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**Do you mind? Using biologging tools to
study anthropogenic disturbance effects
on wildlife behavior and energetics
– a case study on moose**

PhD in Applied Ecology and Biotechnology
2024



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To my parents

Sammendrag

Boreale skogområder er under påvirkning av klimaendringer og økt menneskelig aktivitet. I dette økosystemet er elgen (*Alces alces*) en nøkkelart. Elgen er av høy kulturell og økonomisk betydning og viktig for livsopphold i bygdesamfunn. Nedgang i elgbestander flere steder i nyere tid kan knyttes til økosystemendringer og mulige effekter av menneskelig aktivitet og infrastruktur. I denne avhandlingen har jeg utviklet modeller for å studere effekter av forstyrrelse på atferd og energiforbruk til ville elger ved hjelp av biologgingsdata samlet inn fra GPS- og akselerasjonssensorer festet på elghalsbånd. I første artikkel brukte jeg atferdsobservasjoner av merkede elger i fangenskap til å utvikle en maskinlæringsmodell som klassifiserer et gitt intervall i akselerasjonsdataene til én av syv vanlige atferdskategorier. I andre artikkel brukte jeg data fra hjerteloggere og akselerasjonssensorer på elg i fangenskap til å predikere hjertefrekvens fra akselerasjonsdata. Jeg illustrerer bruken av denne modellen sammen med en publisert ligning som kvantifiserer forholdet mellom elgens hjertefrekvens og energiforbruk til å beregne elgens energiforbruk fra akselerasjonsdataene. I tredje artikkel brukte jeg modellene utviklet i artikkel I og II til å undersøke i detalj hvordan ville elger responderte på eksperimentelle forstyrrelser. Jeg designet en atferdsstudie der jeg systematisk nærmet meg ville elger som var merket med halsbånd med GPS- og akselerasjonssensorer, enten til fots eller med truger, om sommeren, under elgjakten, og om vinteren. Jeg kvantifiserte elgenes atferd og energiforbruk under tilnæringsforsøket sammenlignet med kontrollperioder, og undersøkte effekten av avstand til forstyrrelsen, årstid, og tid på døgnet. Tilnæringsforsøkene førte til at elgen brukte mer tid på forflytning og mindre tid på matinntak, spesielt i de første ti minuttene etter forstyrrelsen, med generelle endringer i atferd og energiforbruk som varte i opptil tre timer. Elgenes respons varierte med årstid; tilnæringsforsøk med kortere avstand ga en kraftigere fluktrespons om sommeren og om vinteren enn i jaktseasonen, mens flukten startet tidligere og varte lenger om vinteren. Elgens energiforbruk var høyest etter tilnæringsforsøk om morgenen sommerstid. Mine funn beskriver elgers respons på forstyrrelse på et detaljnivå som ikke er gjort tidligere, og belyser de negative effektene av forstyrrelse for ville elgers energibudsjett. Funnene kan informere fremtidige studier som tar sikte på å kvantifisere kumulative effekter av forstyrrelse og konsekvenser av gjentatte forstyrrelser for ville elger.

Abstract

Boreal forests are experiencing disturbances from climatic changes and increased human activity. In this ecosystem, moose (*Alces alces*) are a keystone species. They are of high cultural and economic significance and important for subsistence in rural communities. Recent declines in several moose populations have implicated ecosystem changes and potential effects from human activity and infrastructure. In this thesis, I developed models to study the effects of disturbances on the behavior and energy expenditure of wild moose using biologging data collected by collar-mounted GPS and accelerometer units. In Paper I, I used behavioral observations on collared captive moose to develop a machine learning model predicting one of seven common behaviors for any given interval in the accelerometer data. In Paper II, I used data from heart rate loggers and accelerometer collars in captive moose to predict heart rate from accelerometer data. I illustrate the use of my model in concert with a published equation quantifying the relationship between moose heart rate and energy expenditure, to calculate moose energy expenditure from accelerometer data. In Paper III, I used the models developed in Papers I and II to investigate the detailed responses of wild moose to experimental disturbances. I designed a behavioral response study during which I systematically approached collared moose on foot or snowshoes in the summer, during the hunting season and in winter. I quantified the behavior and energy expenditure of the moose during the approaches relative to control periods and investigated the effect of distance to the disturbance source, season, and time of day. The disturbances resulted in increased locomotor activity and decreased foraging activity, particularly in the first ten minutes following the approach, with overall changes in behavior and energy expenditure lasting up to three hours. The disturbance response varied by season; close approaches elicited a stronger flight response in summer and winter than in the hunting season, while the onset of flight was sooner and lasted longer in the winter. Energy expenditure was highest following approaches during summer mornings. My findings describe moose disturbance response in unprecedented detail and elucidate the negative effects of disturbances on the energy budget of wild moose. The models I developed in this thesis can improve the study of wild moose behavior and energy budgets. They can inform future studies aiming to quantify cumulative effects of disturbances and consequences of repeat disturbances on wild moose.

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Abbreviations

GPS – Global Positioning System

ODBA – Overall dynamic body acceleration

bpm – beats per minute

List of papers

- Paper I Predicting moose behaviors from tri-axial accelerometer data using a supervised classification algorithm
Kirchner TM, Devineau O, Chimienti M, Thompson DP, Crouse J, Evans AL, Zimmermann B, Eriksen A
Animal Biotelemetry (2023) 11:32
<https://doi.org/10.1186/s40317-023-00343-0>
- Paper II Predicting energy expenditure from dynamic body acceleration in a large boreal ungulate
Kirchner TM, Devineau O, Thompson DP, Thiel A, Chimienti M, Evans AL, Crouse J, Eriksen A
Manuscript
- Paper III Do you mind? Behavioral responses of moose to experimental disturbance and implications for energy expenditure
Kirchner TM, Devineau O, Chimienti M, Zimmermann B, Versluijs E, Evans AL, Mathisen KM, Eriksen A
Manuscript

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Introduction

Wildlife in the Anthropocene

Humans have been exerting such large influences on natural systems that they were proposed as namesake for the current geological epoch (Crutzen 2002). This epoch, the Anthropocene, is seeing a shifting of climatic zones and a steady encroaching of humans and their infrastructure on wildlife habitat (Alkemade et al. 2009, Pirootta et al. 2022). The perception of human activity by wildlife can resemble the threat they perceive in the presence of a predator (Frid & Dill 2002). Wildlife perceiving a threat may try to avoid it by adjusting what they do, when they do it, where and how (Lima & Dill 1990). For example, increasing human activity can lead to increased nocturnality of animals to minimize temporal overlap, thereby sharing space while simultaneously minimizing the chance of an encounter (Gaynor et al. 2018). This example illustrates the continuous adjustment of an animal's decisions in order to survive in a "landscape of fear" – a landscape with spatio-temporal variation in perceived predation risk (Brown et al. 1999, Laundre et al. 2010, Gaynor et al. 2019). Responding to perceived predation risk can lead to risk effects; changes in behavior, space use and energy expenditure (Frid & Dill 2002, Preisser & Bolnick 2008, Creel et al. 2009, Suraci et al. 2019). For example, increased home range sizes of eagles (*Aquila fasciata*) (Perona et al. 2019) and increased distances of bighorn sheep (*Ovis canadensis nelson*) to hiking trails (Longshore et al. 2013) on weekends illustrate the "weekend effect"; changes in animal movement and behavior resulting from increased risk effects of increased human recreational activity on weekends. On a larger scale, changes in wildlife behavior and distribution during the "Anthropause", a period of suppressed human mobility due to lockdown policies during the COVID-19 pandemic (Rutz et al. 2020), illustrate the restrictions imposed on wildlife by human activity (Bates et al. 2021, Tucker et al. 2023).

Using biologging tools to study wildlife behavior and energetics

Animal-borne devices that transmit or store information on the animal's position, behavior and physiology are commonly referred to as biologging tools (Rutz & Hays 2009, Wilmers et al. 2015) and frequently used in studies of human disturbances effects on wildlife (MacArthur et al. 1979, Johnson & Tyack 2003, Tucker et al. 2023). The field of wildlife biologging benefits

from improvements in sensor technology driven by the high demand for personal electronics like smartphones and fitness trackers (Wilmers et al. 2015, Majumder & Deen 2019, Fahlman et al. 2021). An important type of sensor in personal electronics, accelerometers record fine-scale movements in a functional principle analogous to the vestibular system in the inner ear of vertebrates (Angelaki & Cullen 2008, Khan & Chang 2013, Pfaff et al. 2019). Worn on the body, they can be used for a wide range of purposes, for example to count steps and detect falls (Preset et al. 2018, Majumder & Deen 2019). In wildlife biologging studies, accelerometers facilitate the study of a wide range of phenomena from disease infection in cockroaches (*Blaberus craniifer*) (Wilson et al. 2014) to the heart rate of blue whales (*Balaenoptera musculus*) (Czapanskiy et al. 2022). They can also be used to distinguish between active and inactive states and among a range of distinct behaviors in a variety of species (Watanabe et al. 2005, Shepard et al. 2008, Wilson et al. 2008, Nathan et al. 2012). Furthermore, overall dynamic body acceleration (ODBA) – a signal extracted from the accelerometer data – is a metric of body movement that is correlated with energy expenditure and can thus be used as accelerometer-derived proxy for energy expended on body movement (Wilson et al. 2006, Green et al. 2009, Halsey et al. 2009). For example, a recent study deployed collars with accelerometers on wild pumas (*Puma concolor*) and used overall dynamic body acceleration to show that navigating a landscape of fear of humans increased puma energy expenditure (Nickel et al. 2021).

Ecological importance of moose

Moose (*Alces alces*) are a keystone species of the boreal forests with a circumboreal range (Molvar et al. 1993, Bowyer et al. 1997, McCulley et al. 2017, Schmitz et al. 2018, Leroux et al. 2020, Petersen et al. 2023). Their English name is derived from Algonquian words describing the tendency of moose to eat twigs and bark (Fraser et al. 1984, Reeves & McCabe 2007, Jackson 2008), illustrating the importance of browsing activity (the consumption of woody vegetation) for this species (Bowyer et al. 1997). Through their browsing activity, moose can alter plant composition in their habitats (Pastor et al. 1988, Molvar et al. 1993, Bowyer et al. 1997, Kielland & Bryant 1998). The high lignin content of their browse promotes rapid passage of food through their digestive tract, leading to a high through-put of ingested plant material (Schwartz 1992) and a rapid deposition and distribution of excreted nutrients in their surroundings (Molvar et al. 1993). The fertilizing effects of moose activity, together with

effects of browsing activity on plant growth and community composition, illustrate the ecological role of moose as ecosystem engineers (Pastor et al. 1988, Molvar et al. 1993, Bowyer et al. 1997, Kielland & Bryant 1998, Persson et al. 2000). Furthermore, moose (especially calves) are important prey for many species including bears (*Ursus americanus*, *U. arctos*), wolves (*Canis lupus*), red foxes (*Vulpes vulpes*), ravens (*Corvus corvax*), wolverines (*Gulo gulo*) pine marten (*Martes martes*), Eurasian jays (*Garrulus glandarius*) and goshawks (*Accipiter gentilis*) (Timmermann & Rodgers 2005, Wikenros et al. 2013, Ausilio et al. 2023). Moose take advantage of the high productivity of the boreal forests during the short vegetation period in high latitudes to deposit fat and protein reserves before entering a period of negative energy balance during long, cold winters (Schwartz 1992, Sand et al. 1995). Physiological adaptations, including seasonal hypometabolism and reduced activity, lower energy requirements during winter (Renecker & Hudson 1986, Risenhoover 1986, Cederlund 1989, Græsli et al. 2020b). Due to the tight coupling of moose biology to the productivity pulses of the boreal forest, moose can be seen as indicator species for the state of this ecosystem (Snaith & Beazley 2002, Moen et al. 2006, Gaillard 2007, Gauthier et al. 2015).

Morphological adaptations of moose

Many descriptions of moose consider their – in the words of Henry David Thoreau – “grotesque and awkward” (Thoreau 1864, Jackson 2008) appearance a trademark of the species. Some of the most prominent features of moose are adaptations facilitating survival in habitats characterized by high predator abundances and long periods of cold winters and deep snow: Their legs are long and jointed in a way that allows a greater range of motion and the small hoofs and dewclaws are splayable, together facilitating long-strided locomotion on soft substrate and in rough terrain and deep snow (Schwartz 1992, Geist 1999, Bubenik 2007) and enabling moose to outperform predators in the obstacle course of uneven terrain (McMillan 1954, Lindstedt et al. 1991, Geist 1999, Wirsing et al. 2021). Females accompanied by calves with limited locomotor abilities, and moose that sink into deep snow while their lighter predators are able to run on the hardened surface, can successfully stand their ground and confront predators, aided by their large body sizes (Geist 1999, Ballard & Ballenberghe 2007) which also reduce heat loss in low temperatures (Geist 1987, Bowyer et al. 1997). Such aggressive anti-predator behavior appears to be more prominent in moose in North America

compared to moose in Europe, which may result from higher densities of large carnivores in North America (Geist 1999, Sand et al. 2006, Ericsson et al. 2015).

Adaptations that allow moose to thrive in cold conditions, such as their large body size and thick, insulating fur, may hamper their tolerance of elevated temperatures. Moose do not sweat and thus have to rely on behavioral thermoregulation at high temperatures, such as seeking out thermal refuges characterized by shade, wet soil and increased wind speeds (McCann et al. 2013, 2016, Thompson et al. 2021, Verzuh et al. 2021, 2023), clearing bed sites from plant debris to increase contact with cold soil (Olson et al. 2016) and reducing activity (Dussault et al. 2004, van Beest & Milner 2013, Thompson et al. 2021, Verzuh et al. 2023). Where a reduction in activity limits time spent foraging, behavioral thermoregulation can affect energy intake (Renecker & Hudson 1992, van Beest et al. 2012). The ability to adequately adjust behavior to prevailing climatic conditions can affect body condition and ultimately survival (van Beest & Milner 2013), emphasizing the importance of availability of thermal refuges connected to foraging habitat for moose population health (van Beest & Milner 2013, Elmore et al. 2017, Thompson et al. 2020, 2021, Verzuh et al. 2023).

Impacts of environmental stressors on moose populations

The availability of browse and thermal cover (such as conifer canopies) limits moose distributional range in cold climate zones, and heat and the availability of thermal refuges in warm climate zones (Timmermann & McNicol 1988, Karns 2007, Nadeau et al. 2017). Several populations in warmer climate zones in North America, often located at the southern edge of the distributional range, have declined in recent years (Murray et al. 2006, Lenarz et al. 2010, Monteith et al. 2015, Timmermann & Rodgers 2017, Nadeau et al. 2017), likely due to a combination of factors: Warmer temperatures can negatively affect female body condition, reproductive rates, and calf survival due to increased thermoregulatory costs and accelerated vegetation growth in spring (Monteith et al. 2015). Warmer temperatures can also lead to increased parasite loads and may interact with disease transmission and malnutrition, resulting in lower pregnancy and increased mortality rates (Murray et al. 2006, Jones et al. 2019). Declining body size and life span of moose in Isle Royal National Park, USA, over the last four years were correlated with increasing temperatures (Hoy et al. 2018).

Uncertainty around estimated impacts of risk effects on individual moose

Risk effects from human activity and infrastructure can have effects similar to, and may also compound, environmental stressors: Short relative telomere lengths – an indicator of chronic stress – were found in moose in southern Sweden in areas characterized by high levels of human activity and infrastructure as well as increased temperatures (Fohringer et al. 2022). Comparably short relative telomere lengths were found in moose living in extreme environmental conditions including deep snow and limited forage availability (Fohringer et al. 2022). In contrast, moose living in areas with less anthropogenic activity and infrastructure and in a less extreme environment had longer relative telomere lengths (Fohringer et al. 2022). Cortisol concentrations in moose hair – an indicator of stress – were correlated with proximity to wolf territories and average temperatures, but not with indicators of human activity and infrastructure (Spong et al. 2020). This might suggest that anthropogenic factors did not affect the stress levels of moose on this study. However, risk effects from humans may be expressed not in hormonally mediated chronic stress but in behavioral changes depressing foraging activity and thus causing nutritional stress (Creel et al. 2009), as observed in elk (*Cervus elaphus*) under wolf (*Canis lupus*) predation in the Greater Yellowstone Ecosystem (Creel et al. 2009). The contrasting results of these studies illustrate the uncertainty that currently exists regarding long-term impacts of risk effects on individuals. Risk effects can also be confounded by other factors (such as climate) (Fohringer et al. 2022), especially when exposure to disturbance is inferred from proxies (such as distance to or density of roads and settlements) (Spong et al. 2020) rather than explicitly measured (Colman et al. 2017). Understanding disturbance effects on individuals is important because disturbance-induced changes to behavior and physiology affect individual survival and reproduction, which can translate to population-level consequences (DeRuiter et al. 2017, Pirotta et al. 2018). Models investigating population consequences of disturbances often use nutritional status (body condition) as link between individual disturbance effects and population consequences (Nowacek et al. 2016, Pirotta et al. 2018, Gallagher et al. 2021), illustrating the importance of understanding how risk effects impact energy acquisition (foraging behavior) and expenditure (Creel et al. 2009).

Historical importance of moose for humans

The lives of moose and humans have been intricately linked for thousands of years. Moose hunting was a critical source of food for hunter-gatherers and sometimes the main food source ensuring survival in the absence of other prey species during winter (Timmermann & Rodgers 2005, Reeves & McCabe 2007, LeBlanc et al. 2011, Larsson et al. 2012, Westman et al. 2022). This dependence on provisioning by moose was mirrored in the cultural reverence of moose throughout their distributional range (Volokitin & Kosinskaya 2002, Ashihmina 2002, Reeves & McCabe 2007). Artifacts of apparent ritual nature – staffs ending in the shape of a moose head – were found throughout boreal forest in Eurasia and used for thousands of years, starting ca. 8000 years ago (Zhulnikov & Kashina 2010). In up to ca. 6500 years-old rock carvings and paintings from Fennoscandia, moose were a central and recurring motif (Sognnes 1998, Bolin 2000, 2010, Blehr 2014). Several depictions even suggest the belief in kinship of moose and humans (Bolin 2000, 2010, Hill 2011). Petroglyphs between 2000 and 3000 years old featuring moose were also found in North America (Reeves & McCabe 2007). People in the Northern Ural and Siberia associated moose with both the sun and earth itself (Ashihmina 2002, Zhulnikov & Kashina 2010).

Current importance of moose hunting

Today, moose are still an important food source for First Nations and rural communities, and moose hunting remains a significant cultural and recreational activity (Loring & Gerlach 2009, LeBlanc et al. 2011, Priadka et al. 2022, Westman et al. 2022). Where moose browsing inflicts significant damage on commercial forestry plantations, hunting is also used as management tool for population control (Lavsund et al. 2003, Lykke 2005). In Scandinavia, the meat can be sold commercially, and its revenues can exceed those of the timber harvest from the same area (Andersen et al. 1996). Scandinavia hosts some of the highest moose densities in the world with approx. 0.7 moose/km² in Norway in 2000 and an estimated population size ranging from 90,000-117,000 moose between 1991-2000. (Lavsund et al. 2003, Timmermann & Rodgers 2005). Approximately 25% of the population is harvested every year by ca. 56,000 registered moose hunters, who are the main source of mortality for moose in Scandinavia (Solberg et al. 1999, Ericsson & Wallin 2001, Lavsund et al. 2003). Over 50% of hunting approaches on moose are unsuccessful, suggesting that a significant proportion of the moose

population in Norway experiences a direct hunting attempt during each hunting season (Heberlein 2000, Græsli et al. 2020a).

