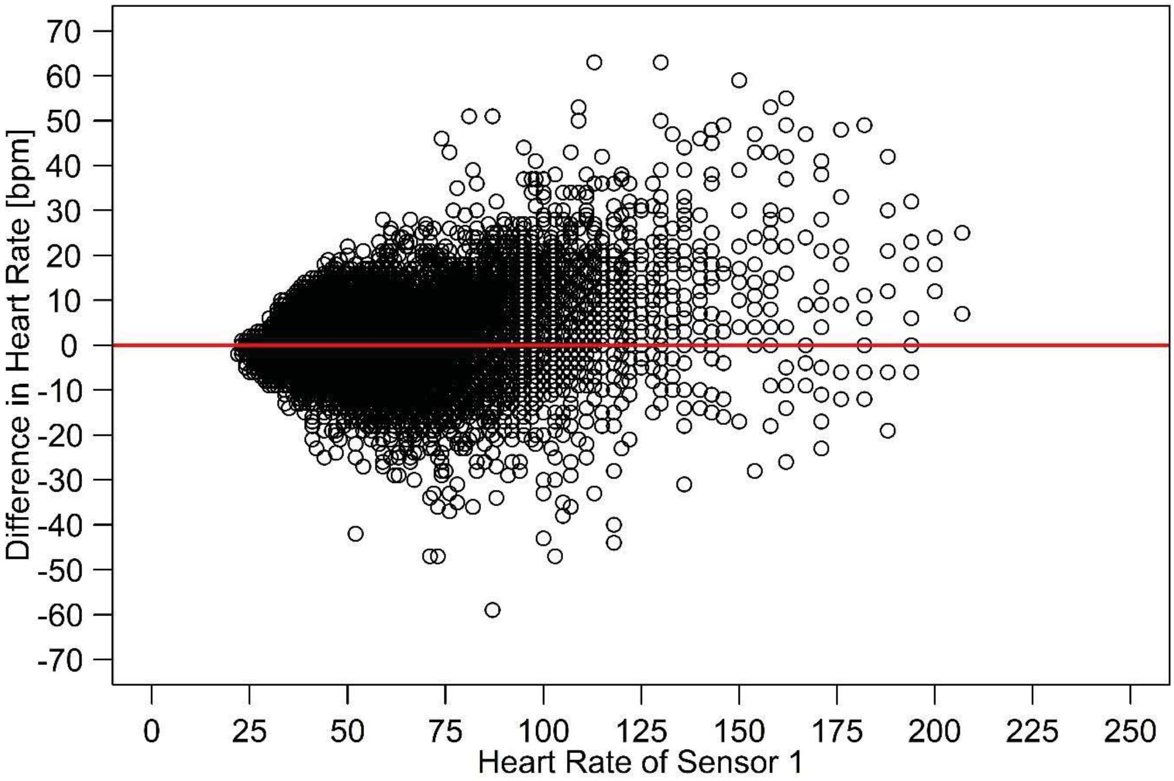


Figure A.2.1: Electrocardiogram (ECG) of the bear. The green lines in the lower plot indicate where the installed software in the cardiac biologger estimates the presence of a beat (R peaks). The "R" indicate real R peaks and the blue arrows indicate where the software made a mistake. This plot was obtained from the software Pdd EGM waveform tool (Medtronic, Minnesota, USA).