Effects of non-consumptive disturbances on moose

While hunting is a popular activity; on a global scale, even more people engage in the non-consumptive activity of wildlife viewing (Filion 1983, Silverberg et al. 2003). Moose can be exposed to people engaged in wildlife viewing or in recreational activities that take place in moose habitat but do not directly target wildlife, such as gathering forage, hiking and cross-country skiing (Neumann et al. 2010a). Such activities are an important part of the Scandinavian lifestyle and facilitated by unrestricted access to land and a widespread network of forestry roads (Gelter 2000, Gundersen et al. 2006, Helseth et al. 2022). Thus, moose can incur a variety of non-lethal anthropogenic disturbances in addition to unsuccessful hunting attempts, and the same individuals are likely exposed repeatedly, particularly in areas with easy access for people (Neumann et al. 2009, 2010a)

Previous studies of moose behavioral disturbance response

In some of the first studies of moose disturbance responses in the mid-1960s, scientists approached wild moose and observed their response (McMillan 1954, Altmann 1958). They noted that a variety of factors such as nutritional and reproductive status, hunting activity, time of day, distance to cover and type of approach can influence the distance at which a moose responds to an observer (a metric of the intensity of the disturbance response), but their findings were limited to what could directly be observed (McMillan 1954, Altmann 1958). Advances in biotelemetry and biologging technology such as the development of radio tracking collars that enable tracking with a receiver (Mech 1979) and of implantable heart rate monitors and transmitters allowed post-disturbance movement and physiological parameters to be monitored (MacArthur et al. 1979, Andersen et al. 1996). Andersen et al. (1996) exposed moose bearing radio collars and heart rate transmitters to a variety of disturbances from a hiker to a platoon of soldiers, to a variety of vehicles, and even a fighter jet. This study revealed a stronger flight and heart rate response (a longer time for heart rate to return to pre-disturbance level) following approaches of humans compared to mechanical stimuli, and among approaches by humans, a stronger response the closer the disturbance stimulus was to the moose (Andersen et al. 1996). The development of GPS collars enabled the recording,

storage and transmission of frequent locations (Rodgers et al. 1996), disposing of the need to place a receiver in the field, thereby facilitating wildlife monitoring by alleviating logistic constraints (Dettki et al. 2004). Studies using GPS or radio collars to quantify the response of moose to experimental disturbances from hikers or snowmobiles (Neumann et al. 2010b), cross-country skiing (Baskin et al. 2004, Neumann et al. 2010a), helicopters (Støen et al. 2010) and hunting dogs (Ericsson et al. 2015) generally found increased movement rates during the first few hours after the approaches and spatial displacement from the area of disturbance immediately following the approach.

Previous estimates of energetic costs of moose disturbance response

Neumann et al. (2010 a,b) calculated energy expenditures of moose following experimental disturbances, using an estimated moose weight and movement rates (distance moved per hour) calculated from GPS positions recorded from the disturbed moose. These calculations were based on an equation that links energy expenditure during terrestrial locomotion to body mass and movement speed in a wide range of species (also referred to as “Taylor’s treadmill menagerie” (Kram 2012)) (Taylor & Heglund 1982). There are several reasons why estimates of moose energy expenditure calculated using this equation and substituting movement rates for movement speeds are likely inaccurate. First, energy expenditure estimates that are derived from an equation that is not species-specific and that substitute hourly movement rates for movement speed likely have limited accuracy. Fleeing moose likely vary their speed during flight, and higher movement speeds are more energetically costly than lower movement speed (Taylor & Heglund 1982, Kram 2012). Second, the calculated movement rates (derived from the length of spatial displacement and the time it took to achieve this spatial displacement) are influenced by the frequency with which GPS positions were recorded, which can also depend on the habitat variables (e.g. canopy cover) (Moen et al. 1996). Third, the actual movement path of fleeing moose is likely more tortuous than straight-line distances between two GPS locations (Baskin et al. 2004, Græsli et al. 2020a). Fourth, moose in flight might try to shake off a pursuing predator in uneven terrain (Geist 1999) and thereby incur greater energetic costs compared to movement at equivalent speed on even terrain or even a treadmill (Halsey 2016). For example, Støen et al. (2010) noted that moose fled into rough terrain following approaches with a helicopter.

Græsli et al. (2020a) studied the response of moose to approaches by hunting dogs using dual-axis accelerometers in GPS collars in combination with implanted heart rate logger. The accelerometers allowed the distinction between active and inactive behavioral states in the moose and revealed overall reduced activity on the days after approaches, suggesting increased resting behavior compensating for the energy-consuming flight following the approach (Græsli et al. 2020a). Heart rates were higher on the approach day compared to controls before and after, but were not used to calculate energy expenditure (Græsli et al. 2020a). Changes in foraging behavior on the day after the approach might elucidate compensation for the energy expended during flight but were not investigated (Græsli et al. 2020a).

Thesis objectives

The goal of this thesis was to use a combination of biologging tools to advance our understanding of the detailed behavioral responses of moose to anthropogenic disturbances, and the resulting energetic costs. To this end, I designed a behavioral response study in which I systematically exposed collared wild moose to a disturbance: An approaching observer. The moose collars collected two data sets: GPS locations and high-frequency tri-axial accelerometer data. These data allowed me to not only quantify the intensity of the disturbance stimulus (proximity to the observer using the GPS data), but also the response of the moose, which was encoded in the accelerometer data. Because accelerometer data sets are extremely large and difficult to interpret, I developed models that could analyze the accelerometer data and return the information I was interested in. My first two thesis papers each concern themselves with one of these models. Predicting the behavior of the moose at a given point in time was the goal of Paper I. Quantifying the energy expenditure at a given point in time was the goal of Paper II. Applying the models from Papers I and II to investigate the behavioral response of collared moose to experimental disturbances, and to quantify energetic consequences for the moose, was the goal of Paper III.

Methods

Paper I: Behavioral classification model

My goal for Paper I was to use a random forest model to predict the behavior of collared moose from accelerometer data. Random forest is a type of supervised machine learning that enabled me to train a model on accelerometer data with known behavioral context, so that the model could then predict behavior from accelerometer data for which the behavior was not known. To collect accelerometer data and simultaneously record the behavioral context, I conducted behavioral observations on collared captive moose in two facilities: The Kenai Moose Research Center (Alaska Department of Fish and Game) in Alaska and the Norwegian Moose Center in Norway. All captive moose were equipped accelerometer-GPS collars (Vertex Plus, Vectronic Aerospace GmbH, Berlin, Germany) recording tri-axial accelerometer data continuously at 32 Hz (Figure 1).



Figure 1: Captive moose with accelerometer-GPS collar during a behavioral observation in spring 2022 at the Kenai Moose Research Center, Alaska.

I conducted behavioral observations during different seasons (summer, fall and winter) on 12 individual moose belonging to two subspecies; 10 female Alaskan moose (*A. a. gigas*) in Alaska, and two European moose (*A. a. alces*) in Norway (one female, one male). At the start of the study, the moose were between 1-18 years old and five were pregnant. The first step

of the modeling procedure focused on training the model. I split the accelerometer data into regular (three-second-long) intervals and trained the model to predict one of seven behaviors for each accelerometer data interval, based on properties of the accelerometer data. The seven behaviors of interest are common and important behaviors of moose: Lying with the head down or tucked, lying with the head up, ruminating, standing, foraging, walking, and running. The second step of the modeling procedure focused on testing the model to evaluate its performance in predicting behaviors from accelerometer data. First, I evaluated the overall performance of the model by training it on a subset of the data, then running it on the withheld data and comparing the behavior predicted for each data interval to the actual behavior observed during this interval. Second, I evaluated the generalizability of my model to individuals it was not trained on. I achieved this by training and testing the model iteratively, with each iteration withholding data from one specific individual during model training and using the withheld data for model testing.

Paper II: Energy expenditure model

My goal for Paper II was to create a model that could predict the heart rate of collared moose from accelerometer data. Together with an existing equation calculating energy expenditure from heart rate in moose (Renecker & Hudson 1985), I could then use my model to estimate energy expenditure in collared moose from accelerometer data. In order to collect heart rate data together with accelerometer data, we implanted heart rate loggers (DST centi-HRT, Star Oddi, Iceland) (Figure 2) in eight moose at the Kenai Moose Research Center collared with GPS-accelerometer collars (Vertex Plus, Vectronic Aerospace GmbH, Berlin, Germany). All moose were non-pregnant and non-lactating females and between 2-13 years old at the start of the study. These loggers calculated heart rate every 30 seconds on three consecutive days per season in early and late summer, fall and spring. The sampling periods coincided with the behavioral observations conducted for Paper I. I quality-checked the heart rate data by manually validating the logger-calculated heart rates with raw electrocardiograms recorded prior to each sampling period. I included in the final analysis only those measurements that an internal algorithm in the loggers categorized as high-quality measurements, and only those that fell within the range of values that I could manually validate. To link the heart rate data from each moose to the accelerometer data recorded by the collar, I calculated the overall dynamic body acceleration from the accelerometer data recorded at the time of each heart

rate logger measurement. Then, I used a generalized additive mixed model to quantify the effect of overall dynamic body acceleration and several other variables on moose heart rate.



Figure 2: Surgical implantation of a heart rate logger in an anesthetized captive moose at the Kenai Moose Research Center, Alaska (Alaska Department of Fish and Game Division of Wildlife Conservation Institutional Animal Care and Use protocol no. 0086-2020-40). Image credit: Alaska Department of Fish and Game.

Paper III: Behavioral response study

My goal for Paper III was to evaluate the effect of disturbance on the behavior and energy expenditure of wild moose. To do so, we immobilized eight wild female moose from a helicopter in winter and spring 2021 in Innlandet county, Norway, to deploy GPS-accelerometer collars (Vertex Plus, Vectronic Aerospace GmbH, Berlin, Germany). The collars remained deployed for one year, recording accelerometer data continuously and transmitting their GPS location regularly via the GSM mobile service network, which allowed me access to the locations of the moose. Using these locations, I conducted experimental approaches on the moose in summer, fall and winter of 2021/2022. Fall approaches were conducted in the middle of the hunting season (October 18-29, 2021). I approached each moose twice per season, once in the morning, and once in the afternoon. The approaches followed a standardized protocol: I approached the last known position of the moose from 1 km away in a linear fashion at normal walking speed (using snowshoes in the winter). Once I passed the last known position, I proceeded another 500 m. I tried to minimize additional disturbance when leaving the area. I recorded my track using a handheld GPS unit. Once we retrieved the

collars, I had access to both the GPS and the accelerometer data recorded during the approaches. From the GPS data, I calculated the distance between the observer and moose every second during the approach, to identify the time when the observer passed the moose (the minimum distance between the moose and the observer, which I defined as contact distance). From the accelerometer data, I predicted behavior and energy expenditure of the moose, using the models from Papers I and II. To understand how an approach changed the behavior and energy expenditure of the moose, I compared each individual's time budget (how much time they spent engaging in each of the seven behaviors) and energy expenditure during the approach to the same time period on the day before, which I considered the control period (Neumann et al. 2010a). Specifically, I investigated changes relative to the control during different time periods leading up to and following contact with the observer (for example, 60 min to 30 min before contact, 30 min to 10 min before contact, 10 min before contact to contact etc.), to investigate changes in the disturbance response over time. I compared my findings of energy expenditure during the first hour following contact with published estimates of moose energy expenditure during other approach studies. I also investigated the effect of contact distance on moose flight behavior (the amount of time they spent running after contact with the observer).

Ethical statement

Animal handling followed established protocols as cited in the individual manuscripts. Collars were deployed without anesthesia in Alaska, and with anesthesia in Norway. Heart rate loggers were surgically implanted and removed in captive moose at the Kenai Moose Research Center following anesthesia. The surgeries resulted in a mild infection and subsequent rejection of the logger in one animal presumably due to a foreign body reaction, which has also been documented in other species (Mayer et al. 2022). In Norway, two moose died shortly after chemical immobilization for collar deployment or removal (one wild moose, one captive moose at the Norwegian Moose Center). While cause of death could not conclusively be established, mortality within 30 days after capture is considered capture-related (Arnemo et al. 2006, Hampton & Arnemo 2023). During capture efforts of wild moose in Norway, some collared moose were captured repeatedly (with approximately one year in between capture events), in order to remove an old collar and deploy a new collar. The capture team observed hair loss at the top of the neck of the moose, where the animals likely experiences the highest

pressure due to weight from the collar, suggesting the hair loss resulted from friction or weight of the collars (Hampton & Arnemo 2023).

Results

Paper I: Behavioral classification model

I collected over 390 hours of behavioral observations as training data for the behavioral classification model (Figure 3). Predictive performance of the model varied among the seven behaviors and, as is common for random forest models (Pagano et al. 2017), was higher for behaviors with a higher sample size. At least 80% of predictions of the most common behaviors (lying with the head elevated, ruminating and foraging, each constituting at least 21% of the training data) were correct. The behavior with the most misclassifications (72%) was running (lowest precision), which was the behavior with the lowest overall sample size (< 1%), and which was most often confused with walking. Similarly, generalizability of the model to other individuals was variable and generally related to the amount of training data I had collected for each individual.

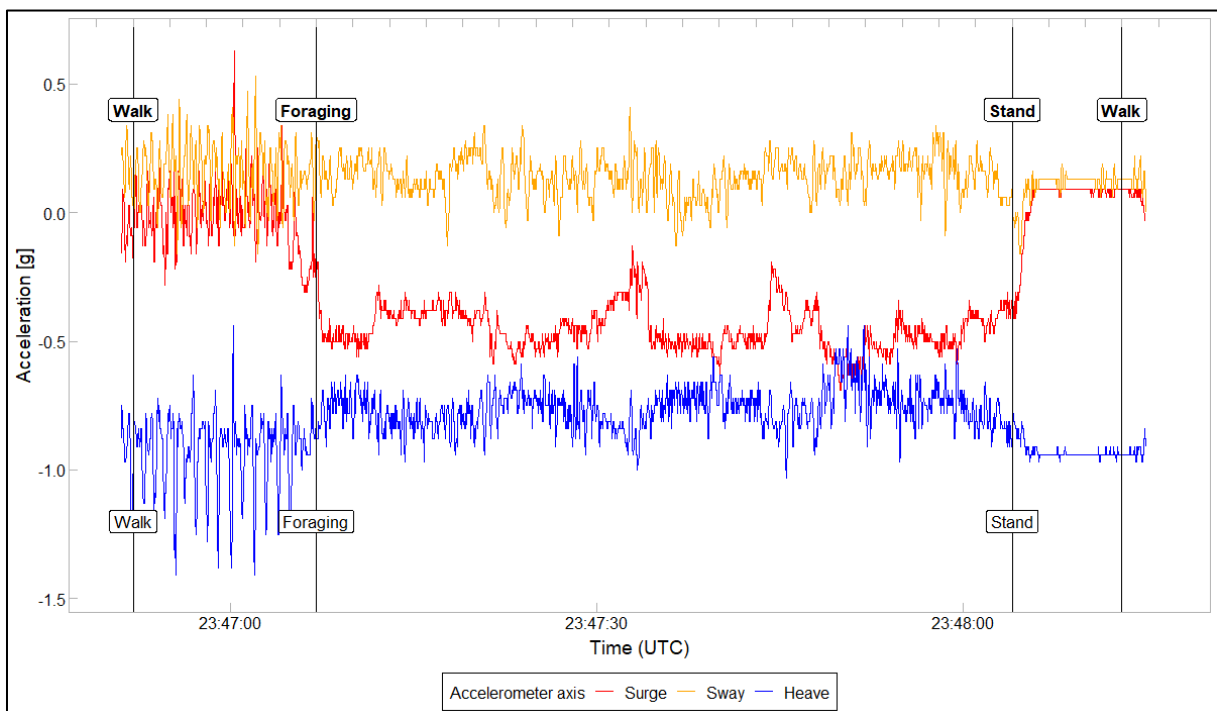


Figure 3: Raw data from a tri-axial accelerometer collar deployed on a captive moose. The corresponding behavior is predicted from the random forest model (top labels) and compared to the behavioral observation (bottom label). The start of a new behavior is indicated by a vertical line.

Paper II: Energy expenditure model

I collected 224,973 high-quality measurements of moose heart rate within the manually validated range between 17 and 154 beats per minute from seven individuals (one logger was rejected during the deployment and not recovered). Average heart rate was 34 bpm (beats per minute) in the fall, 39 bpm in the spring and 57 bpm in the summer. The heart rate model predicted an effect of overall dynamic body acceleration, season, time of day and individual on heart rate. The model likely underestimated the energy expenditure at the high values of overall dynamic body acceleration commonly recorded during running behavior (Figure 4).

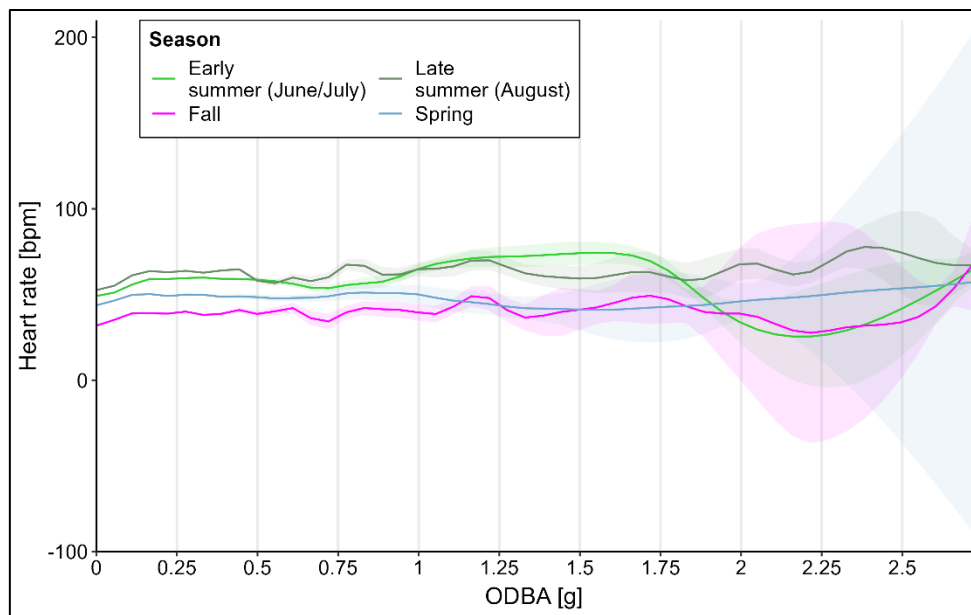


Figure 4: Smooths of the general additive mixed model predicting heart rate from accelerometer data in captive moose.