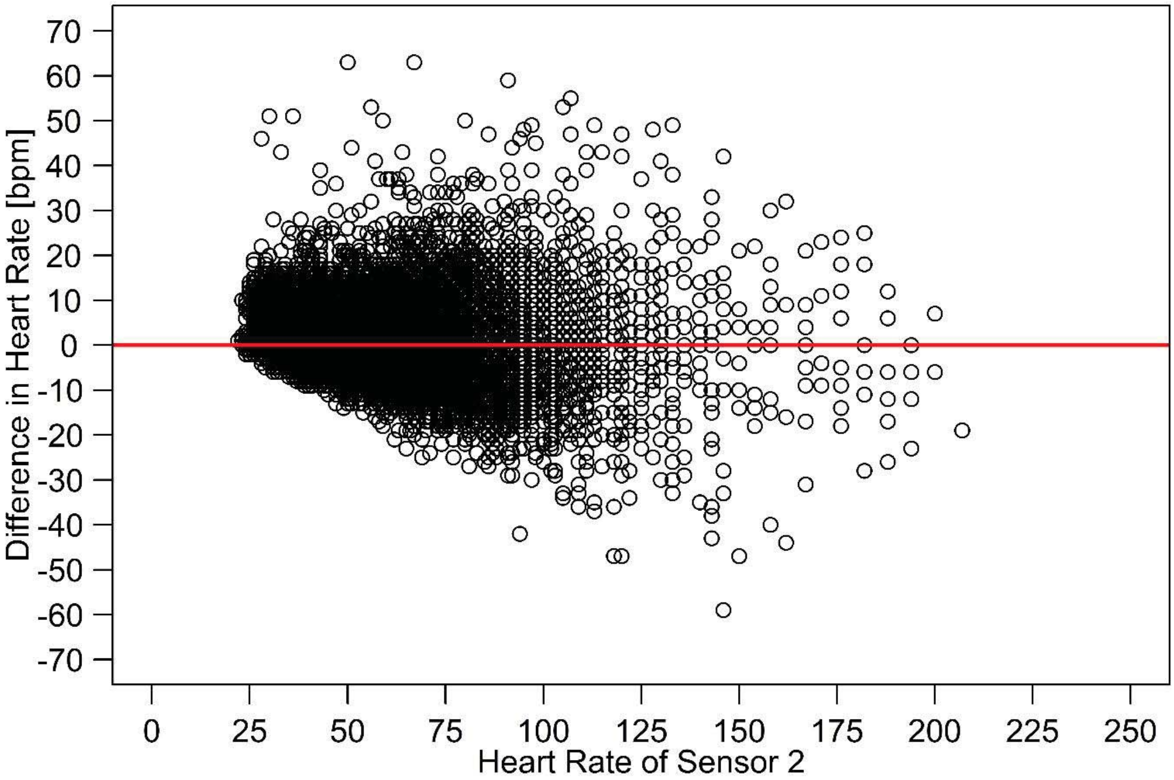


Figure A.2.2: Comparison of the heart rate measured simultaneously in the same bear by two sensors. The plots are in the shape of cone-shaped clouds pointing towards the left. This indicates a decreasing quality of the measurement at higher heart rates.

Appendix 3: T_bAREA Example

A T_bAREA value was calculated for each day (24 hours, local time) as the area situated under the body temperature (T_b) curve and above the median T_b of the bear (Figure A.3.1-A). The median T_b (here = 37.48°C) was calculated from all the T_b values of the bear recorded from 1st June to 30th September. Days involving research activities that could have affected the bear were however not included in this data. To compute the area, all the T_b values situated under the median T_b were assigned the value 0 and all the T_b values situated above the median T_b were changed by subtracting the median T_b (e.g. 42 became 4.52 (42 - 37.48 = 4.52)) (Figure A.3.1-B). The AUC function from the DescTools package, version 0.99.23 (Signorell 2017) was then used to calculate the area under the curve using a trapezoidal approximation. Figure A.3.1-C illustrates the trapezoidal approximation with non-real points. All points are connected by a direct line and the area of each trapezoid is measured and summed to give the total area.

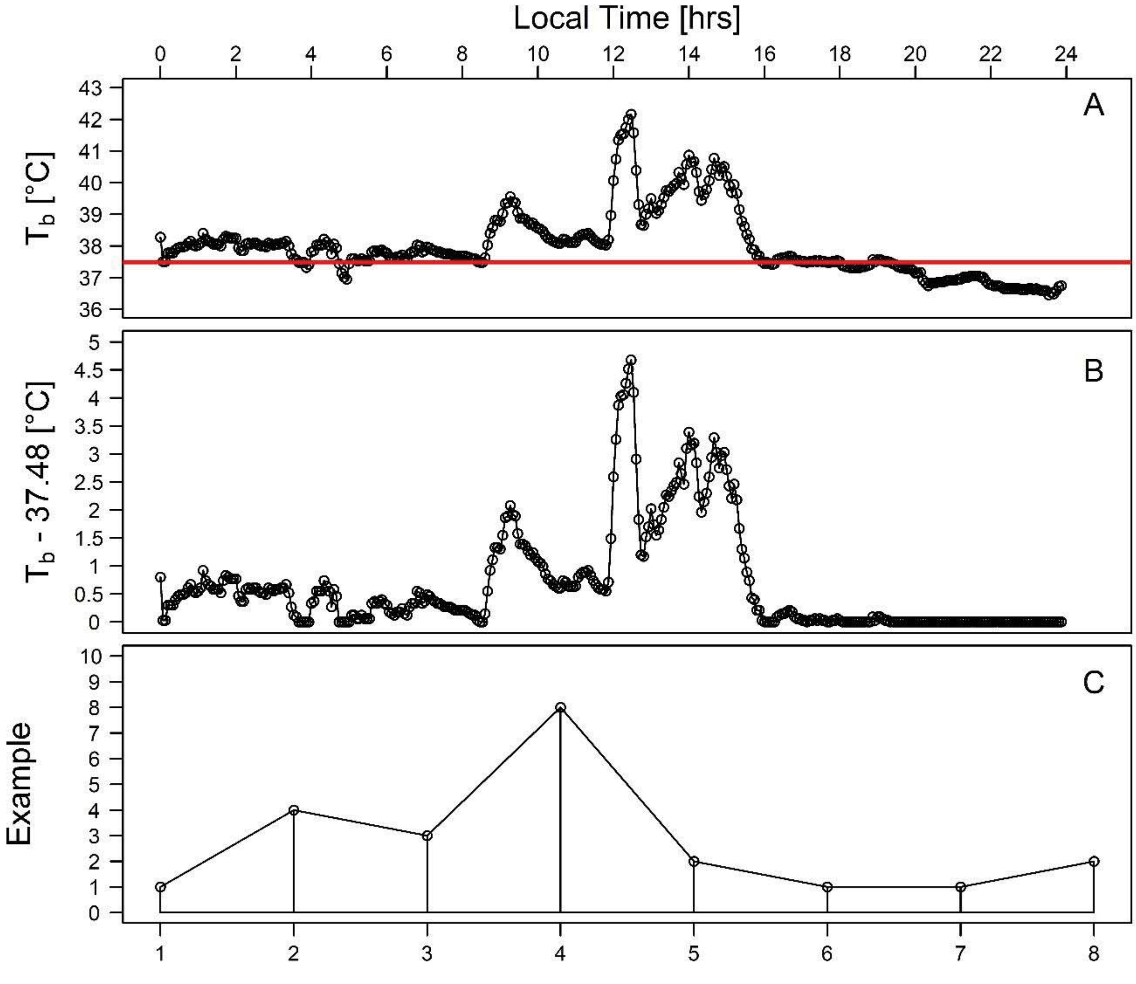


Figure A.3.1: Illustration of the method used to measure the T_bAREA values. (A) Body temperature (T_b) recorded during the day (24 hours, local time) of a simulated hunt (black line) and the median T_b of the bear (red line). (B) Illustration of the mathematical operation allowing to only consider the area above the median T_b and below the T_b values. (C) Illustration of the trapezoidal approximation allowing to measure the area under the curve (points presented in C are not real T_b values).

Appendix 4: ANOVA Tables, EMM Tables and Contrast Tables

Table A.4.1: ANOVA table (Type III Wald chi-square tests) of the LME model for the effect of the explanatory variables PERIOD, TYPE and the interaction on the response variable TRAVEL (square root transformed). This is the final model after carrying out the backward selection method. In the model, the ID of the bears and the ID of the experiments were considered as random factors, with the experiment ID factor nested in the bear ID factor.

Model TRAVEL ~ PERIOD*TYPE

	Chisq	**Df**	**Pr(>Chisq)**
Intercept	810.9	1	< 0.0001
PERIOD	11.8	3	0.0083
TYPE	0.8	1	0.3739
PERIOD:TYPE	63.4	3	< 0.0001

Table A.4.2: ANOVA table (Type III Wald chi-square tests) of the LME model for the effect of the explanatory variables PERIOD, TYPE and the interaction on the response variable MAXSPEED (square root transformed). This is the final model after carrying out the backward selection method. In the model, the ID of the bears and the ID of the experiments were considered as random factors, with the experiment ID factor nested in the bear ID factor.

Model MAXSPEED ~ PERIOD*TYPE

	Chisq	**Df**	**Pr(>Chisq)**
Intercept	977.7778	1	< 0.0001
PERIOD	19.9446	3	0.0002
TYPE	0.1	1	0.7434
PERIOD:TYPE	92.0	3	< 0.0001

Table A.4.3: ANOVA table (Type III Wald chi-square tests) of the LME model for the effect of the explanatory variables PERIOD, TYPE and the interaction on the response variable HEARTRATE30 (square root transformed). This is the final model after carrying out the backward selection method. In the model, the ID of the bears and the ID of the experiments were considered as random factors, with the experiment ID factor nested in the bear ID factor.