Paper III: Behavioral response study

I conducted 50 approaches on eight collared wild moose. Forty-eight approaches resulted in a contact distance less than 600 m (range: 17-266 m) and were included in the analysis (Figure 5).

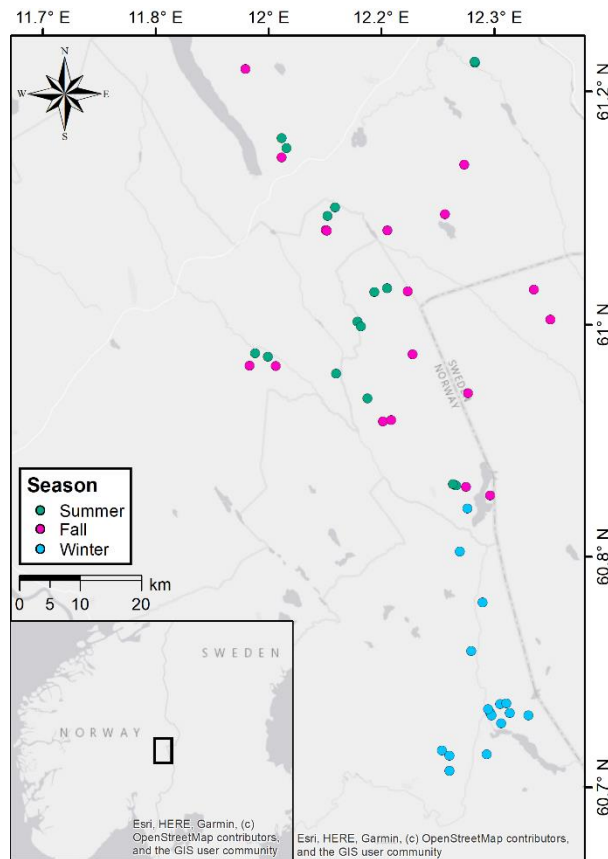


Figure 5: Location of the study area on the southern border of Norway and Sweden. Passing positions of 50 experimental approaches conducted on collared moose are color-coded by season.

The general response of the moose to the approaches was a clear increase in locomotor activity, particularly running, in the first 10 min after contact, and a decrease in foraging and ruminating activity (Figure 6). Over the course of the first hour, running and walking activity decreased but remained elevated compared to the control period (Figure 7). In contrast, foraging activity remained lower compared to the control during the first two hours after contact. Energy expenditure varied over the course of the approaches. It was highest in the first half hour after contact, particularly during summer morning approaches, with an average increase of 25% in the first 10 min after contact compared to the control period. Compared to studies estimating energetic costs of moose disturbance response from movement rates, I estimated much lower relative increases in energy expenditure during the first hour after contact (Table 1).

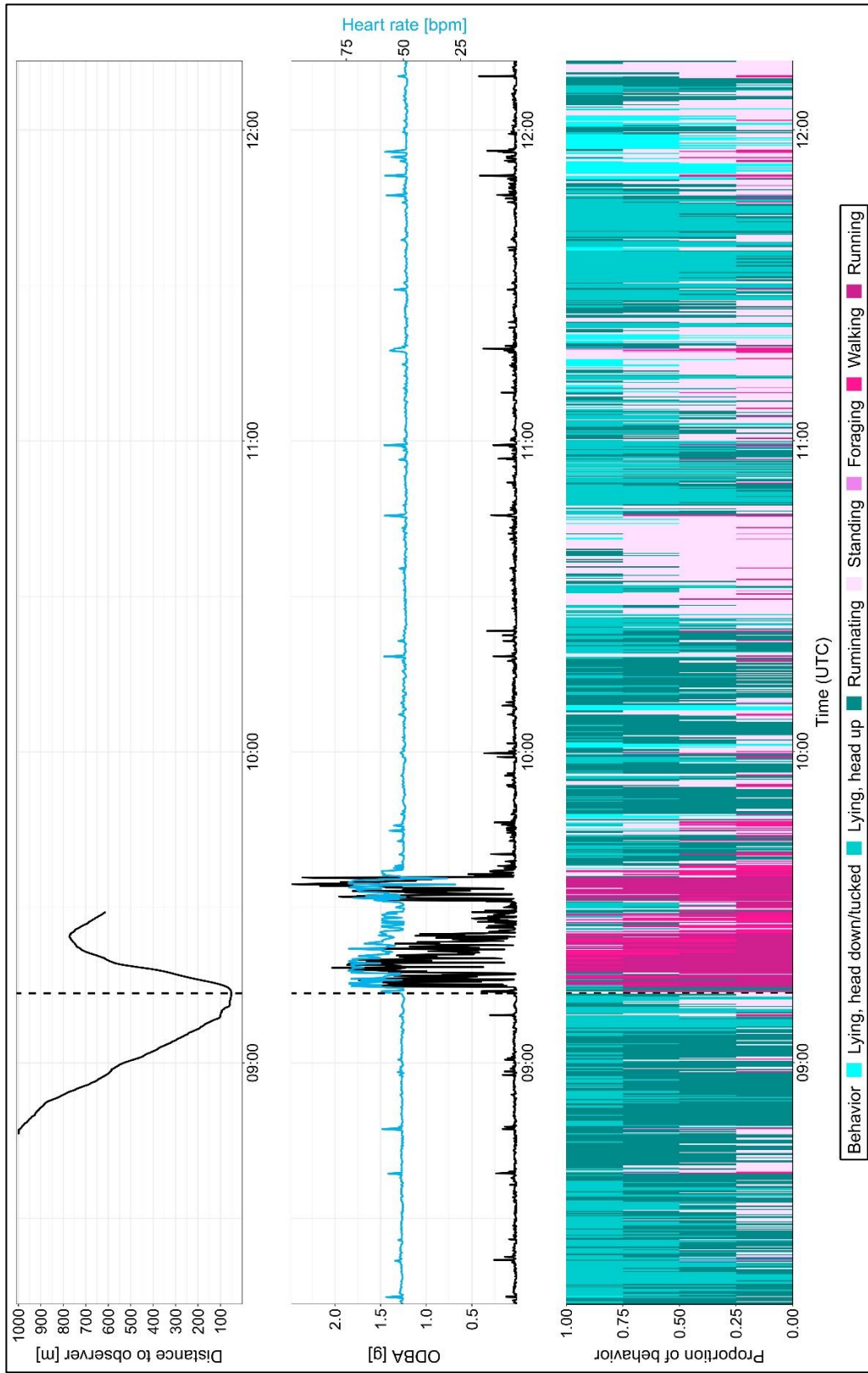


Figure 6. Moose-human contact distance during an experimental approach trial (top), overall dynamic body acceleration (ODBA) calculated from accelerometer data and heart rate predicted from ODBA (middle) and behavior predicted from accelerometer data (bottom) for one summer morning approach with a contact distance of 52 m. Vertical dashed line indicates time of minimum contact distance. Plot of contact distance ends when the observer reached the observer end position of the approach route.

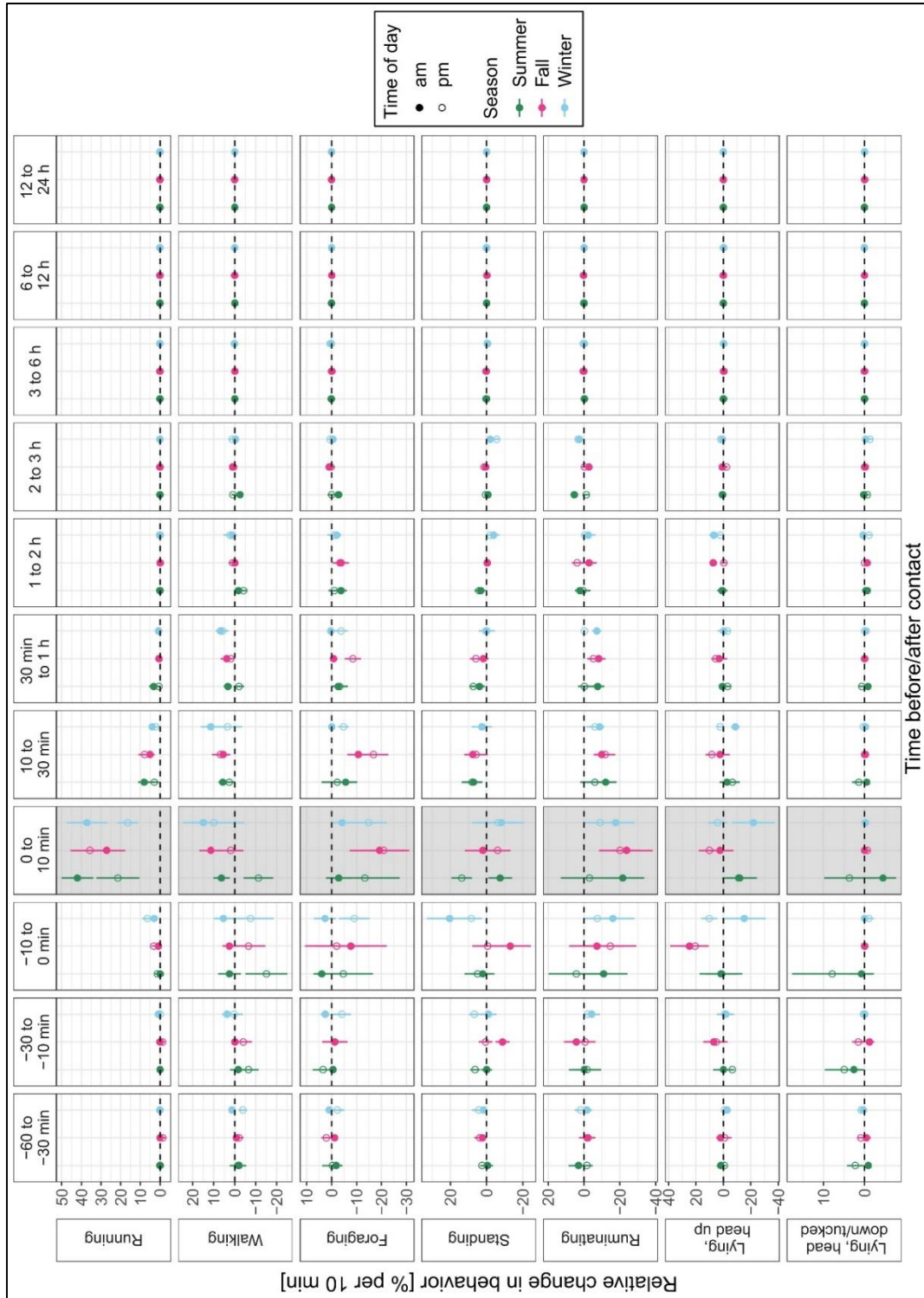


Figure 7: Mean and standard error of the proportion of each behavior predicted from accelerometer data for different time bins before and after contact to observer during experimental approaches on wild collared moose. Each time bin compares the data from the approach to the control period during the same time of day the day before. The data is split by season and time of day during the approach.

Table 1: Energy expenditure calculated from predictions of heart rate from accelerometer data during first 10 min and first 60 min after contact for 48 approaches on wild collared moose (highlighted in grey) compared to results from other studies estimating energy expenditure from movement rates *(Neumann et al. 2010b) ^ (Neumann et al. 2010a). Moose silhouette from Colourbox.

Approach method	Season	Energy expenditure (mean \pm SD) [kJkg ⁻¹ h ⁻¹]					
		0-10 min since contact			0-60 min since contact		
		Approach	Control	Relative increase [%]	Approach	Control	Relative increase [%]
Hike	Summer	6.0 \pm 0.8	5.3 \pm 0.5	14.6 \pm 19.7	5.4 \pm 0.6	5.2 \pm 0.4	4.5 \pm 13.0
Hike	Fall	3.1 \pm 0.2	2.9 \pm 0.2	6.8 \pm 11.7	2.9 \pm 0.2	2.9 \pm 0.2	1.0 \pm 8.2
Snowshoe	Winter	3.3 \pm 0.1	3.3 \pm 0.2	0.3 \pm 7.5	3.4 \pm 0.1	3.3 \pm 0.2	1.8 \pm 5.3
Hike*	Summer				4.3 \pm 0.2	3.7 \pm 0.1	16
Ski^	Winter				5.4 \pm 0.5	3.6 \pm 0.1	48
Snowmobile*	Winter				4.4 \pm 0.1	3.7 \pm 0.1	19



The behavioral response to the approaches varied by season and contact distance. In summer and winter, close approaches (short contact distances) triggered a stronger flight response compared to approaches with longer contact distances. I observed the opposite trend in the fall, when long contact distances elicited an intense flight response (comparable to that of moose fleeing from a close approach in the summer), and close approaches elicited a much less intense running response (Figure 8).

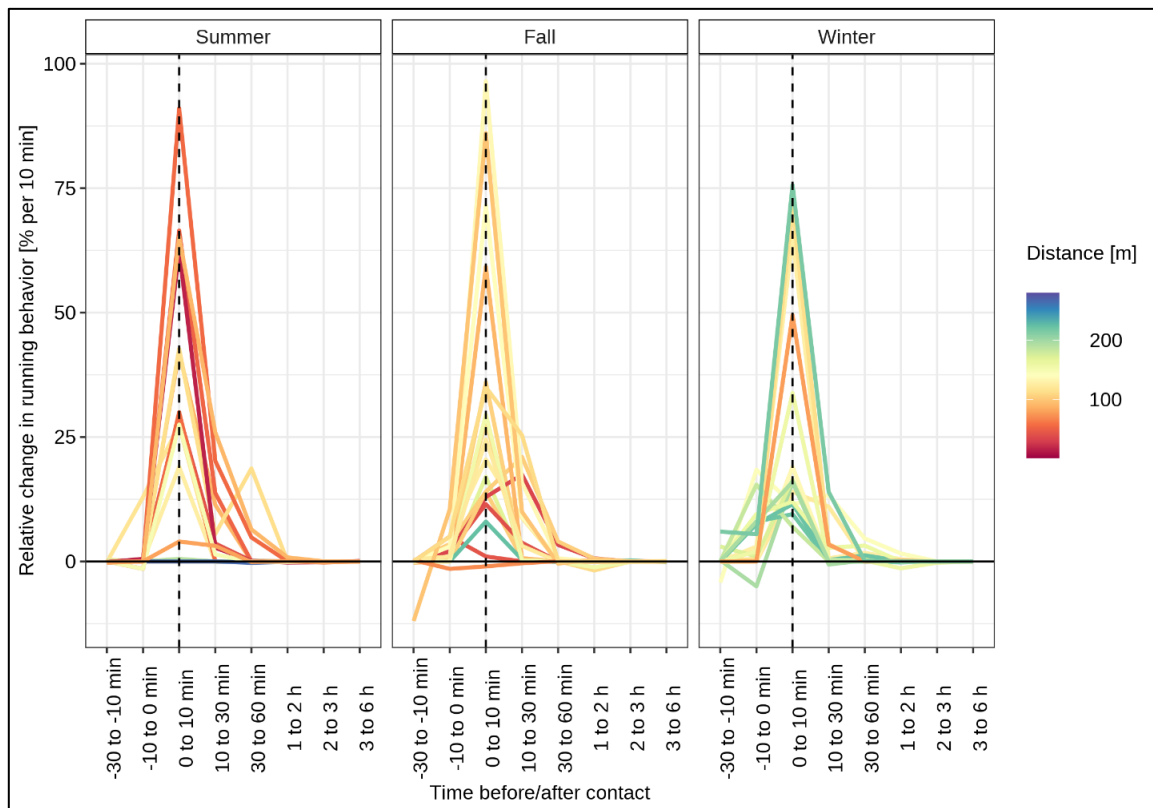


Figure 8: Proportion of running behavior predicted from accelerometer data on wild collared moose during different time bins before and after contact during experimental approaches relative to the control period on the same time of day the day before.

Discussion

Effects of disturbances on moose behavior and energy budget

It is evident from my data that increased locomotor activity (flight) during the first hour after contact occurred at the cost of time spent foraging and ruminating. The behavioral classification model had the highest performance for these behaviors, suggesting that misclassifications are unlikely to be responsible for this trend. I did not observe a compensatory increase in foraging activity during the 24 hours following the approaches, suggesting that either the overall time for foraging that was lost during these approaches did not have significant impacts on the energy budget of the moose, or the compensation occurred more than 24 hours after the disturbance.

Assuming a weight of 300 kg for the moose in my study (Milner et al. 2013), their energy expenditure during the first hour after contact in summer was on average ca. 60 kJ higher compared to the control. Renecker & Hudson (1986) determined a summer maximum daily energy expenditure of $940 \text{ kJkg}^{-0.75}\text{h}^{-1}$, which translates to $2,883 \text{ kJh}^{-1}$ for a moose of 300 kg. Based on this data, the locomotor response of moose weighing 300 kg to an approach in the summer increased its energy expenditure in the first hour after contact by ca. 2%, suggesting a small overall impact of the disturbance on the energy expenditure of the moose. However, the actual energy expenditure resulting from locomotor activity is likely higher than this estimate, as my model tended to underestimate heart rates predicted for movement falling in the high range of ODBA values that I observed in running moose. Still, the overall (absolute) range of energy expenditures I calculated matched that calculated from movement rates of experimentally disturbed moose (Neumann et al. 2010 a, b).

Calculating moose energy expenditure from accelerometer data

My model for estimating heart rate and resulting energy expenditure from accelerometer data is an improvement over the more established general model, which quantifies energy expenditure during terrestrial locomotion from movement speed (Taylor & Heglund 1982, Neumann et al. 2010a, b), by predicting seasonal variation in energy expenditure, an important characteristic of moose metabolism (Renecker & Hudson 1986). Furthermore, the fine temporal resolution of my analysis revealed previously undocumented high variation in

the behavioral and energetic response of moose to a disturbance over time. Importantly, high variation in the proportion of locomotor behaviors in the time budget of disturbed moose suggests high variation in movement speed and therefore energy expenditure, suggesting that averaging energy expenditure over an entire hour following disturbance oversimplifies the behavioral response and obscures the true range of the resulting energy expenditure.

Context-dependence of behavioral disturbance response of moose

Wildlife disturbance responses depend on many factors, including characteristics of the disturbance itself (e.g., type and intensity), characteristics of the animal (e.g., body condition, reproductive status), and spatio-temporal context (e.g., type of habitat, overall level of predation risk) (Altmann 1958, Stankowich 2008, St Clair et al. 2010, Tablado & Jenni 2017). For example, the distance at which Two-banded Plovers (*Charadrius falklandicus*) moved away from humans during experimental approaches depend on whether mammalian predators are present in their habitat (St Clair et al. 2010). The response of blue whales to exposure to simulated sonar depends on their behavior at the time of exposure (Goldbogen et al. 2013, DeRuiter et al. 2017). The disturbance response of the moose in my study appeared to be dependent on characteristics of the disturbance stimulus (proximity to the observer) and temporal context (season).