Model HEARTRATE30 ~ PERIOD*TYPE

	Chisq	**Df**	**Pr(>Chisq)**
Intercept	2188.8	1	< 0.0001
PERIOD	16.7	3	0.0008
TYPE	0.1	1	0.7874
PERIOD:TYPE	58.1	3	< 0.0001

Table A.4.4: ANOVA table (Type III Wald chi-square tests) of the LME model for the effect of the explanatory variables PERIOD, TYPE and the interaction on the response variable T_bAREA (square root transformed). This is the final model after carrying out the backward selection method. In the model, the ID of the bears and the ID of the experiments were considered as random factors, with the experiment ID factor nested in the bear ID factor.

Model T_BAREA ~ PERIOD*TYPE

	Chisq	**Df**	**Pr(>Chisq)**
Intercept	320.6	1	< 0.0001
PERIOD	7.8	3	0.0494
TYPE	0.6	1	0.4571
PERIOD:TYPE	28.3	3	< 0.0001

Table A.4.5: ANOVA table (Type III Wald chi-square tests) of the LME model for the effect of the explanatory variables PERIOD, TYPE and the interaction on the response variable REST. This is the final model after carrying out the backward selection method. In the model, the ID of the bears and the ID of the experiments were considered as random factors, with the experiment ID factor nested in the bear ID factor.

Model REST ~ PERIOD*TYPE

	Chisq	**Df**	**Pr(>Chisq)**
Intercept	1644.4	1	< 0.0001
PERIOD	8.4	3	0.0393
TYPE	3.9	1	0.0484
PERIOD:TYPE	35.2	3	< 0.0001

Table A.4.6: ANOVA table (Type III Wald chi-square tests) of the LME model for the effect of the explanatory variables PERIOD, TYPE and the interaction on the response variable HRV. This is the final model after carrying out the backward selection method (the variable PERIOD was the only significant variable). In the model, the ID of the bears and the ID of the experiments were considered as random factors, with the experiment ID factor nested in the bear ID factor.

Model HRV ~ PERIOD*TYPE

	Chisq	**Df**	**Pr(>Chisq)**
Intercept	574.4	1	< 0.0001
PERIOD	34.9	3	< 0.0001

Table A.4.7: EMMs of the distances travelled by the bears (TRAVEL square root transformed). EMMs are in square root kilometres. This table numerically summarizes Figure 4. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts. The 2 last columns indicate the limits of the confidence intervals.

PERIOD	TYPE	EMM	SE	df	lower.CL	upper.CL
Control period	Human	2.83	0.10	140.9	2.64	3.03
DD	Human	3.13	0.10	140.9	2.93	3.33
D1	Human	2.92	0.10	140.9	2.72	3.11
D2	Human	3.04	0.10	140.9	2.84	3.24
Control period	Hunt	2.72	0.11	155.9	2.50	2.94
DD	Hunt	3.60	0.11	155.9	3.38	3.82
D1	Hunt	2.46	0.11	155.9	2.24	2.68
D2	Hunt	2.54	0.11	155.9	2.32	2.75

Table A.4.8: EMMS of the maximum running speed of the bears (MAXSPEED square root transformed). EMMs are in square root kilometres / hour. This table numerically summarizes Figure 5. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts. The 2 last columns indicate the limits of the confidence intervals.

PERIOD	TYPE	EMM	SE	df	lower.CL	upper.CL
Control period	Human	1.24	0.04	174.7	1.16	1.31
DD	Human	1.40	0.04	174.7	1.32	1.48
D1	Human	1.24	0.04	174.7	1.16	1.32
D2	Human	1.29	0.04	174.7	1.21	1.37
Control period	Hunt	1.22	0.04	196.8	1.13	1.30
DD	Hunt	1.81	0.04	196.8	1.72	1.89
D1	Hunt	1.18	0.04	196.8	1.09	1.26
D2	Hunt	1.17	0.04	196.8	1.09	1.26

Table A.4.9: EMMs of the maximum heart rates (HEARTRATE30 square root transformed). EMMs are in square root bpm. This table numerically summarizes Figure 6. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts. The 2 last columns indicate the limits of the confidence intervals.

PERIOD	TYPE	EMM	SE	df	lower.CL	upper.CL
Control period	Human	10.32	0.22	109.9	9.88	10.76
DD	Human	11.05	0.22	109.9	10.61	11.49
D1	Human	10.10	0.22	109.9	9.66	10.54
D2	Human	10.34	0.22	109.9	9.90	10.78
Control period	Hunt	10.24	0.20	83.7	9.85	10.63
DD	Hunt	12.89	0.20	83.7	12.50	13.28
D1	Hunt	9.95	0.20	83.7	9.56	10.34
D2	Hunt	10.06	0.20	83.7	9.67	10.45

Table A.4.10: EMMS of the body temperature areas (T_bAREA square root transformed). EMMs are in square root T_bAREA. This table numerically summarizes Figure 7. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts. The 2 last columns indicate the limits of the confidence intervals.

PERIOD	TYPE	EMM	SE	df	lower.CL	upper.CL
Control period	Human	110.09	6.17	141.9	97.89	122.29
DD	Human	110.16	6.17	141.9	97.96	122.36
D1	Human	97.97	6.17	141.9	85.78	110.17
D2	Human	96.33	6.17	141.9	84.13	108.53
Control period	Hunt	103.68	6.48	96.4	90.82	116.54
DD	Hunt	144.28	6.48	96.4	131.42	157.14
D1	Hunt	86.76	6.48	96.4	73.89	99.62
D2	Hunt	98.24	6.48	96.4	85.38	111.11

Table A.4.11: EMMs of amount of time the bears rested in 24 hours (REST). EMMs are in minutes. This table numerically summarizes Figure 8. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts. The 2 last columns indicate the limits of the confidence intervals.

PERIOD	TYPE	EMM	SE	df	lower.CL	upper.CL
Control period	Human	658.68	16.29	133.4	626.47	690.89
DD	Human	664.35	16.29	133.4	632.14	696.56
D1	Human	631.24	16.29	133.4	599.03	663.45
D2	Human	630.08	16.29	133.4	597.87	662.29
Control period	Hunt	618.58	17.22	135.0	584.53	652.63
DD	Hunt	619.15	17.22	135.0	585.11	653.20
D1	Hunt	695.89	17.22	135.0	661.84	729.93
D2	Hunt	653.39	17.22	135.0	619.34	687.43

Table A.4.12: EMMs of the HRV. EMMs are in milliseconds. This table numerically summarizes Figure 10. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts. The 2 last columns indicate the limits of the confidence intervals.

PERIOD	EMM	SE	df	lower.CL	upper.CL
Control period	195.71	8.18	35.4	179.12	212.31
DD	224.38	8.18	35.4	207.78	240.98
D1	218.01	8.18	35.4	201.41	234.61
D2	207.08	8.18	35.4	190.48	223.67

Table A.4.13: Results of the pairwise analyses of the EMMs of the distance travelled by the bears in 24 hours (TRAVEL) depending on the explanatory variables PERIOD and TYPE. The variable TRAVEL was square root transformed to improve the normality of the residuals. The values presented here are based on a 0.95 confidence level with the Tukey correction method. This table numerically summarizes Figure 4. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts.

Contrast	estimate	SE	df	t.ratio	p.value
Control period,Human - DD,Human	-0.298	0.094	531.0	-3.177	0.034
Control period,Human - D1,Human	-0.085	0.094	531.0	-0.902	0.986
Control period,Human - D2,Human	-0.205	0.094	531.0	-2.190	0.360
Control period,Human - Control period,Hunt	0.113	0.127	466.6	0.885	0.987
Control period,Human - DD,Hunt	-0.766	0.127	466.6	-6.024	< 0.0001
Control period,Human - D1,Hunt	0.372	0.127	466.6	2.924	0.070
Control period,Human - D2,Hunt	0.296	0.127	466.6	2.329	0.280
DD,Human - D1,Human	0.213	0.094	531.0	2.275	0.309
DD,Human - D2,Human	0.093	0.094	531.0	0.987	0.976
DD,Human - Control period,Hunt	0.411	0.127	466.6	3.227	0.029
DD,Human - DD,Hunt	-0.468	0.127	466.6	-3.681	0.006
DD,Human - D1,Hunt	0.670	0.127	466.6	5.267	< 0.0001
DD,Human - D2,Hunt	0.594	0.127	466.6	4.672	< 0.0001
D1,Human - D2,Human	-0.121	0.094	531.0	-1.288	0.903
D1,Human - Control period,Hunt	0.197	0.127	466.6	1.550	0.780
D1,Human - DD,Hunt	-0.682	0.127	466.6	-5.359	< 0.0001
D1,Human - D1,Hunt	0.457	0.127	466.6	3.589	0.009
D1,Human - D2,Hunt	0.381	0.127	466.6	2.994	0.058
D2,Human - Control period,Hunt	0.318	0.127	466.6	2.499	0.198
D2,Human - DD,Hunt	-0.561	0.127	466.6	-4.409	< 0.0001
D2,Human - D1,Hunt	0.577	0.127	466.6	4.539	< 0.0001
D2,Human - D2,Hunt	0.502	0.127	466.6	3.944	0.002
Control period,Hunt - DD,Hunt	-0.879	0.101	531.0	-8.711	< 0.0001
Control period,Hunt - D1,Hunt	0.259	0.101	531.0	2.571	0.169
Control period,Hunt - D2,Hunt	0.184	0.101	531.0	1.821	0.606
DD,Hunt - D1,Hunt	1.138	0.101	531.0	11.282	< 0.0001
DD,Hunt - D2,Hunt	1.063	0.101	531.0	10.532	< 0.0001
D1,Hunt - D2,Hunt	-0.076	0.101	531.0	-0.750	0.995