Previous studies of disturbance response on moose observed a positive correlation between increased disturbance response (i.e., flight intensity) and characteristics of the disturbance stimulus that likely increased the threat perceived by moose (e.g., close proximity of observer, high approach speed, high directionality of approach, continued pursuit) (McMillan 1954, Andersen et al. 1996, Stankowich 2008, Neumann et al. 2010a). While my observations from summer and winter support this trend, my observations of reduced flight intensity during close approaches during the hunting season contradict it. Moose that detect a disturbance from far away may not be able to discern the type of approaching threat, but they might flee as long as sufficient distance to the approaching threat gives them a chance at escape – which may be a favorable adaptation in a heavily hunted population where hunting dogs are used to detect and pursue moose (Sand et al. 2006, Græsli et al. 2020a). If moose do not detect an approaching observer until the observer is close (for example due to unfavorable wind conditions, or ground cover muffling the sound of the approach), they may be able to evaluate

the level of threat posed by the observer. A single observer (without a dog) may not be considered a high-level threat and may therefore not elicit a strong flight response. Given the prominence of moose hunting activity in the study area in fall, fleeing in response to a low-level threat could relocate the moose to an active hunting area with a much higher risk (Ericsson & Wallin 1996, Baskin et al. 2004) that they may not know well, which might impede their escape (Geist 1999, Little et al. 2016, McLaren & Patterson 2021).

The seasonal variation in disturbance response of the moose in my study suggests an awareness of the larger spatio-temporal context of risk during the hunting season. This awareness could be mediated by survival of recent hunting attempts (Heberlein 2000, Græsli et al. 2020a), or by an overall increase in the presence and activity of humans and off-leash dogs in the area associated with the start of small game hunting season or start of training season for baying dogs, which precede the moose-hunting season (Neumann et al. 2009). A similar awareness of variation in risk levels has been observed in other species. For example, survival rate is higher in male red deer (*Cervus elaphus*) that abruptly shift their habitat in response to the onset of the hunting activity (Lone et al. 2015). White-tailed deer (*Odocoileus virginianus*) exhibit an abrupt reduction in movement, concurrently with an increase of human activity on the landscape during the scouting period that precedes the hunting season (Little et al. 2016, Marantz et al. 2016). Their movement is reduced during hunting season even in hunting-free zones adjacent to hunting areas (Little et al. 2016). The proportion of time that elk are vigilant depends on the distance to the nearest wolf pack several kilometers away, and to the size of the pack (Liley & Creel 2008).

Importance of fine-scale investigations of disturbance responses

I observed large variation in moose disturbance response – within seasons, and within each approach in the form a modulation of the behavioral response and energy expenditure over time. High variation in disturbance response among individuals and treatments has been found in a variety of species (Neumann et al. 2009, St Clair et al. 2010, DeRuiter et al. 2017). In fact, the magnitude of this variation can be comparable to the disturbance response itself (DeRuiter et al. 2017). Therefore, investigations of disturbance responses on the scale and level on which these responses occur (changes in behavior and physiology), as I have presented here, improve our understanding of different factors that cause this variation, and

improve our assessment of how individual disturbance effects can propagate to population-level impacts (Pirotta et al. 2021).

Conclusions

In this thesis I demonstrated the use of biologging tools to investigate risk effects of human recreational activities on wildlife, using moose as model species. I developed models that advance our understanding of moose by enabling a more fine-scale analysis of their behavior and energy expenditure. Furthermore, my calibration of accelerometer data with heart rate facilitates the estimation of energy expenditure from the collar data of wild moose, reducing the need for implanting loggers to record energy expenditure. Applying my models to data from experimental approaches, my results illustrate that risk effects from human recreational activities affect the energy budget of moose by increasing energetically costly locomotor behaviors and decreasing foraging activity. These findings fill in the gaps from previous investigations of human disturbance response in moose that were conducted on comparatively coarse spatio-temporal scales: My results show that the disturbance response is graded; most intense immediately after contact and subsiding over the course of one to two hours. The models presented in this thesis improve our understanding of moose population dynamics, by providing the link between individual disturbances responses and population consequences.

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Dissertation articles

1

METHODOLOGY

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Predicting moose behaviors from tri-axial accelerometer data using a supervised classification algorithm

Theresa M. Kirchner^{1*} , Olivier Devineau¹, Marianna Chimienti², Daniel P. Thompson³, John Crouse³, Alina L. Evans¹, Barbara Zimmermann¹ and Ane Eriksen¹

Abstract

Background Monitoring the behavior of wild animals in situ can improve our understanding of how their behavior is related to their habitat and affected by disturbances and changes in their environment. Moose (*Alces alces*) are keystone species in their boreal habitats, where they are facing environmental changes and disturbances from human activities. How these potential stressors can impact individuals and populations is unclear, in part due to our limited knowledge of the physiology and behavior of moose and how individuals can compensate for stress and disturbances they experience. We collected data from collar-mounted fine-scale tri-axial accelerometers deployed on captive moose in combination with detailed behavioral observations to train a random forest supervised classification algorithm to classify moose accelerometer data into discrete behaviors. To investigate the generalizability of our model to collared new individuals, we quantified the variation in classification performance among individuals.

Results Our machine learning model successfully classified 3-s accelerometer data intervals from 12 Alaskan moose (*A. a. gigas*) and two European moose (*A. a. alces*) into seven behaviors comprising 97.6% of the 395 h of behavioral observations conducted in summer, fall and spring. Classification performance varied among behaviors and individuals and was generally dependent on sample size. Classification performance was highest for the most common behaviors lying with the head elevated, ruminating and foraging (precision and recall across all individuals between 0.74 and 0.90) comprising 79% of our data, and lower and more variable among individuals for the four less common behaviors lying with head down or tucked, standing, walking and running (precision and recall across all individuals between 0.28 and 0.79) comprising 21% of our data.

Conclusions We demonstrate the use of animal-borne accelerometer data to distinguish among seven main behaviors of captive moose and discuss generalizability of the results to individuals in the wild. Our results can support future efforts to investigate the detailed behavior of collared wild moose, for example in the context of disturbance responses, time budgets and behavior-specific habitat selection.

Keywords Accelerometer, Biologging, Behavior, Cervid, Moose, *Alces alces*, Machine learning, Behavioral analysis, Alaska, Norway

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Background

Understanding the behavior of wild animals can facilitate effective conservation and management [1–3]. Such knowledge can be acquired through direct observations of wild animals, which is time-consuming, challenging and expensive [4]. One alternative is to use location data of wild animals to infer their behavior from characteristics of their movement trajectories [5–7]. However, behavioral inference is limited by the spatial and temporal resolution of the location data, which in turn can be influenced by the behavior itself (e.g. by collar position and habitat choice impacting GPS fix rate) [8–11]. Advances in biologging technology alleviate this limitation by enabling the recording of near-continuous data [12, 13]. In particular, animal-attached accelerometers enable a fine-scale biomechanical approach to the study of behavior [13–15].

Tri-axial accelerometers quantify inertial forces along three orthogonal axes [16, 17]. Attached to an animal, they record acceleration that is the result of both static or gravitational acceleration reflecting the posture of the animal relative to the earth's gravitational field, and dynamic or specific acceleration resulting from changes in speed due to movement of the animal [18–20] and vibrations due to effects of tag attachment [21, 22]. The resulting datasets are large (especially at high sampling frequencies) and complex and commonly, machine learning tools are used to classify the accelerometer data into discrete behaviors, using predictor variables that quantify characteristics of the accelerometer traces [14, 23, 24]. Supervised machine learning algorithms are trained by linking behavioral observations to simultaneously recorded accelerometer data, thereby creating a labeled data set, in order to distinguish the observed behaviors based on characteristic differences in the accelerometer traces, allowing for the quantification of model performance [11, 14, 25]. Such behavioral observations are commonly collected on accelerometer-bearing animals in captivity to facilitate the interpretation of accelerometer data collected on wild, unobserved animals [11, 13, 25].

Moose (*Alces alces*) are a keystone species of the boreal forests and tundra in the northern hemisphere [26–28]. Humans highly regard moose for their high cultural significance, for trophy and recreational hunting, and as a food source [29–31]. However, in some areas, browsing damage to commercial forestry plantations and frequent moose–vehicle collisions result in management decisions aimed at limiting population sizes [29, 32]. Throughout much of their range, moose face changes in environmental conditions and disturbances due to human activities [33–35]. The effects of these potential stressors are not yet well-understood due to our limited knowledge of moose physiology and behavior, and of how much

behavioral plasticity can compensate for stress and disturbances experienced by individuals [36, 37].

Monitoring the behavior of moose in situ can improve our understanding of how their behavior is affected by disturbances and changes in their environment [38]. Most previous studies aimed at remotely monitoring moose behavior used radio-telemetry or activity counts from dual-axis motion sensors and distinguished only between active and inactive periods lasting several minutes [35, 39, 40]. Ditmer et al. validated activity counts averaged over 1 min with behavioral observations of a single collared captive moose during one season [41]. Resulting behavior-specific activity counts were then used to improve a model predicting the behavior of collared wild moose from year-round GPS data, assigning one of three potential behaviors (resting, foraging, traveling) per 15- or 20-min movement interval [41]. To predict moose behavior in greater detail (i.e. to predict a higher number of behaviors over multiple seasons), it is important to consider the effect of time of year on the motion signatures of behaviors [38, 40]. For example, collar fit can vary over the course of the year [21, 38], the same locomotor behavior can be associated with varying activity counts depending on ground cover including snow [40, 42], the activity count can vary with seasonal changes in insect harassment and resulting movement [40, 43], and different types of food consumed over the course of the year can be associated with different head movements and consequently, activity counts [40, 44, 45]. Furthermore, it is important to account for inter-individual variation in the motion signatures of behaviors [46–48]. Notably, Herberg used behavioral observations conducted on eight collared captive moose during four seasons in combination with dual-axis accelerometer measurements of moose averaged over 5-min intervals as well as GPS-based location data to predict the proportion of time spent resting, foraging or moving within each 5-min interval [38]. Activity within most of their 5-min intervals comprised multiple behaviors associated with behavior-specific variations in energy expenditures [38, 49], and they proposed the use of continuous accelerometer recordings to improve distinction among behaviors and refine the temporal resolution of the behavioral predictions [38]. Increasing the temporal resolution is important because biologically relevant and energetically costly behaviors such as bouts of locomotion or alertness, can occur on time scales that are shorter than the recording intervals of the technology previously used for detecting behaviors [35, 39]. Accelerometer sampling frequency should be at least twice the frequency of the fastest body movement of interest [51–53]. Investigating moose behavior on a finer temporal scale and distinguishing among a higher number of behaviors can facilitate the

early detection of individual responses to changes in the environment resulting from anthropogenic activities, which can serve as foundation for the assessment of population-level responses [54–56].

Our goal was to train a random forest algorithm to classify continuous high-frequency accelerometer data collected from captive moose over several seasons into discrete behaviors, to detect changes in behavior on the temporal scales on which the behaviors can occur. The aim was to enable future studies to quantify fine-scale disturbance responses, behavior-specific habitat selection and detailed time budgets in wild moose.

Methods

Data collection

To study moose behavior, we fitted 12 individuals of subspecies *A. a. gigas* in Alaska (all female) and two individuals of subspecies *A. a. alces* in Norway (one female, one male) with Vectronic Vertex Plus accelerometer-GPS neck collars (Vectronic Aerospace GmbH; Berlin, Germany), which recorded tri-axial accelerometer data at 32 Hz with a sensor range of $\pm 4 g$ and a resolution of 8 bit (Additional file 1: Table S1). Accelerometer data were recorded continuously, and accelerometer time stamps were synchronized with GPS time during GPS fixes (every 15 min in collars in Alaska, every 60 min in collars in Norway). We conducted behavioral observations on individual collared moose and distinguished 21 mutually exclusive behaviors, including multiple foraging, locomotor, grooming and inactive behaviors, expanding on Herberg [38] (Additional file 1: Table S2). The protocol for data capture varied between the two locations as described below.

Alaska

Twelve captive female moose at the Kenai Moose Research Center (Alaska Department of Fish and Game, Alaska) were collared without anesthesia three times for data collection over the course of 3 years. Deployment periods were October 1–11 2020, May 7–November 23 2021, and March 24–July 14 2022. Collars were fitted with a 6-cm gap between the collar and the neck to allow for seasonal changes in neck diameter. The moose were kept in two large (2.6 km²) enclosures with varying terrain and vegetation consisting of boreal and black spruce forest, meadows, bogs and lakes [57]. Supplemental feed was provided from January through April. Supplemental water was provided in one enclosure during June and early July when warm, dry conditions depleted the natural water supplies from wetlands, and in October and November when natural water sources were frozen prior to adequate snow fall. Each animal was observed for at least six hours per observation day during daylight hours.

During the observations, moose were followed on-foot by one of five observers, who logged time-stamped behaviors to the nearest second using GPS time on a tablet running ArcGIS QuickCapture software (Esri, Redlands, CA, USA) and connected to a handheld GPS unit (Bad Elf GPS Pro, Bad Elf, West Hartford, CT, USA).

Norway

One female and one male moose at the Norwegian Moose Center (Inland Norway University of Applied Sciences, Norway) were collared on November 23 2020, following anesthesia with etorphine and xylazine [58]. The moose were kept in a 0.02 km² enclosure with vegetation and undulating terrain, a stream and an artificial water station. A salt lick and daily rations of feed pellets were provided, as well as supplemental browse every second day. The moose were filmed from the outside perimeter of the enclosure between November 23 and December 5 2020, using a Canon XA40 (Canon Europe Ltd, Middlesex, U.K.) handheld video camera mounted onto a tripod. The camera was infrared-enabled to film during low-light conditions. On a few occasions, filming without tripod was conducted in order to maintain visibility of active moose during a filming interval. Filming each day was opportunistic and depended on the activity level of the moose, visibility of the moose from the perimeter of the enclosure, and available daylight. Filming took place in approximately 1-h intervals, and the camera was briefly switched off between intervals. At the start and end of each filming interval, the video was synchronized with GPS time by filming the screen of a handheld GPS unit (GPSMAP 64s, Garmin, Southampton, U.K.). Each filming interval focused on one moose, unless both moose were in close proximity to each other. Collars were removed on December 4, 2020 (Mattis, male) and December 9, 2020 (Idun, female) following anesthesia with etorphine and xylazine [58]. Using the software BORIS v.7.9.22 [59], the videos were then transcribed by a single observer with experience in the data collection on Alaskan moose to ensure comparability between the data sets from the two locations. To avoid errors during the transcription process, exclusion criteria for mutually exclusive behaviors were set to ensure the logical sequence of transcribed behaviors (e.g., standing excluded lying).

Data preparation

Behavioral data

Observation data from Alaska were downloaded from ArcGIS QuickCapture and checked manually. Duplicated entries were removed (e.g. the same button was pressed repeatedly by accident). Within observations, time periods with nonsensical behavioral sequences were excluded

from the analysis (e.g. lying followed by running, without any recording of the moose standing up in between). Observations with many errors were entirely excluded from the analysis. Transcribed observation data from Norway were exported from BORIS for further analysis. All behavioral data were imported into R Studio [60] v. 2022.7.2.576 running R [61] v. 4.2.2 for subsequent analysis.

Accelerometer data

The accelerometer data were downloaded from the collars using Vectronic GPS Plus X software v.10.7.2 (Alaska) or v.10.7.1. (Norway), extracted using Vectronic MotionData Monitor software v.1.2.0 and imported into R Studio [60]. Inspection of the data revealed a delay in the date switching of the timestamps after midnight each day. We therefore excluded the first 20 s after midnight for all observations. Inspection of the data also revealed gaps in the accelerometer data of each collar (<1 min) that occurred at least once per 24-h period, due to rebooting of the unit, as well as inconsistencies in the values of consecutive seconds of time stamps assigned during GPS time synchronization during GPS fixes. Because of these data gaps and the inconsistencies in time stamps assigned during GPS fixes, we summarized the 32-Hz raw accelerometer data in intervals, rather than correcting each individual time stamp, which also facilitated the temporal matching of the behavioral data with the accelerometer data intervals. Based on a preliminary analysis of the data with interval lengths varying from 1 to 10 s, we summarized the accelerometer data in 3-s intervals to maintain a high temporal resolution of individual behaviors (the shortest mean duration of a behavior in our ethogram was two seconds, Additional file 1: Table S2) while maximizing classification performance (i.e. maximizing recall and precision for the largest number of behaviors). Inspection of the data revealed that one collar (Individual: Minnie) recorded at 8 Hz, while the remaining accelerometers recorded at 32 Hz. However, because we summarized our data into intervals, this data was included in the analysis. Opportunistic video recordings revealed that two accelerometer axes were reversed in the collars from Norway compared to Alaska. The data from Norway were adjusted to standardize axis orientation across all collars (Fig. 1).

From the raw accelerometer data, we calculated variables that were frequently used in other studies [14, 23, 25] and did not require continuous time series, to accommodate the aforementioned gaps and inconsistencies in the data. We then summarized the variables in each 3-s interval (Table 1). Most variables described the distribution of raw accelerometer values within each 3-s interval on each axis (X–Z). In addition, pitch (corresponding to

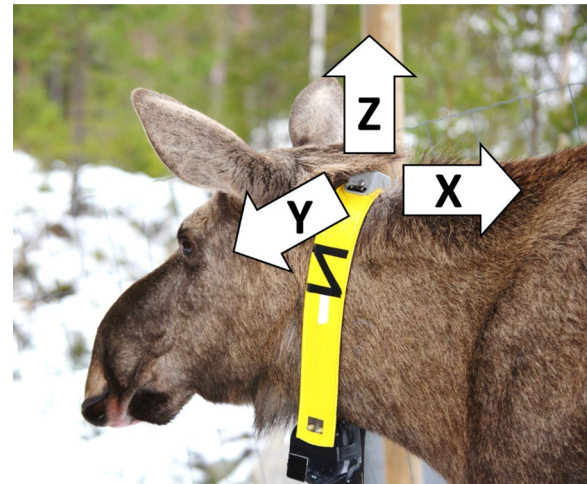


Fig. 1 Accelerometer collar on Idun while standing. Arrows represent axis orientation of the accelerometers mounted in the housing on top of the neck and point towards positive values. X: surge (cranio-caudal axis), Y: sway (medio-lateral axis), Z: heave (ventro-dorsal axis)

Table 1 Predictor variables in the random forest model

Predictor variable	Number of variables per interval
Mean (X, Y, Z, pitch, MSA)	5
Median (X, Y, Z, pitch, MSA)	5
SD (X, Y, Z, pitch, MSA)	5
Min (X, Y, Z, pitch, MSA)	5
Max (X, Y, Z, pitch, MSA)	5
Range (X, Y, Z, pitch, MSA)	5
Interquartile range (X, Y, Z, pitch, MSA)	5
Absolute value of skew (X, Y, Z, pitch, MSA)	5
Kurtosis (X, Y, Z, pitch, MSA)	5
Girth	1
Length	1
Season	1
Sex	1
Subspecies	1

Predictor variables described either the 3-s interval accelerometer data or the time and location of data collection and morphometrics of the collared moose and were used in the random forest model to predict behaviors from the accelerometer data

vertical neck orientation) (Eq. 1) and Minimum Specific Acceleration (MSA) (Eq. 2) were calculated from the raw accelerometer data in each interval. We also included individual metrics which are easy to record in the field: Subspecies, sex, body length, girth and season. Such metrics could improve the generalizability of our model to individuals not seen during model training [25].