Table A.4.14: Results of the pairwise analyses of the EMMs of the maximum speed of the bears in 24 hours (MAXSPEED) depending on the explanatory variables PERIOD and TYPE. The variable MAXSPEED was square root transformed to improve the normality of the residuals. The values presented here are based on a 0.95 confidence level with the Tukey correction method. This table numerically summarizes Figure 5. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts.

Contrast	estimate	SE	df	t.ratio	p.value
Control period,Human - DD,Human	-0.163	0.042	531.0	-3.895	0.003
Control period,Human - D1,Human	-0.002	0.042	531.0	-0.055	1.000
Control period,Human - D2,Human	-0.055	0.042	531.0	-1.314	0.894
Control period,Human - Control period,Hunt	0.017	0.051	576.6	0.326	1.000
Control period,Human - DD,Hunt	-0.571	0.051	576.6	-11.285	< 0.0001
Control period,Human - D1,Hunt	0.056	0.051	576.6	1.103	0.956
Control period,Human - D2,Hunt	0.062	0.051	576.6	1.232	0.922
DD,Human - D1,Human	0.160	0.042	531.0	3.840	0.003
DD,Human - D2,Human	0.108	0.042	531.0	2.581	0.165
DD,Human - Control period,Hunt	0.179	0.051	576.6	3.537	0.010
DD,Human - DD,Hunt	-0.409	0.051	576.6	-8.075	< 0.0001
DD,Human - D1,Hunt	0.218	0.051	576.6	4.314	< 0.0001
DD,Human - D2,Hunt	0.225	0.051	576.6	4.442	< 0.0001
D1,Human - D2,Human	-0.053	0.042	531.0	-1.259	0.913
D1,Human - Control period,Hunt	0.019	0.051	576.6	0.371	1.000
D1,Human - DD,Hunt	-0.569	0.051	576.6	-11.240	< 0.0001
D1,Human - D1,Hunt	0.058	0.051	576.6	1.149	0.946
D1,Human - D2,Hunt	0.065	0.051	576.6	1.277	0.907
D2,Human - Control period,Hunt	0.071	0.051	576.6	1.409	0.853
D2,Human - DD,Hunt	-0.516	0.051	576.6	-10.202	< 0.0001
D2,Human - D1,Hunt	0.111	0.051	576.6	2.186	0.362
D2,Human - D2,Hunt	0.117	0.051	576.6	2.315	0.287
Control period,Hunt - DD,Hunt	-0.588	0.045	531.0	-13.098	< 0.0001
Control period,Hunt - D1,Hunt	0.039	0.045	531.0	0.877	0.988
Control period,Hunt - D2,Hunt	0.046	0.045	531.0	1.022	0.971
DD,Hunt - D1,Hunt	0.627	0.045	531.0	13.975	< 0.0001
DD,Hunt - D2,Hunt	0.634	0.045	531.0	14.120	< 0.0001
D1,Hunt - D2,Hunt	0.007	0.045	531.0	0.145	1.000

Table A.4.15: Results of the pairwise analyses of the EMMs of the maximum heart rate measured in the bears for 24 hours (HEARTRATE30) depending on the explanatory variables PERIOD and TYPE. The variable HEARTRATE30 was square root transformed to improve the normality of the residuals. The values presented here are based on a 0.95 confidence level with the Tukey correction method. This table numerically summarizes Figure 6. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts.