Calculation of pitch [62]:

$$\text{Pitch(radians)} = \text{atan}\left(\frac{\text{raw}_x}{\sqrt{\text{raw}_y^2 + \text{raw}_z^2}}\right) \times \frac{180}{\pi} \quad (1)$$

Calculation of Minimum Specific Acceleration (MSA) [19]:

$$\text{MSA}\left(\frac{m}{s^2}\right) = \left| \sqrt{\text{raw}_x^2 + \text{raw}_y^2 + \text{raw}_z^2} - 1 \right| \quad (2)$$

Labeling of accelerometer data

Visual comparison of the start times of recorded behaviors with the raw accelerometer data for a subset of the data revealed that the recorded start time lagged behind the accelerometer signatures. Therefore, we applied an offset to all behaviors (1 s for data from Alaska, 2 s for data from Norway). The non-overlapping 3-s accelerometer data intervals were labeled with the respective behavior recorded during the observations. Intervals during which more than one behavior was recorded were excluded from analysis. The frequency with which different behaviors were observed varied greatly. Because our goal was to obtain a model that could reliably distinguish the main behaviors of moose, we excluded rare behaviors such as head shaking, scratching and urinating, which represented 2.4% of observations. We summarized all foraging behaviors into a coarser foraging category. To identify when the moose were lying with their head tucked, which has been reported as their energetically

least costly behavior [49], we distinguished between two separate lying behaviors based on their head position: lying with the head down or tucked (“lying_o”) and lying with the head up (“lying_u”) (Additional file 1: Table S2). Head position of lying moose was assumed to be up unless otherwise noted during the observations (the head position was not recorded for moose in Norway, and therefore whenever these moose were lying, we considered the behavior to be “lying_u”). Our final analysis included 394.7 h of labeled data (380.4 h of observations collected on-foot in Alaska and 14.3 h of annotated video footage from Norway) of the following seven behavioral categories: Foraging, lying_o, lying_u, ruminating, running, standing, walking (Table 2).

Predicting behaviors from accelerometer data

To classify the accelerometer data into behavioral categories, we used a random forest algorithm, which is frequently used for the classification of accelerometer data [23, 47, 63]. A random forest grows many decision trees on bootstrapped subsamples of the data and combines the predictions of all trees to predict the out-of-bag data that were not used to grow the trees, in order to quantify prediction error [64, 65]. Random forest is a comparatively fast supervised classification algorithm that, through the combination of many decision trees and introduced stochasticity in the modeling process, increases classification performance and can process correlated and interacting predictor variables as well as missing values [64–67]. To accommodate the unbalanced nature of our dataset, we assigned weights to the

Table 2 Samples sizes for each individual and behavior

Animal ID	Foraging	Lying_o	Lying_u	Ruminating	Running	Standing	Walking	Total
Stella	12,308	3763	19,247	13,242	18	5408	1661	55,647
Babe	15,732	2791	15,832	9787	89	8462	2590	55,283
Wilma	6970	1383	20,242	15,274	16	9465	1474	54,824
Sky	13,126	1354	15,733	15,999	49	5226	1715	53,202
Shiner	7397	1390	23,916	11,784	9	6359	2176	53,031
Cayenne	13,149	732	12,568	12,927	7	8536	2197	50,116
Roxanne	9392	1386	16,271	10,006	41	7243	3716	48,055
Minnie	6349	1678	22,927	8434	28	5253	1988	46,657
Winnie	4326	99	3426	4078	0	1128	266	13,323
Vicky	3205	49	4034	4451	37	709	236	12,721
Mattis	753	0	2729	2036	50	3897	727	10,192
Idun	865	0	2614	929	13	1894	637	6952
Lily	2832	0	1277	2203	7	362	203	6884
Olivia	2303	10	1392	1930	0	1035	121	6791
Total	98,707	14,635	162,208	113,080	364	64,977	19,707	473,678

Number of labeled 3-s accelerometer data intervals for each behavior and individual moose used to train the random forest model classifying animal-borne accelerometer data into seven discrete behaviors

observations of each behavior that were inversely proportional to the class size of the respective behavior (i.e., we weighed observations so that the weight of observations of behavior X was equal to the number of observations of the rarest behavior divided by the number of observations of behavior X). Assigning greater weight to observations of rare behaviors reduces the error rate of classifications of the rare classes [67]. We used the random forest implementation from H2O through the h2o R package [68] v. 3.38.0.1 with 200 trees. To test the generalizability of our model to new individuals not included during model training, we performed leave-one-individual-out cross-validation, where the model was repetitively trained on all but one of the individuals and evaluated with the labeled data of the remaining, held-out individual [69–71]. We first ran a random forest with the full set of predictor variables. Random forests are capable of handling both correlated and non-informative predictor variables [65–67] and, while a higher number of predictor variables might increase computation time, our priority was to maximize behavioral classification performance. To assess the effect of variable selection on model performance, we then re-ran the model with only those predictor variables that had scored the highest variable importance ($\geq 3\%$) in the full model [67]. To evaluate classification performance, accuracy is a commonly used metric [72]. However, it is a suboptimal metric for evaluating classification performance in imbalanced datasets (such as ours) [72–74]. Thus, modeling with the goal of maximizing accuracy may not be the best procedure for our dataset. Therefore, we focus the discussion of the performance of our model on the metrics recall and precision (but also give accuracy values since this is a common metric used in other studies) [73].

Results

Model performance

Out of 50 predictor variables in the full model, 16 scored a variable importance of at least 3% and were included in the reduced model. Recall and precision of most behaviors in the full model were slightly higher than or equal to recall and precision of the reduced model, except for lying with the head down/tucked and ruminating (Table 3). Therefore, we focus the description of our results and the discussion on the full model.

Across all individuals and behaviors, our model classified 473678 3-s accelerometer data intervals from 14 moose into seven behaviors (Fig. 2) with mean recall of 0.75 (± 0.10) and mean precision of 0.62 (± 0.24) (Table 3).

Across all individuals, classification performance varied by behavior and was generally best for the three most common behaviors (lying with the head up, ruminating, foraging) constituting 79% of our data, with recall and precision

Table 3 Effect of variable selection on model performance

	Full RF		Reduced RF	
	Recall	Precision	Recall	Precision
Foraging	0.86	0.90	0.84	0.89
Lying_o	0.78	0.34	0.75	0.41
Lying_u	0.74	0.84	0.74	0.83
Ruminate	0.79	0.80	0.82	0.78
Run	0.74	0.28	0.73	0.24
Stand	0.55	0.56	0.52	0.53
Walk	0.79	0.62	0.79	0.60

Comparison of model performance between the full random forest model run with all 50 predictor variables and subsequent reduced random forest model run with only the 16 most important variables

ranging from 0.74 to 0.90. Model performance was more variable among the four rarer behaviors constituting the remaining 21% of our data, with recall and precision ranging from 0.28 to 0.79. Among these behaviors, performance was best for walking and lying with the head down/tucked, while standing had the most misclassifications and was most frequently confused with lying behaviors and foraging (Table 4).

Among individuals, classification performance was variable with overall accuracy ranging from 0.38 (Mattis, the only male in our study) to 0.82 (Sky) (Additional file 1: Table S4). Sample sizes among individuals were highly variable, with six moose each contributing less than 3% to the total data in this study, and eight moose each contributing at least 10%. The six individuals with smaller sample sizes scored lower mean recall (mean \pm SD: 0.67 ± 0.05) and mean precision (mean \pm SD: 0.55 ± 0.06) values than the eight moose with larger sample sizes (mean recall \pm SD: 0.75 ± 0.04 , mean precision \pm SD: 0.64 ± 0.06).

Among individuals, the rarest behaviors (lying_o, running) showed the highest variation in classification performance, particularly precision (Table 5, Additional file 1: Tables S5–S18).

Variable importance

The most important variable in our model was the standard deviation of acceleration along the heave axis with an overall contribution of 5% to the classification performance of the model (Additional file 1: Table S3). Sixteen variables contributed at least 3%, of which five were metrics of pitch, four metrics of surge and three metrics of heave.

Discussion

Animal-borne accelerometers have wide-ranging applications, from investigating the energy budget [75–77] and health status [78, 79] of individuals to identifying behavior-specific habitat use [80, 81]. By facilitating the

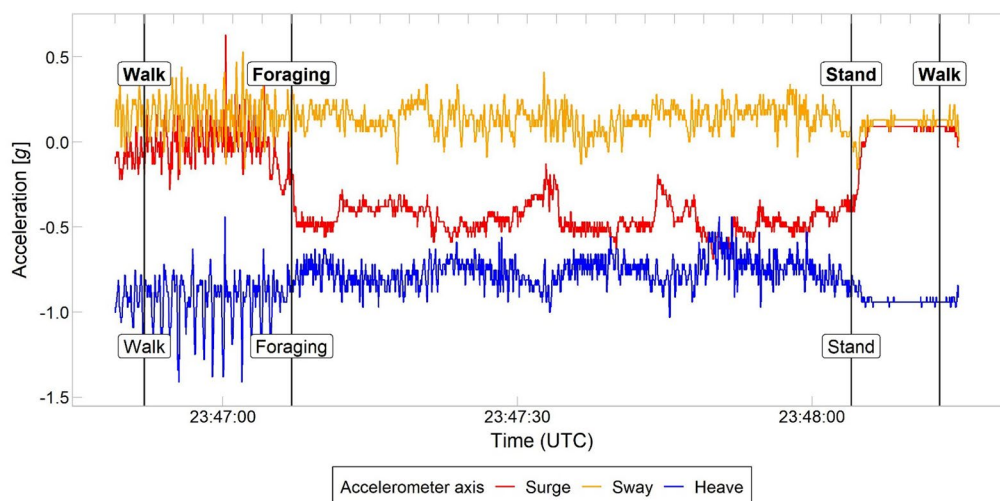


Fig. 2 Example raw accelerometer traces (sampling frequency of 32 Hz) of one captive moose (Stella). Vertical lines indicate the start of a new behavior predicted from the 3-s accelerometer data intervals (bold top labels) and observed during the behavioral data collection (bottom labels). Tick marks on the top axis indicate the start of a new accelerometer data interval

identification of areas important for species conservation [3, 80] and the assessment of effects of disturbances and environmental changes on individual behavior and energy balance [56, 75], this technology can improve wildlife conservation and management efforts. Here, we show that data from animal-borne accelerometers can be used to distinguish among the most common behaviors in moose.

Classification performance

With the three most prevalent behaviors (lying with the head up, ruminating, foraging) scoring the highest recall and precision values between 0.74 and 0.90, classification performance was generally related to class prevalence, which might suggest that the model performed better when the training data contained greater variation in the ways a certain behavior was expressed. While the most prevalent behaviors scored comparable values for both recall and precision, the rarest behaviors (running, lying with the head tucked/down, walking) scored higher recall than precision values. This indicates that our model had fewer false negative predictions of these behaviors, which means that it was able to identify these rare behaviors when the moose were engaging in them, and had a higher number of false positive predictions, which means that it incorrectly predicted these behaviors when other behaviors were occurring. While we assigned greater weights to rare behaviors in order to reduce their classification error [67], it is possible that the weighting was more effective at reducing the number of false negative predictions (and thus increasing recall) than at limiting the number of false positive predictions (and thus increasing precision).

Failing to reduce false positive predictions would lead to a reduction in precision, particularly for behaviors with small numbers of true positive predictions, i.e., behaviors with small sample sizes. Increasing the sample sizes of rare behaviors might improve classification performance for these behaviors but was not feasible in the current study.

Behaviors characterized by little body movement can be difficult to distinguish based on accelerometer data (while predictor variables based on static acceleration might facilitate this distinction, we could not calculate these in the current study), and attempting to distinguish among several inactive behaviors with our model (lying with the head down/tucked, lying with the head up, standing) comes at the risk of reducing the overall classification performance [63, 82]. Nonetheless, we did not group these behaviors together because we wanted to evaluate the performance of our model in distinguishing among these important behaviors. Renecker and Hudson recorded the lowest heart rates in moose lying with the head folded against the abdomen, and an increase in energy expenditure of up to 79% during standing compared to lying with the head tucked [49]. Therefore it was important that our model could distinguish periods of minimal energy expenditure during lying with the head down/tucked from times when moose engage in behaviors associated with increased metabolic rates that serve other functions such as energy gain (ruminating), and increased awareness of and interaction with the surroundings (e.g. during lying with the head up or standing, compared to lying with the head down/tucked). Despite being one of the rarest behaviors in our study, the recall

Table 4 Cross-validation confusion matrix for all individuals

Behavior	Predictions							Recall	Precision	Prevalence (%)	
	Lying_u	Ruminating	Foraging	Standing	Lying_o	Walking	Running				Total
Observations											
Lying_u	120,623	17,762	713	11,612	11,003	378	117	162,208	0.74	0.84	34
Ruminating	10,499	89,245	603	8649	3948	104	32	113,080	0.79	0.80	24
Foraging	275	553	84,485	5709	544	7063	78	98,707	0.86	0.90	21
Standing	11,232	4430	5305	35,571	6304	1973	162	64,977	0.55	0.56	14
Walking	54	50	2860	624	167	15,647	305	19,707	0.79	0.62	4
Lying_o	1576	131	56	1416	11,423	30	3	14,635	0.78	0.34	3
Running	2	18	3	2	1	68	270	364	0.74	0.28	0
Total	144,261	112,189	94,025	63,583	33,390	25,263	967	473,678			

The confusion matrix combines the cross-validation confusion matrixes of the random forest model classifying accelerometer data across all 14 moose observed in captivity in Alaska and Norway. Values in columns represent the number of 3-s accelerometer data intervals predicted for each of the seven behaviors, split into rows based on the behavioral labels of the intervals recorded during the observations. Recall and precision quantify the model classification performance for the respective behavior across all animals in the study. Prevalence indicates the contribution of each behavior to the total sample size of accelerometer data intervals

Table 5 Behavior-specific individual variation in model performance

Performance metric	Behavior						
	Lying_u	Ruminating	Foraging	Standing	Walking	Lying_o	Running
Recall	0.69±0.17	0.74±0.18	0.86±0.04	0.53±0.18	0.73±0.14	0.78±0.15	0.74±0.21
Precision	0.82±0.09	0.78±0.12	0.89±0.07	0.56±0.18	0.57±0.19	0.31±0.31	0.28±0.26
Prevalence (%)	34	24	21	14	4	3	0

Behavior-specific variation in classification performance among 14 individuals of the random forest model classifying seven different behaviors from accelerometer data. Mean and standard deviation of precision and recall are given together with the prevalence of the behaviors in the observational data

of lying with the head down/tucked ranged among the highest values of all behaviors, with 78% of all events that were labeled as lying with the head down/tucked being correctly identified by our model. While the unique neck postures during this inactive behavior might facilitate its distinction, false predictions of this behavior did occur (34% in total) and involved mostly other, more common inactive behaviors (lying with the head up, standing, ruminating), illustrating the challenges of distinguishing inactive behaviors from accelerometer data. We did not distinguish lying with the head down/tucked from the generally much more common behavior lying with the head up during the transcription of videos from Norway and therefore labeled all lying behaviors of these moose as lying with the head up. As a consequence, some data had incorrect labels (the small proportion of data that were labeled as lying with the head up when it should have been labeled as lying with the head down/tucked) that trained the model to incorrectly predict the behavior in these instances as lying with the head up. Similarly, some data with incorrect labels (i.e. lying with the head up) were used to falsify predictions that were actually correct (i.e. lying with the head down/tucked). It is likely that this contributed to the comparatively low precision of our models' predictions of lying with the head down/tucked.

In an accelerometer study on reindeer (*Rangifer tarandus*) that grouped all inactive behaviors (including standing, sleeping and ruminating) into one behavior class, this class had the best classification performance among all behaviors [71], which was better than the classification performance for any of the inactive behaviors in our study. However, the focus of the study on reindeer was the distinction among three foraging behaviors (browsing low, browsing high and grazing) [71]. In contrast, we grouped three foraging behaviors into one overall foraging class, which in turn had a better classification performance than the three foraging behaviors investigated in the study on reindeer (precision of foraging in our study scored higher than precision of all three behaviors in the study on reindeer, and recall of foraging in our study scored higher than recall of two out of the three behaviors in the study on reindeer) [71]. This comparison illustrates

the potential effect of grouping of behaviors on model classification performance and the behavioral inferences that can be drawn from the predictions, emphasizing that behavioral grouping needs careful consideration in studies using supervised classification algorithms to analyze accelerometer data.

Classification performance in our model was comparable to that in Martiskainen et al. classifying accelerometer data from dairy cows [83]. While their model performed better at classifying standing, our model performed better at classifying foraging behavior. Similar to our study, Martiskainen et al. reported misclassifications among less active behaviors (lying, ruminating and standing), which they also suspected was due to the similarities in neck posture of the cows during these behaviors [83]. Their model confused among the behaviors foraging, standing and (lame) walking [83] which is also evident in our predictions. During our observations, we considered a moose to be foraging until it took more than two consecutive steps without bites of food; which prompted a switch to walking. Consequently, some instances where the moose was walking were still recorded as foraging, likely contributing to the misclassifications of these two behaviors. Furthermore, foraging and walking can occur simultaneously in browsing animals, complicating their distinction using accelerometer data.

Model generalizability

Given the goal of classifying unlabeled data in wild animals, cross-validating the model on labeled data from unseen individuals, can provide insights into the generalizability of the model [25, 70, 71]. Therefore, variation in classification performances among individuals is a useful indicator of the generalizability of our model [69–71].

In an effort to maximize model generalizability, we aimed to maximize the amount of variation in our training data by pooling data from as many individuals as possible and including individuals from both sexes and two subspecies [83]. The lowest overall prediction performance (accuracy and mean recall) was observed when our model classified data from the only male moose in our study (Mattis). A possible interpretation is that our model might have limited applicability to male moose.

Morphological differences such as the large weight of the head due to the presence of antlers and resulting increased neck circumference [84] could result in different neck posture and movement of male moose compared to female moose during the same behaviors, precluding the generalizability to male moose of a model that was trained on data from female moose to classify data from neck-mounted accelerometers. This notion is supported by the high total number of false predictions of lying with the head down/tucked for Mattis; a behavior characterized by unique neck postures that is confused mainly with behaviors characterized by limited body movement where neck posture might be an important predictor (standing, lying with the head up and ruminating). However, we did find that these misclassifications also occurred particularly often in Shiner, the female moose with the largest measured chest girth and weight in our study, where a large and heavy head and large neck circumference might have resulted in similar misclassifications to those observed for a (younger and) smaller male with small antlers. This might suggest that the reduced performance of our model in classifying Mattis' data did not stem from a lack of generalizability of our model to (young) male moose with small antlers. Instead, the low sample sizes for several of Mattis' behaviors as well as overall individual variability in model performance, which we discuss below, might have resulted in the comparatively low performance of our model when classifying his data. However; ultimately, due to our small sample size of male moose, we cannot evaluate the generalizability of our model to male moose. European moose constituted only 3.6% of the data, hence their predictions were largely based on data from Alaskan moose. Yet, mean recall and precision of the behavioral classification of the one female European moose in our study, Idun, were higher than the mean values of Alaskan moose with similar sample sizes. While the successful application of our model to Idun's accelerometer data might have been facilitated by the similarities in size between Idun and the yearling Alaskan moose in our study (Babe, Vicky and Winnie), ultimately our sample size is too small to evaluate the generalizability of our model to European moose.

Variation in overall accuracy and behavior-specific recall and precision among individuals with comparable sample sizes (e.g. Shiner and Sky) suggests the influence of factors other than sample size, sex and subspecies on model performance. Such individual differences in classification performance have been observed on a wide range of species from penguins [48] to pinnipeds [25, 47] and caprids [46]. Including individual characteristics as predictor variables might account for some of this individual variation and has been shown to increase the generalizability of classification models [25]. However,

individual length and girth had comparatively low variable importance in our model. Other variables such as age or weight might have been more important [25] but were not included in our model because these metrics are difficult to determine in the field when collaring wild moose. Furthermore, length and girth were not measured on all animals in our study and were inferred from other data for several individuals, potentially confounding the importance of these metrics on the behavioral classification of moose accelerometer data.

Fine-scale differences in placement of the accelerometers among individuals might have contributed to the individual variation in the classification performance of our model [48, 69]. Because most collars were deployed for several months at a time, they were fitted to account for seasonal changes in neck diameter, potentially resulting in changes in how the collars responded to body movement over the course of the deployments, thereby increasing within- and among-individual variation of the data [22, 38, 85]. Because collar fitting in our study was similar to collar fitting on wild moose in the field, our training data included such variation. While this might have reduced the classification performance of our model, it increases generalizability of our model to data from wild animals, where some fine-scale differences in accelerometer placement among individuals can be expected. In our model, season had a variable importance of 2%, suggesting that variation in collar fit over the course of the deployments, or other seasonal variation such as the effect of snow on locomotor behaviors, exerted some influence on the classification in our model. In addition to within- and among-animal variation among collar placement, variation may exist among the accelerometer units themselves [22]. Addressing such variation requires calibration of the units prior to deployment [22, 86, 87]; but calibration data are often not available for existing accelerometer data where collars were deployed in the field without prior calibration [22].

Limitations of our study and recommendations for futures studies

The quality of the time stamps of our accelerometer data prevented a time series analysis of the data at a sub-second level. It was therefore not possible to distinguish between static and dynamic acceleration [17, 18] and analyze the frequency composition of the accelerometer signals [14, 18], to calculate predictor variables that were among the most important for the classification of accelerometer data in other studies [46, 63, 71]. For example, frequency analysis of accelerometer data using fast Fourier transform can facilitate the distinction among simultaneous, rhythmic behaviors such as foraging and walking [63]. In moose, such a frequency

analysis might help distinguish among lying and ruminating, standing, foraging and walking behaviors from accelerometer data. Improving the quality of the time stamps recorded by the accelerometers built into the collars would enable the calculation of these important predictor variables, thus offering a promising way to further improve the performance of behavioral classification models on fine-scale tri-axial accelerometer data of moose.

For the sake of this study, we considered postures (e.g. lying, standing) as separate categories from behaviors (e.g. foraging, ruminating, walking). Postures and behaviors are not mutually exclusive as, for example, a foraging moose is usually standing. Consequently, there was overlap in the accelerometer signatures of the behavioral classes, which we considered exclusive. This could explain some of the misclassifications among these behaviors like for example, foraging and standing, and lying with the head up and ruminating. In future studies, recording posture and behavior separately might facilitate the distinction among these behaviors [63]. However, such a distinction is logistically challenging when logging behaviors in real time in the field.

When applying our model to accelerometer data from wild moose, our model will not be able to classify behaviors that were not included in model training, for example swimming which can occur when moose are foraging on aquatic vegetation [88]. Instead, such behaviors unknown to the model will be misclassified as one behavior (or multiple behaviors) known to the model based on similarity in the accelerometer variables [25]. Increasing the sample size of observations of male and European moose and of rare behaviors would improve the generalizability of our model to new individuals.

Conclusions

We demonstrate the use of accelerometer data to distinguish among seven important behaviors of moose. Potential applications include the quantification of the time budget of wild moose and, by relating behavioral predictions to environmental variables, the investigation of behavior-specific habitat selection as done for other species [80, 81, 89]. Quantifying behavioral responses of moose to changes in their environment can elucidate the effect of disturbances on their time budget. Relating accelerometer data to metabolic rate could elucidate the energetic consequences of behavioral responses of moose to disturbances [15, 56].

Abbreviation

MSA Minimum specific acceleration

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-023-00343-0>.

Additional file 1: Table S1. Details on individual moose included in the study. **Table S2.** Ethogram used to record observations of captive moose including sample sizes and durations of all behaviors and grouping of behaviors to label accelerometer data intervals. **Table S3.** Variable importance of the random forest model. Importance of all predictor variables of the random forest model used to predict moose behavior from 3-s intervals of animal-borne accelerometer data. **Table S4.** Summary of the individual classification performance of the random forest model in predicting behavior from accelerometer data for each of the 14 moose in the study. **Tables S5–S18.** Confusion matrices for the 14 moose. Values in columns represent the number of 3-s accelerometer data intervals predicted for each of the seven behaviors, split into rows based on the behavioral labels of the intervals recorded during the observations. Recall and precision quantify the classification performance of the model for each behavior of each individual. Prevalence indicates the contribution of each behavior to the total sample size of accelerometer data intervals for the respective individual.

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Author contributions

AE, ALE, BZ, DT, JC, OD and TK conceived the study and planned the experiments. JC, DT, BZ, AE and ALE acquired funding. TK, DT and JC collected the data. TK performed the analyses with support from OD and MC. TK wrote the manuscript with input from all co-authors. All authors reviewed the manuscript.

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Availability of data and materials

Data for this project are available upon reasonable request from the Alaska Department of Fish and Game and subject to a data sharing agreement.

Declarations

Ethics approval and consent to participate

Animal care and handling procedures in Alaska were approved by the Animal Care and Use Committee, Alaska Department of Fish and Game, Division of Wildlife Conservation (protocol number 0086-2020-40). Animal handling in Norway did not require a permit under the Norwegian Food Safety Authority as the collars were deployed during routine hoof trimming and annual veterinary exams.

Consent for publication

All authors agree consent to publish this work to *Animal Biotelemetry*.

Competing interests

The authors declare that they have no competing interests.

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Predicting energy expenditure from dynamic body acceleration in a large boreal ungulate

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Abstract

Energy expenditure is a vital parameter in bioenergetic models aiming to quantify the consequences of disturbances and changing environmental conditions on wildlife. However, energy expenditure is difficult to measure in wild animals. Here, we used biologging data to predict heart rate from accelerometer data in moose (*Alces alces*). We implanted heart rate loggers and deployed accelerometer collars on eight captive female moose. We simultaneously recorded heart rate (every 30 seconds) and accelerometer data (continuously at 32 Hz) during three-day-long sampling periods in early and late summer, fall and spring. At the same time, we conducted behavioral observations in late summer, fall and spring. We fitted a generalized additive mixed model to predict heart rate from overall dynamic body acceleration calculated from the accelerometer data. Using a previously published equation, we then calculated energy expenditure from the predicted heart rates. Using our behavioral observations, we predicted energy expenditures for seven different behaviors by season and compared our results to previously published values. Season, overall dynamic body acceleration, time of day and individual were important predictors in our model and together explained 66% of the deviance in the moose heart rate data. Our model tended to underestimate heart rate at high values of overall dynamic body acceleration due to low sample sizes and imbalanced sampling for the different behaviors. We observed large seasonal and individual variation in the behavior-specific energy expenditure, with lowest energy expenditure during lying in the fall ($12.5 \pm 4.8 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-0.75}$) and highest during running in the fall ($69.7 \pm 46.2 \text{ kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-0.75}$). Our range of predicted behavior-specific energy expenditure was comparable to published values but slightly lower in the fall and summer and higher in the spring. The method presented here facilitates the estimation of moose energy expenditure from collar-mounted accelerometers, circumventing the need for surgical logger implantation.

Introduction

Energy is a central currency in ecology (Brown et al. 2004, Butler et al. 2004). Animals expend energy on a variety of metabolic functions such as maintenance, growth, reproduction and movement, and gain energy only through foraging (Pontzer & McGrosky 2022). The ability of an individual to meet its metabolic demands determines its survival (Kleiber 1961). Through the effect of maternal condition on recruitment, the energy balance of individuals can ultimately affect population growth (Bernardo 1996, Shallow et al. 2015, Ruprecht et al. 2016); individual energy budgets are therefore of interest for population management and conservation.

Changing environmental conditions, anthropogenic disturbances and predation risk effects can affect the energy balance and survival of individuals by increasing energy expenditure (e.g., increased costs of locomotor activity or thermoregulation, increased vigilance) (Fancy & White 1987, Feist & White 1989, Dickinson et al. 2021, Díaz et al. 2024) or reducing energy intake (via reduction in foraging activity or forage availability) (Creel et al. 2009). For example, in recent years, negative effects of climatic factors on plant phenology and thus maternal body condition were implicated in declining recruitment of several ungulate populations including woodland caribou (*Rangifer tarandus caribou*) (DeMars et al. 2021), roe deer (*Capreolus capreolus*) (Gaillard et al. 1997, 2013) and moose (*Alces alces*) (Monteith et al. 2015). At the same time as caribou recruitment is affected by climatic effects on plant phenology, anthropogenic landscape change facilitates the range expansion of other cervids and their predators into the range of endangered woodland caribou, increasing predation and predation risk effects on caribou (DeMars et al. 2021). To predict the effect of a multitude of factors on population growth, energy use and

gain are important parameters in population models (Nisbet et al. 2000, Nabe-Nielsen et al. 2014, Pirota et al. 2022).

Several methods exist for studying animal energy expenditure. Field metabolic rate, the rate of energy expenditure under natural conditions (Kleiber 1961, Speakman 1999, Weibel & Hoppeler 2005), can be measured indirectly from doubly labeled water or estimated from heart rate (Speakman 1999, Green 2011). In wild animals, these methods can be difficult to implement as they are invasive and/or logistically challenging (Speakman 1999, Butler et al. 2004, Halsey et al. 2008). In recent years, accelerometry has become a prominent method to quantify animal energy expenditure due to its comparable ease of implementation (Wilson et al. 2006, Halsey et al. 2011). This method uses body-mounted accelerometers to quantify the movement of an animal's body resulting from energy-consuming muscle contractions (Cavagna et al. 1963, Wilson et al. 2006, Halsey et al. 2008, Gleiss et al. 2011). To quantify the rate of energy expenditure during body movement, measurements of body acceleration are calibrated with concurrent measurements of the rate of oxygen consumption (Wilson et al. 2006, Halsey et al. 2008).

Moose are the largest deer species and occur in the boreal forests of the northern hemisphere (Karns 2007, Niedziałkowska et al. 2022) where they are of high ecological and cultural importance (Molvar et al. 1993, Snaith & Beazley 2002, LeBlanc et al. 2011). A variety of factors have been suggested to contribute to recent population declines and declines in cow/calf ratios observed in several areas, including food limitation or nutritional deficits (Lavsund et al. 2003, Murray et al. 2006, Pettorelli et al. 2007, Monteith et al. 2015), increased parasite loads (Murray et al. 2006, Jones et al. 2020), increased predation (Wikenros et al. 2020) and increased energetic costs of thermoregulation (Post & Stenseth 1999, Murray et al. 2006, Monteith et

al. 2015). Moose in an area with high anthropogenic activity and increased temperatures had short relative telomer lengths – a signs of chronic stress (Fohringer et al. 2022). Another study did not find an effect of human activity on cortisol concentrations in moose hair, another indicator of stress (Spong et al. 2020), illustrating that the effect of human disturbance on moose health is currently unclear.

Our goal was to predict moose energy expenditure from accelerometer data to facilitate future studies of the energy budgets of wild moose, for which more direct methods such as isotope dilution techniques or heart rate measurements are difficult to implement. In captive moose, we simultaneously recorded accelerometer data as proxy for body movement and heart rate as proxy for energy expenditure. We first built a model to estimate heart rate from the accelerometer data, and then used an existing equation quantifying energy expenditure from heart rate in moose (Renecker & Hudson 1985) to link accelerometry directly to energy expenditure.

Methods

Moose husbandry

At the Kenai Moose Research Center (MRC) run by the Alaska Department of Fish and Game, female captive moose were housed in two 2.6 km² enclosures with varying seral states of mixed boreal forest, black spruce forest, meadows, wetlands, and lakes in varying terrain. Moose foraged on natural vegetation throughout the year and were provided supplemental pellet ration from January to April (ca. 3.5 kg/day; Reindeer 13% Pellet, Alaska Garden and Pet Supply, Anchorage, AK, USA). Water was supplemented in June and early July in one enclosure when wetland water sources were depleted, and prior to adequate snow fall in October and November when natural water sources were frozen. The moose were weighed

approximately once every season (April, October and December 2021 and March 2022) on a platform scale (MP Series Load Bars; ± 2 kg; Tru-Test Limited, Auckland, NZ).

Data collection: Heart rate logger implantation and programming

Star-Oddi Centi heart rate loggers were implanted into 8 female non-pregnant, non-lactating moose aged 2-12 years (Appendix: Table 4) at the Kenai Moose Research Center in July 2021 and removed in July 2022. For immobilization prior to the surgeries, we used Thiafentanil oxalate (0.001– 0.004 mg/kg estimated body mass; 10 mg/mL; Wildlife Pharmaceuticals Inc., Windsor, CO, USA) and Xylazine (0.03–0.05 mg/kg estimated body mass; 100 mg/mL; Lloyd Laboratories, Shenandoah, IA, USA) (Høy-Petersen et al. 2023). Surgeries followed the protocol described in Græsli et al. (2020b). Loggers were programmed to record raw electrocardiogram (ECG) data for 4 seconds in summer and 10 seconds in the fall and spring. The loggers automatically calculated heart rate (HR) in beats per minute (bpm) from R-R intervals between consecutive ventricular depolarization waves (QRS complexes) detected in the ECG data (Bayés de Luna et al. 2007, Star Oddi 2022). The loggers assigned a quality index for each heart rate measurement, considering factors such as the number of detected QRS complexes and heart rate variability per 4 second measurement interval, with quality index 0 indicating the highest and quality index 3 indicating the lowest quality (Star Oddi 2022). We programmed each logger to record heart rate every 30 for three consecutive days in late summer (August 7- 30, 2021), fall (October 25-November 17, 2021), spring (March 25-April 17, 2022) and early summer (June 15-July 8, 2022). Loggers recorded heart rate once every two hours between the three-day sampling periods. Sampling periods did not overlap among the loggers deployed in each animal; only one logger was recording at a time, and the next logger started recording in the next animal when the previous loggers stopped recording. For manual validation of the logger-based heart rate calculation, we programmed

the loggers to save the raw ECG data in addition to the HR data calculated from the ECG as follows: All loggers recorded HR and saved the raw ECGs every 5 minutes over the course of two days between August 4 and August 5. Additionally, every logger recorded HR and saved the raw ECG data once per hour for 24 hours prior to that logger's high frequency sampling period each season.

Data collection: Accelerometer data

Moose with heart rate loggers were also equipped with Vertex Plus accelerometer-GPS collars (Vectronic Aerospace GmbH, Berlin, Germany). For the two deployment periods (May 7-November 23 2021, and March 24-July 14 2022), collars were fitted and removed without anesthesia. To accommodate seasonal changes in neck diameter, a gap of approximately 6 cm was left between the collar and the neck. The collars recorded tri-axial accelerometer data at 32 Hz (except for Minnie's collar; this collar recorded data at 8 Hz; however the data was still included in the analysis) and one GPS position every 15 min, during which the accelerometer time stamps were synched with GPS time (Kirchner et al. 2023).

Data collection: Behavioral observations

During each heart rate logger's high-frequency recording periods, we conducted behavioral observations for a minimum of six hours per day during daylight hours. One of five observers followed the moose on foot or snowshoes, logging start times of behaviors to the nearest second in ArcGIS Quick Capture software (Esri, Redlands, CA, USA) running on a tablet linked to a GPS unit (Bald Elf GPS Pro, Bad Elf, West Hartford, CT, USA) (Kirchner et al. 2023). Our ethogram consisted of 21 behaviors building on Herberg (2017). Only one behavior was recorded at any point in time. Additionally, we recorded opportunistic video footage of bedded moose during observations in summer 2021 and spring 2022 using a handheld video camera (Canon X40; Canon Europe Ltd, Middlesex, U.K.).

Validation of heart rate measurements

After immobilization of the moose and surgical removal of the loggers, we downloaded the heart rate data using the program Mercury (Star Oddi, Gardabaer, Iceland). We plotted the voltage of the raw ECG signal recorded during each 4-second sampling interval and manually calculated heart rate from this data as the mean time between the R waves of two consecutive QRS complexes. For each logger, we plotted ECGs from which the logger calculated low, medium, and high heart rates, and manually validated at least 5 ECGs for each heart rate category and quality index 0 and 1 (HR measurements with quality index lower than 1 were not considered for inclusion in the analysis). We compared the manually calculated HR to that calculated by the logger and considered a measurement reliable if it did not deviate from the manually validated heart rate by more than 10% (Trondrud et al. 2021).

Time drift correction of heart rate measurements

Prior to deployment, the clock in each logger was synchronized with the computer used for logger programming. After logger recovery, the time in each logger was compared to the time stamp of the same computer. From the time difference between the computer and the recovered logger, we calculated a linear drift correction factor for each logger and corrected the time stamp of each heart rate measurement for time drift.

Preparation of accelerometer data

After removal of the collars, we downloaded the data and extracted the accelerometer data recorded during heart rate measurement intervals using the program Vectronic MotionData Monitor (v.1.2.0) (Vectronic Aerospace GmbH, Berlin, Germany). We calculated static body acceleration for each accelerometer measurement as a four-second running mean of the raw acceleration in each axis to match the heart rate recording interval (i.e., ECG length). Dynamic body acceleration was

calculated in each axis by subtracting static acceleration from raw acceleration recorded in the respective axis. For each of the 32 accelerometer measurements per second, overall dynamic body acceleration (ODBA) was calculated as sum of the dynamic body acceleration over all axes. Because the accelerometer data contained time gaps at varying length and occasionally also discontinuous timeseries data as detailed in (Kirchner et al. 2023), we ensured that the moving windows used to calculate static acceleration and thus ODBA did not span any time gaps but were in fact limited to a duration of four seconds.

We rounded the start and end time of each heart rate measurement interval and each four-second moving window used to calculate ODBA and calculated the median ODBA for each heart rate measurement. For the remainder of this manuscript, we will refer to the median value of ODBA in each four-second window simply as ODBA.