Contrast	estimate	SE	df	t.ratio	p.value
Human,Control period - Hunt,Control period	0.072	0.269	223.7	0.266	1.000
Human,Control period - Human,DD	-0.731	0.247	201.0	-2.966	0.065
Human,Control period - Hunt,DD	-2.573	0.269	223.7	-9.572	< 0.0001
Human,Control period - Human,D1	0.216	0.247	201.0	0.876	0.988
Human,Control period - Hunt,D1	0.364	0.269	223.7	1.354	0.877
Human,Control period - Human,D2	-0.025	0.247	201.0	-0.101	1.000
Human,Control period - Hunt,D2	0.255	0.269	223.7	0.948	0.981
Hunt,Control period - Human,DD	-0.803	0.269	223.7	-2.988	0.061
Hunt,Control period - Hunt,DD	-2.645	0.210	201.0	-12.595	< 0.0001
Hunt,Control period - Human,D1	0.144	0.269	223.7	0.537	0.999
Hunt,Control period - Hunt,D1	0.292	0.210	201.0	1.392	0.860
Hunt,Control period - Human,D2	-0.097	0.269	223.7	-0.359	1.000
Hunt,Control period - Hunt,D2	0.183	0.210	201.0	0.873	0.988
Human,DD - Hunt,DD	-1.842	0.269	223.7	-6.851	< 0.0001
Human,DD - Human,D1	0.947	0.247	201.0	3.842	0.004
Human,DD - Hunt,D1	1.095	0.269	223.7	4.075	0.002
Human,DD - Human,D2	0.707	0.247	201.0	2.865	0.085
Human,DD - Hunt,D2	0.986	0.269	223.7	3.669	0.007
Hunt,DD - Human,D1	2.789	0.269	223.7	10.376	< 0.0001
Hunt,DD - Hunt,D1	2.937	0.210	201.0	13.987	< 0.0001
Hunt,DD - Human,D2	2.548	0.269	223.7	9.480	< 0.0001
Hunt,DD - Hunt,D2	2.828	0.210	201.0	13.468	< 0.0001
Human,D1 - Hunt,D1	0.148	0.269	223.7	0.550	0.999
Human,D1 - Human,D2	-0.241	0.247	201.0	-0.977	0.977
Human,D1 - Hunt,D2	0.039	0.269	223.7	0.145	1.000
Hunt,D1 - Human,D2	-0.389	0.269	223.7	-1.447	0.834
Hunt,D1 - Hunt,D2	-0.109	0.210	201.0	-0.519	1.000
Human,D2 - Hunt,D2	0.280	0.269	223.7	1.041	0.968

Table A.4.16: Results of the pairwise analyses of the EMMs of the body temperature area (T_bAREA) depending on the explanatory variables PERIOD and TYPE. The variable T_bAREA was square root transformed to improve the normality of the residuals. The values presented here are based on a 0.95 confidence level with the Tukey correction method. This table numerically summarizes Figure 7. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts.

Contrast	estimate	SE	df	t.ratio	p.value
Control period,Human - DD,Human	-0.068	6.578	270.0	-0.010	1.000
Control period,Human - D1,Human	12.117	6.578	270.0	1.842	0.592
Control period,Human - D1,Human	13.760	6.578	270.0	2.092	0.423
Control period,Human - Control period,Hunt	6.409	8.717	241.2	0.735	0.996
Control period,Human - DD,Hunt	-34.192	8.717	241.2	-3.923	0.003
Control period,Human - D1,Hunt	23.334	8.717	241.2	2.677	0.135
Control period,Human - D1,Hunt	11.846	8.717	241.2	1.359	0.875
DD,Human - D1,Human	12.185	6.578	270.0	1.852	0.585
DD,Human - D1,Human	13.828	6.578	270.0	2.102	0.416
DD,Human - Control period,Hunt	6.477	8.717	241.2	0.743	0.996
DD,Human - DD,Hunt	-34.124	8.717	241.2	-3.915	0.003
DD,Human - D1,Hunt	23.401	8.717	241.2	2.685	0.132
DD,Human - D1,Hunt	11.914	8.717	241.2	1.367	0.871
D1,Human - D1,Human	1.643	6.578	270.0	0.250	1.000
D1,Human - Control period,Hunt	-5.707	8.717	241.2	-0.655	0.998
D1,Human - DD,Hunt	-46.309	8.717	241.2	-5.313	< 0.0001
D1,Human - D1,Hunt	11.217	8.717	241.2	1.287	0.903
D1,Human - D1,Hunt	-0.270	8.717	241.2	-0.031	1.000
D1,Human - Control period,Hunt	-7.350	8.717	241.2	-0.843	0.990
D1,Human - DD,Hunt	-47.952	8.717	241.2	-5.501	< 0.0001
D1,Human - D1,Hunt	9.574	8.717	241.2	1.098	0.957
D1,Human - D1,Hunt	-1.913	8.717	241.2	-0.219	1.000
Control period,Hunt - DD,Hunt	-40.602	6.722	270.0	-6.040	< 0.0001
Control period,Hunt - D1,Hunt	16.924	6.722	270.0	2.518	0.193
Control period,Hunt - D1,Hunt	5.437	6.722	270.0	0.809	0.993
DD,Hunt - D1,Hunt	57.526	6.722	270.0	8.557	< 0.0001
DD,Hunt - D1,Hunt	46.038	6.722	270.0	6.849	< 0.0001
D1,Hunt - D1,Hunt	-11.487	6.722	270.0	-1.709	0.682