Estimating heart rate from accelerometer data

All analyses were conducted in R (R Core Team 2023) (v.4.3.1) using R Studio (v.2023.6.1.524) (Posit team 2023). Fitting a generalized additive mixed (GAM) model using the *bam* function in the *mgcv* package (v. 1.9-0) (Wood 2011, 2017), we modeled heart rate as function of ODBA with fast restricted maximum likelihood estimation and a scaled t-distribution (scat family) with an identity link function to account for heavy tails in the distribution of the heart rate data. We used a thin plate regression spline with 25 knots on ODBA with a random slope by season to account for seasonal variation in the effect of dynamic body acceleration on heart rate. To account for seasonal hypometabolism in moose we included season as a fixed effect. We added a smooth with a cyclic cubic regression spline with 10 knots for time of day (in seconds) to account for circadian variation in heart rate, and to address temporal autocorrelation in the heart rate data. We included a random effect for individual with varying intercept by season to account for

individual differences in the heart rate data, and an AR(1) structure to account for observed autocorrelation in the residuals. The final model structure was as follows:

$$\begin{aligned} HR \sim & s(ODBA, k = 25, by \\ & = Season) \\ & + Season \\ & + s(time\ of\ day, k = 10, bs \\ & = cc) \\ & + s(Individual, by \\ & = Season, bs = re) \end{aligned}$$

We inspected the value of k using the *gam.check* function and checked for residual autocorrelation. To evaluate model performance, we used the model to predict heart rate from the data used to fit the model, after removing the effect of individual on heart rate.

Calculating energy expenditure from heart rate data

The next step in predicting energy expenditure from ODBA was to use the heart rate values predicted from our GAM model to calculate energy expenditure using the equations from Renecker & Hudson (1985, 1989).

$$\text{Equation 1: } \textit{norm.HR} = \frac{HR}{M^{-0.25}}$$

$$\text{Equation 2: } \textit{Metabolic rate} = 4.655 \times e^{0.0071 \times \textit{norm.HR}}$$

To calculate normalized heart rate (Equation 1), we first calculated individual spring mass (M) as mean of the weights in April 2021 and March 2022, and summer weight as mean of spring and fall weights (Appendix: Table 4). We used the normalized heart rate to calculate metabolic rate for each 4-second heart rate estimate (Equation 2). To assess our estimates of energy expenditure, we predicted heart rate from ODBA calculated from data recorded during specific, observed behaviors, and visually compared the resulting behavior-specific energy expenditures to the values published in Renecker & Hudson (1989). These data were collected on two captive female moose (average weight: 320 ± 5 kg, age:

2.5 yr) with implanted heart rate loggers observed over a 24-hour period once per month over the course of a year (Renecker & Hudson 1989). For our comparison, we combined the data for some of the behaviors studied in Renecker & Hudson (1989) (see details in Appendix section “Predicting energy expenditure from heart rate data”).

Results

Validation of heart rate measurements

We recovered seven out of eight implanted loggers; one logger was likely rejected over the course of the deployment. Another logger (Sky) stopped recording in January 2022, the remaining six loggers recorded during all programmed sampling periods. Due to a programming error, the heart rate loggers calculated heart rate from four-second ECG for all seasons, and ten-second ECG were only used during the 24-hour validation period prior to each sampling period. During the validation, 99.5% (n = 543) of 546 manually calculated heart rates scored within 10% of the value calculated by the logger for quality class 0, and 80.1% (n =

113) of 141 for quality class 1. A visual inspection of the simultaneous recordings of heart rate and activity data from observation periods revealed a large number of high heart rate measurements of quality class one in two moose (Shiner and Wilma) during bedded periods. A screening of the video footage available for a subset of these measurements revealed that these individuals were bedded on their left side during these periods. In the raw ECG data of these moose collected for the logger measurement validation, we frequently observed a higher heart rate calculated by the logger compared to our calculation for measurements of quality class one; likely resulting from the logger mistaking prominent T-waves in the ECG data for R-waves and thus overestimating the number of QRS complexes and heart rate. It is likely that the placement of the loggers in these moose resulted in an exaggeration of the T-waves in the ECG when the moose were bedded on their left side. For the remainder of the analysis, we used only quality 0 measurements within the validated range (17-155 beats per minute). An example of the variation of heart rate and ODBA over the course of 24 hours for one moose in the summer is shown in Figure 1.

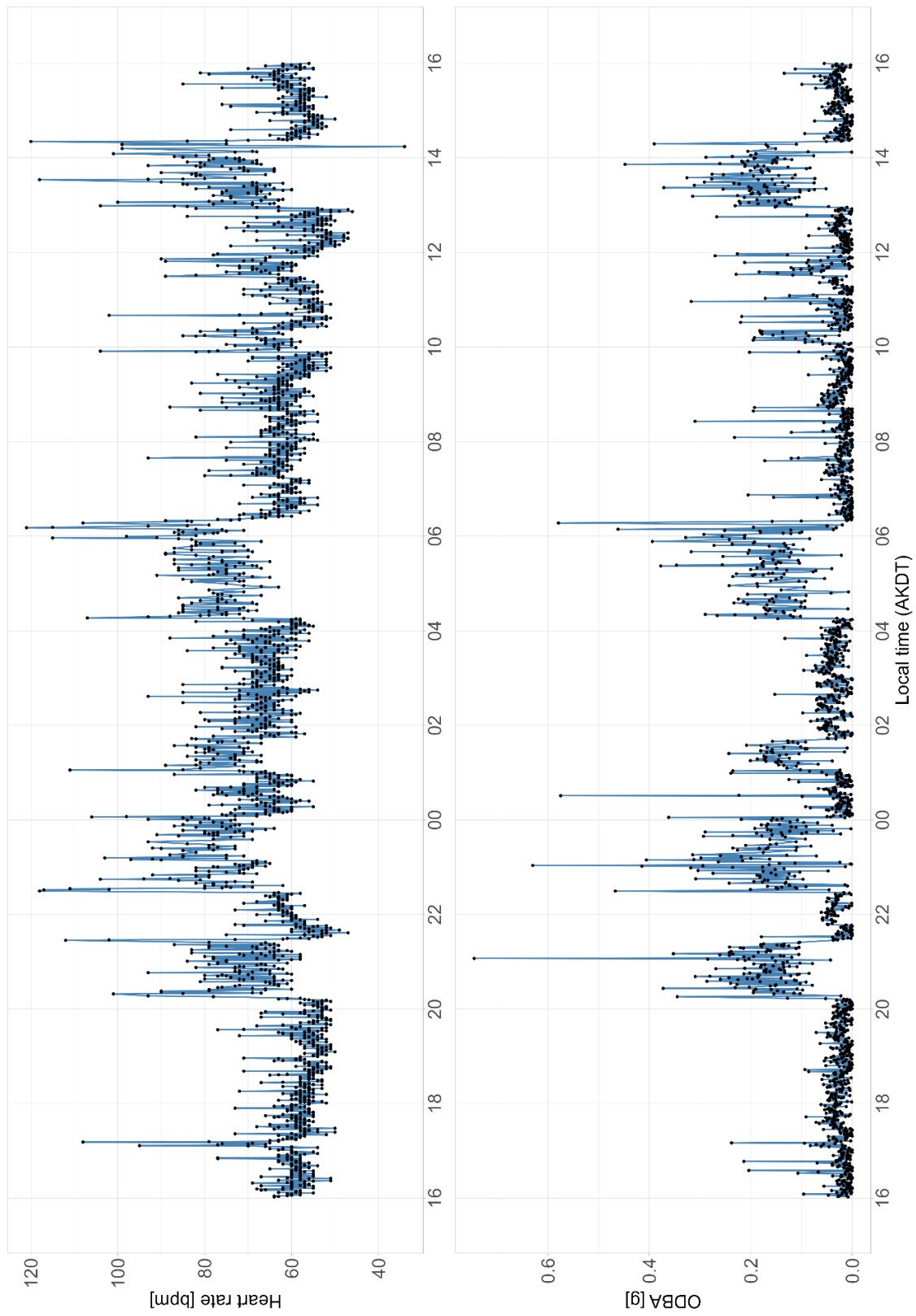


Figure 1: Simultaneous recordings of heart rate from a subcutaneously implanted heart rate logger (top) and overall dynamic body acceleration from a collar-mounted tri-axial accelerometer (bottom) in one captive female moose (Minnie) over the course of 24 hours in August 2021.

Heart rate measurements

Within the sampling periods, the loggers recorded a total of 224,952 measurements; 66.3% (n = 149,152) were of quality class 0 and

fell within the validated range of heart rate measurements. Heart rate varied by season; lowest median heart rate of 33 bpm was recorded in the fall, highest median heart rate of 57 bpm in late summer (Table 1).

Table 1: Moose heart rate recorded by implanted loggers during four seasons in seven captive moose. A detailed overview is also provided over different sample sizes of heart rate measurements depending on data quality: Given are the total number of measurements recorded, the size of the subset of measurements belonging to the highest quality class, and within this quality class, the number of reliable measurements (those that fell within the manually validated range (17-155 bpm)). The number of heart rate measurements within this validated range that were recorded while collar-mounted tri-axial accelerometers recorded an overall dynamic body acceleration of less than 3 g are also given.

Season	Heart rate (median ± SD) [bpm]	Number of heart rate measurements			
		Total	Quality class 0	Quality class 0, within validated range	Quality class 0, within validated range, ODBA < 3g
Spring	38 ± 10	51921	33237	33185	33185
Early summer	54 ± 10	51907	33343	33307	33307
Late summer	57 ± 11	60561	42195	42158	42152
Fall	33 ± 8	60563	40572	40502	40499

Heart rate predictions

Due to the low sample of measurements at ODBA values greater than 3 g (n = 9), we excluded these values from our GAM model of heart rate. This model explained 66% of the deviance of the heart rate data and identified season, ODBA, time of day and individual as important predictors of heart rate in moose (Table 2). The effect of ODBA on heart rate varied across the range of ODBA values and by season. Heart rate increased with increasing ODBA at low values of

ODBA; this relationship plateaued around 0.2 g. Uncertainty in the predictions increased dramatically at high values of ODBA (>1) concurrent with predicted declines in heart rate with increasing ODBA (Figure 2). Keeping all other predictor variables constant, the model predicted the highest heart rates around midnight and the lowest heart rates around 18:00 (Figure 3). We observed significant autocorrelation in the model residuals (Appendix: Figure 6).

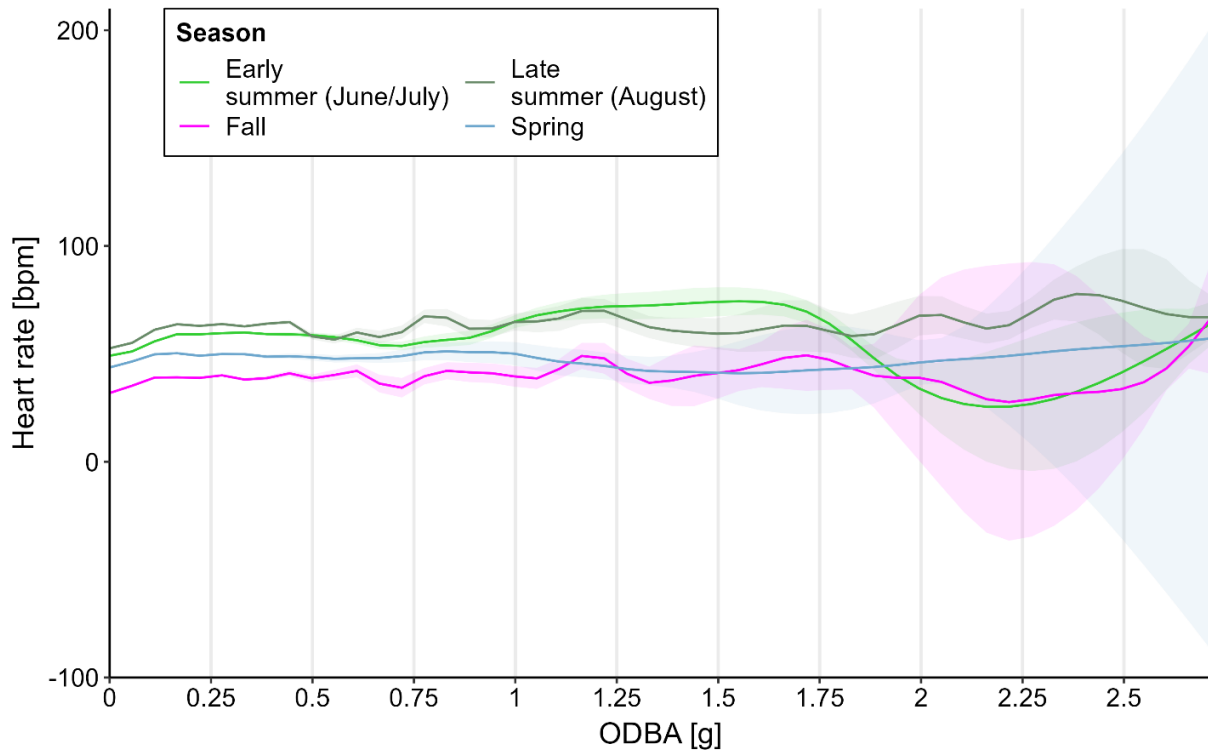


Figure 2: Effect of overall dynamic body acceleration on heart rate in captive moose predicted from a generalized additive mixed model with 95% confidence interval.

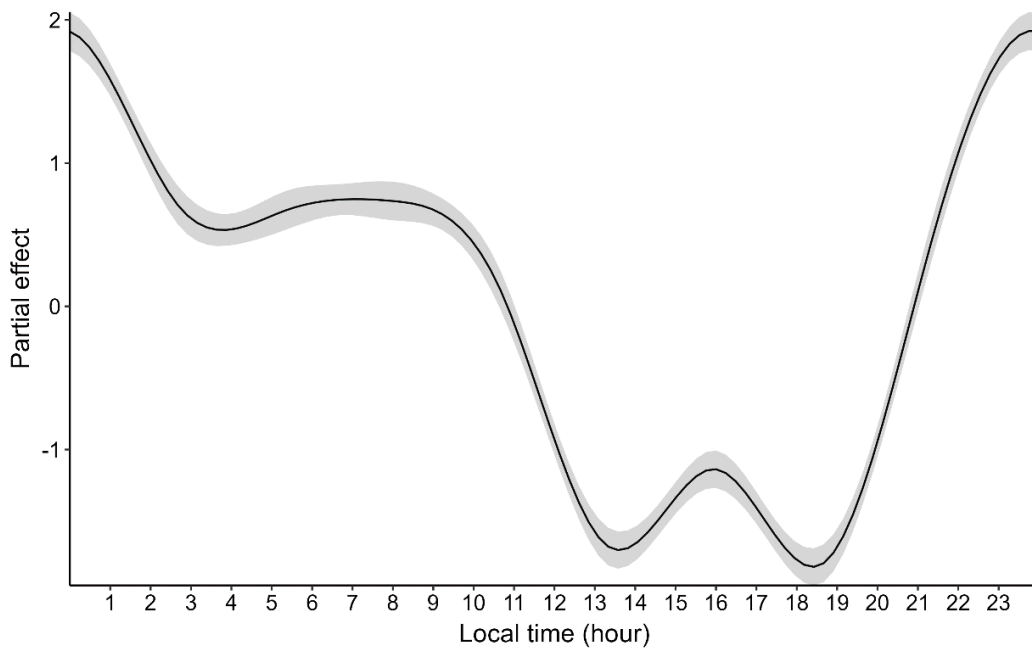


Figure 3: Partial effect of time of day on heart rate in captive moose predicted from a generalized additive mixed model with 95% confidence interval.

Paper II: Energy expenditure model

Table 2: Summary of the generalized additive mixed model quantifying the effect on moose heart rate recorded from implanted loggers of overall dynamic body acceleration (recorded from collar-mounted tri-axial accelerometers), season, time of day and individual. Abbreviations are as follows: ESummer = early summer, LSummer = late summer, day.time = time of day, median_odba = median of the ODBA values recorded at the time of each four-second heart rate logger measurement interval.

Component	Term	Estimate	Std Error	t-value	p-value
A. parametric coefficients	(Intercept)	58.776	2.024	29.043	0.0000 ***
	SeasonFall	-22.075	2.415	-9.140	0.0000 ***
	SeasonLSummer	4.099	2.396	1.711	0.0872 .
	SeasonSpring	-18.603	3.283	-5.667	0.0000 ***
Component	Term	edf	Ref. df	F-value	p-value
B. smooth terms	s(median_odba):SeasonESummer	15.137	16.989	507.206	0.0000 ***
	s(median_odba):SeasonFall	16.841	18.338	335.286	0.0000 ***
	s(median_odba):SeasonLSummer	19.709	21.276	656.215	0.0000 ***
	s(median_odba):SeasonSpring	11.376	12.870	235.995	0.0000 ***
	s(day.time)	7.883	8.000	1,407.713	0.0000 ***
	s(Animal_ID):SeasonESummer	4.997	6.000	1,243.095	0.0000 ***
	s(Animal_ID):SeasonFall	5.992	7.000	680.966	0.0000 ***
	s(Animal_ID):SeasonLSummer	5.993	7.000	713.818	0.0000 ***
	s(Animal_ID):SeasonSpring	4.998	6.000	2,222.429	0.0000 ***

Signif. codes: 0 <= '***' < 0.001 < '**' < 0.01 < '*' < 0.05

Adjusted R-squared: 0.738, Deviance explained 0.662

fREML : 237010.205, Scale est: 1.000, N: 149143

We evaluated our model by using it to predict heart rate from the training data (Figure 4). The model correctly predicted increasing heart rate with increasing ODBA values at the low range of the predictor variable but underestimated heart rate above ODBA values of ca. 0.2 g, illustrating the effect of the plateau of the ODBA model smooths on heart rate predictions.

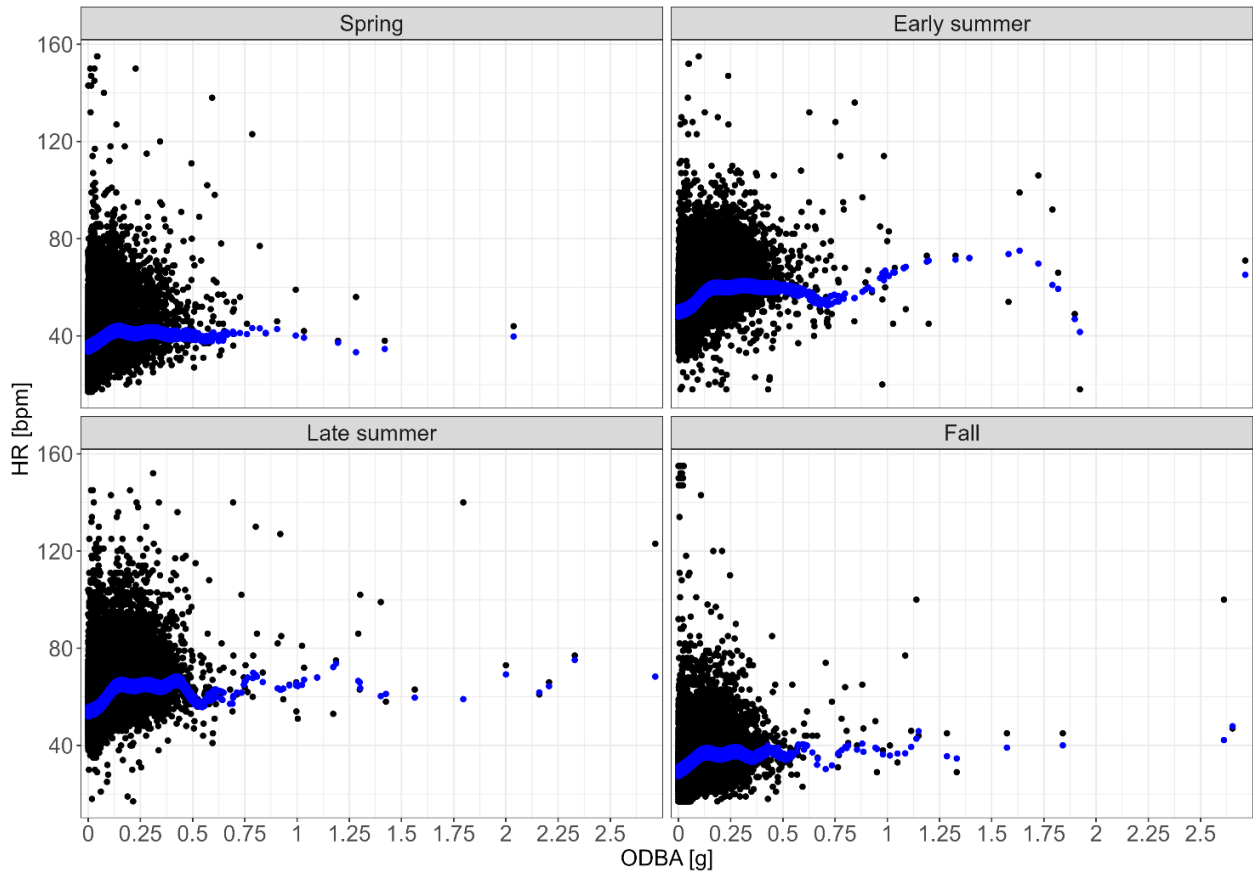


Figure 4: Moose heart rate plotted against overall dynamic body acceleration recorded in seven captive female moose with implanted heart rate loggers and collar-mounted tri-axial accelerometers. Predictions (blue) were derived from a generalized additive mixed model of moose heart rate.

Behavior-specific measurements of heart rate and ODBA

Out of all heart rate measurements qualifying for further analysis (quality 0, within manually validated range), 22,610 coincided with the behavioral observations conducted in fall, spring and late summer. We focused the behavior-specific analysis on seven behaviors constituting 98% of these observations: Lying (42%), ruminating (24%), foraging (17%), standing (11%), walking (4%), alert (0.3%) and running (0.03%). We recorded increasing ODBA among behaviors from lying to running (Figure 5, Appendix: Table 3) but also large variation in heart rate at a given value of

ODBA particularly at lower end of the range of ODBA values. Heart rate tended to increase with increasing ODBA among behaviors in fall and summer but was less dependent on the trend of ODBA in spring. Within each behavior, we observed seasonal variation in ODBA: For most behaviors, ODBA increased from fall to late summer except for ruminating, standing, and foraging, where lowest ODBA was observed in spring, and alert, where ODBA was slightly lower in summer than spring. In contrast, within each behavior, we observed increasing heart rate from fall to summer except for running. Within seasons, we observed individual variation in heart rate normalized by body weight (Appendix: Table 4).

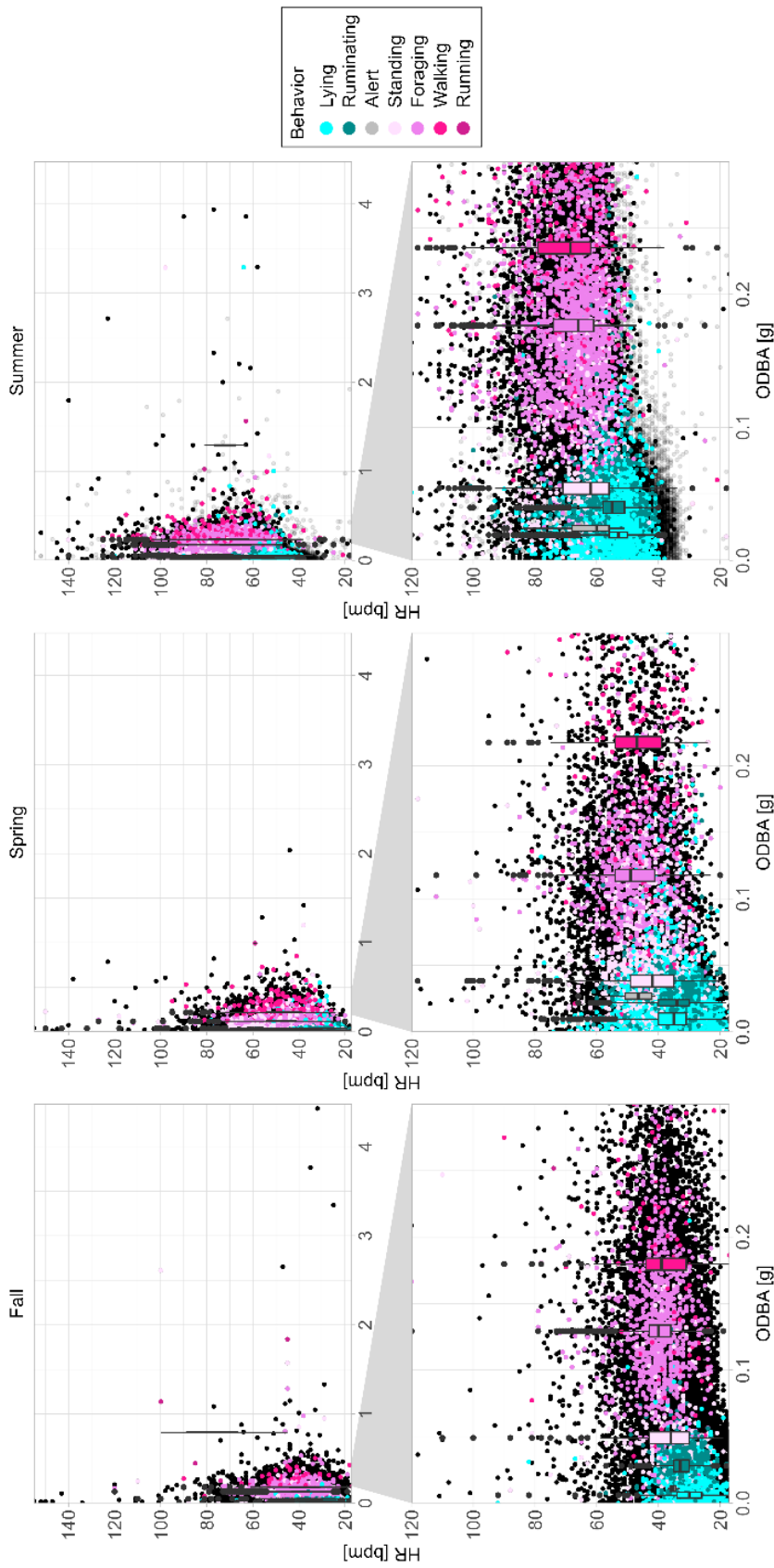


Figure 5: Moose heart rate and overall dynamic body acceleration for seven behaviors by season. The entire data collected during the sampling periods is shown in black. The subset of data collected during behavioral observations is color-coded by behavior. The boxplots are centered on the median ODBA per behavior and season; their center line indicates the median heart rate for the respective behavior and season. The top panels display the entire range of the data, the bottom panels focus on the majority of the data at low ODBA values (note that this range of data excludes running behavior). The opaque data points in the summer panels indicate data collected in early summer 2022, when no corresponding observational data was collected; the remaining data is from late summer 2021.

Predicting energy expenditure from ODBA

We visually compared the calculated energy expenditure by behavior and season to the behavior- and season-specific energy expenditures of moose reported in Renecker & Hudson (1989) (Figure 7). Overall, our range of calculated energy expenditure was comparable to the data published by Renecker & Hudson

(1989). Similar to Renecker & Hudson (1989), we observed large individual variation in behavior-specific energy expenditure. Our calculated energy expenditure tended to be lower than that reported in Renecker & Hudson (1989) for most behaviors and individuals in the fall and summer, and higher in the spring.

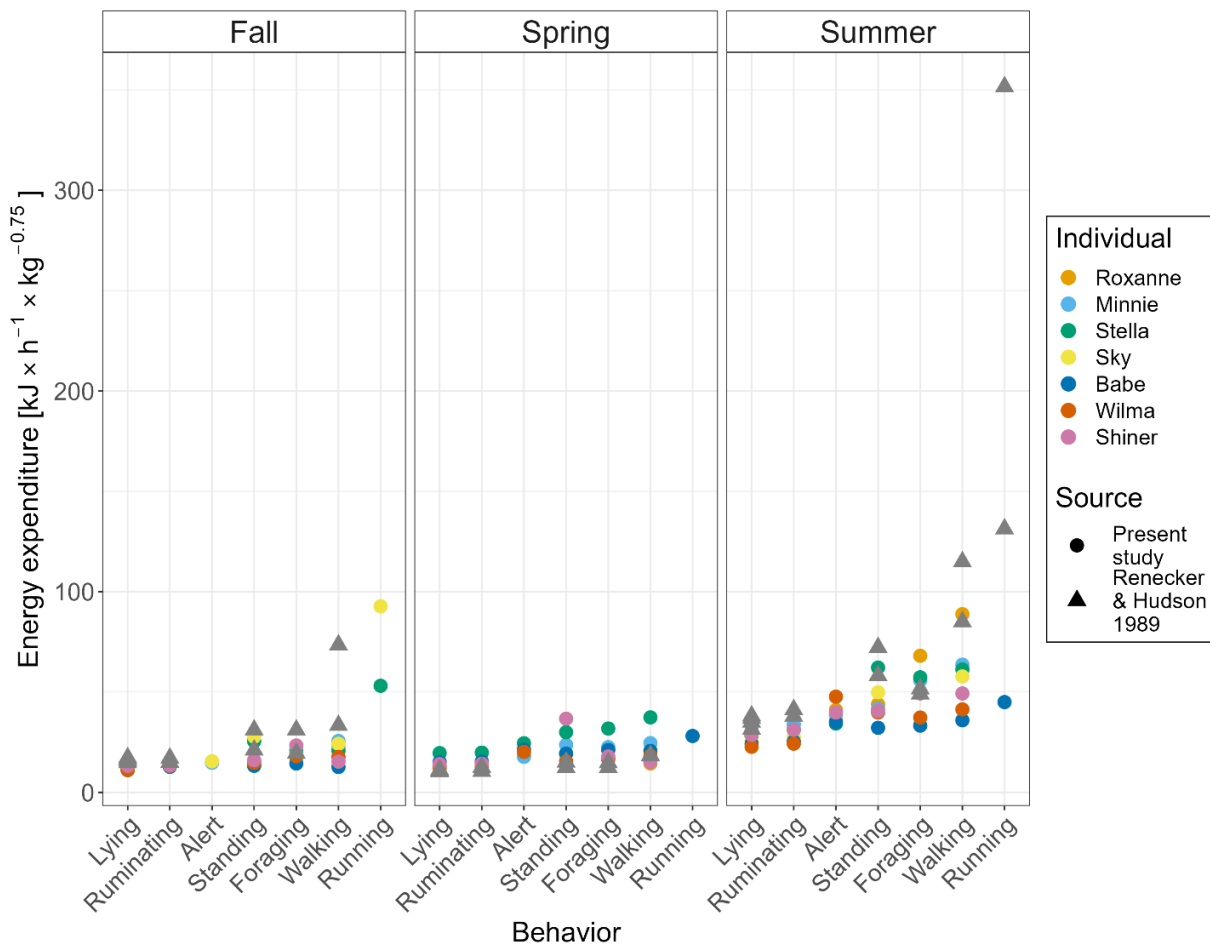


Figure 7: Comparison of energy expenditure per season during different behaviors as predicted by our GAM model of moose heart rate to values published by (Renecker & Hudson 1989). The published values represent mean energy expenditures calculated using Equations 1 and 2 for the heart rate data of each of two individual moose collected over a 24-hour sampling period once per month over the course of a year. Note that the data from Renecker & Hudson (1989) was recorded in July, while our summer observations were conducted in August.

Discussion

Our study is the first to link accelerometry to energy expenditure in moose. We found an increase in heart rate and resulting energy expenditure with increasing overall dynamic body acceleration, similar to other studies on a variety of species from cormorants and shags (*Phalacrocorax* spp.) (Wilson et al. 2006, Hicks et al. 2017), hammerhead sharks (*Sphyrna lewini*) (Halsey et al. 2011) and bovids (Miwa et al. 2015, Dickinson et al. 2021) to humans (*Homo sapiens*) (Halsey et al. 2008). For the remainder of the discussion, we will refer to both direct (e.g., oxygen consumption) and indirect (e.g., heart rate) measures of energy expenditure simply as energy expenditure.

Heart rate: Range and circadian and seasonal variation

The range of heart rate values we were able to validate in this study (17-155 bpm) was wider than the previously published range of 27-144 bpm (Renecker & Hudson 1989). This discrepancy could in part be explained by our short (four seconds-long) ECG recording interval from which heart rate was calculated; in contrast, Renecker & Hudson (1989) recorded heart rate for 10 min. Græsli et al. (2020a) manually validated heart rate up to 195 bpm from 4-second ECG in a study on physiological effects of hunting dog approaches on wild moose with implanted heart rate loggers. Our observed circadian rhythm of heart rate complements the findings by Thompson et al. (2020) of decreasing heart rates from early morning to late afternoon during the summer. Our findings of seasonal variation in heart rate are in agreement with reports of seasonal hypometabolism in moose (Renecker & Hudson 1986, Græsli et al. 2020b). For captive moose in Alberta, Canada, lowest metabolic rate was recorded between January and April (Renecker & Hudson 1986, 1989); in

contrast, we recorded the lowest heart rates normalized by body weight between October and November (for all moose except Roxanne). One possible explanation could be climatic differences between the study locations and years; however, we did not investigate the effect of ambient temperature on heart rate.

Other factors affecting moose heart rate

We observed high variation in heart rate and resulting energy expenditure at a given value of overall dynamic body acceleration after accounting for season and time of day, suggesting that additional factors affect moose energy expenditure. Our model identified individual as an important predictor of heart rate, and we observed individual variation in seasonal median heart rates normalized by body weight. These findings are in accord with other studies reporting on individual variation in heart rate (Careau et al. 2008, White & Kearney 2013, Wascher 2021). Causes for such individual variation could be individual level of stress, hormonal status, personality and costs of thermoregulation (Careau et al. 2008, White & Kearney 2013, Wascher 2021). Air temperature (Renecker & Hudson 1986, Thompson et al. 2020), and digestive activity (Renecker & Hudson 1986) affect heart rate in moose. Furthermore, internal state or excitability is an important determinant of heart rate in both moose (Franzmann et al. 1984, Renecker & Hudson 1989) and mule deer (*Odocoileus hemionus*) (Kautz et al. 1981). Luteal activity affects activity and temperature in moose (Høy-Petersen et al. 2023) and might also affect heart rate. In addition to heart rate, future studies could also investigate heart rate variability in moose, an important indicator of health and stress (Kitajima et al. 2021, Moraes et al. 2021, Wascher 2021). Behavior also affects the relationship between energy expenditure and overall dynamic body acceleration; inactive behaviors are associated with higher uncertainty of predicted energy expenditure (Green et al. 2009) and models that

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account for behavior-specific slopes of the relationship between energy expenditure and overall dynamic body acceleration may provide a better fit than models without (Green et al. 2009, Hicks et al. 2017). Furthermore, the effect of overall dynamic body acceleration on heart rate during locomotion depends on gait and terrain slope (Halsey et al. 2008, Halsey 2016, Dickinson et al. 2021).

Seasonal variation in ODBA

We observed seasonal variation in behavior-specific overall dynamic body acceleration, which could result from a variety of factors. Collar fit might change with seasonal changes in body mass and fur (Herberg 2017, Dickinson et al. 2020, Wilson et al. 2021). Furthermore, seasonal variation in the accelerometer signature of locomotor behaviors may stem from seasonal changes in ground cover (i.e., snow) (Gleiss et al. 2011).

Low predicted energy expenditure at high values of overall dynamic body acceleration

We used a generalized additive mixed model to improve model fit over a wide range of values of overall dynamic body acceleration and a variety of behaviors. However, our sample sizes varied dramatically among behaviors. At the highest values of overall dynamic body acceleration, the behavior we were interested in was running, and this was the behavior with the lowest overall sample size. Its range of values of overall dynamic body acceleration overlapped with that of other behaviors which had higher sample sizes and were associated with lower heart rates – body and head shaking, scratching (during which the moose might have kicked the collar repeatedly while scratching behind their ears with their hoofs) (Appendix: Table 5). It is likely that these behaviors affected the model predictions of heart rate at high values of overall dynamic body acceleration, resulting in an underestimation of heart rate during running behavior. These data points with high values of

overall dynamic body acceleration and low heart rate likely contributed to the stagnation of the relationship between overall dynamic body acceleration and heart rate at overall dynamic body acceleration values around 0.2 g, which did not reflect the trend of increasing heart rate with increasing overall dynamic body acceleration apparent upon visual inspection of the data.

Additional sources of uncertainty

Due to a programming error, our heart rate loggers calculated heart rate from four-second-long ECGs even in fall and spring when we expected moose heart rates to reach their annual minima. Because quality class of the heart rate measurements is, among other things, dependent on the number of QRS complexes detected within an ECG measurement (Star Oddi 2022), we recorded a high number of low-quality measurements, reducing our effective sample size. It is possible that our lowest validated heart rate of 17 bpm does not represent the lowest heart rates occurring in moose in fall and spring.

Our model of moose heart rate showed significant autocorrelation in the residuals. However, other models of ungulate heart rate suggested that residual autocorrelation did not affect model parameter estimates (Leimgruber et al. 2023). Using a different model such as generalized additive models for location, scale and shape (Rigby & Stasinopoulos 2005, Bann et al. 2022, Leimgruber et al. 2023), random forest regression or neural network analysis (Oyeleye et al. 2022) may improve the fit of our model at high values of overall dynamic body acceleration.

Applying the heart rate-energy expenditure equation from Renecker & Hudson (1985) to individuals not assessed during calibration of the equation increases the uncertainty of the resulting estimates of energy expenditure (Green 2011). Quantifying and incorporating the associated error is an important next step to improve estimates of energy expenditure predicted from accelerometer data.

Conclusions

We present a model that enables the prediction of moose heart rate from collar-mounted tri-axial accelerometers and illustrate the calculation of energy expenditure from these predictions. Our analysis facilitates the use of overall dynamic body acceleration in bioenergetic models to improve estimations of moose energy expenditure, and to enable such estimations without the use of implanted heart rate loggers.

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Appendix

Table 3: Overall dynamic body acceleration [g] recorded from collar-mounted accelerometers, heart rate [bpm] recorded from implanted loggers, energy expenditure [$\text{kJ} \cdot \