Table A.4.17: Results of the pairwise analyses of the EMMs of the amount of time the bears rested (REST) depending on the explanatory variables PERIOD and TYPE. The values presented here are based on a 0.95 confidence level with the Tukey correction method. This table numerically summarizes Figure 8. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts.

Contrast	estimate	SE	df	t.ratio	p.value
Human,Control period - Hunt,Control period	40.102	20.438	403.8	1.962	0.509
Human,Control period - Human,DD	-5.671	15.230	474.0	-0.372	1.000
Human,Control period - Hunt,DD	39.526	20.438	403.8	1.934	0.528
Human,Control period - Human,D1	27.439	15.230	474.0	1.802	0.619
Human,Control period - Hunt,D1	-37.205	20.438	403.8	-1.820	0.607
Human,Control period - Human,D2	28.598	15.230	474.0	1.878	0.567
Human,Control period - Hunt,D2	5.295	20.438	403.8	0.259	1.000
Hunt,Control period - Human,DD	-45.773	20.438	403.8	-2.240	0.330
Hunt,Control period - Hunt,DD	-0.577	15.615	474.0	-0.037	1.000
Hunt,Control period - Human,D1	-12.663	20.438	403.8	-0.620	0.999
Hunt,Control period - Hunt,D1	-77.308	15.615	474.0	-4.951	< 0.0001
Hunt,Control period - Human,D2	-11.505	20.438	403.8	-0.563	0.999
Hunt,Control period - Hunt,D2	-34.808	15.615	474.0	-2.229	0.336
Human,DD - Hunt,DD	45.196	20.438	403.8	2.211	0.347
Human,DD - Human,D1	33.110	15.230	474.0	2.174	0.369
Human,DD - Hunt,D1	-31.534	20.438	403.8	-1.543	0.784
Human,DD - Human,D2	34.268	15.230	474.0	2.250	0.324
Human,DD - Hunt,D2	10.966	20.438	403.8	0.537	0.999
Hunt,DD - Human,D1	-12.087	20.438	403.8	-0.591	0.999
Hunt,DD - Hunt,D1	-76.731	15.615	474.0	-4.914	< 0.0001
Hunt,DD - Human,D2	-10.928	20.438	403.8	-0.535	0.999
Hunt,DD - Hunt,D2	-34.231	15.615	474.0	-2.192	0.358
Human,D1 - Hunt,D1	-64.644	20.438	403.8	-3.163	0.036
Human,D1 - Human,D2	1.159	15.230	474.0	0.076	1.000
Human,D1 - Hunt,D2	-22.144	20.438	403.8	-1.084	0.960
Hunt,D1 - Human,D2	65.803	20.438	403.8	3.220	0.030
Hunt,D1 - Hunt,D2	42.500	15.615	474.0	2.722	0.119
Human,D2 - Hunt,D2	-23.303	20.438	403.8	-1.140	0.948

Table A.4.18: Results of the pairwise analyses of the EMMs of the HRV in the bears depending on the explanatory variables PERIOD and TYPE. The values presented here are based on a 0.95 confidence level with the Tukey correction method. This table numerically summarizes Figure 10. DD stands for the experiment day. D1 stands for the day following the experiment. D2 stands for the second day following the experiment. Human stands for human encounters and Hunt stands for simulated hunts.

Contrast	estimate	SE	df	t.ratio	p.value
Control period - DD	-28.667	5.230	303	-5.481	< 0.0001
Control period - D1	-22.294	5.230	303	-4.262	< 0.0001
Control period - D2	-11.363	5.230	303	-2.172	0.133
DD - D1	6.373	5.230	303	1.218	0.616
DD - D2	17.304	5.230	303	3.308	0.006
D1 - D2	10.931	5.230	303	2.090	0.159

Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway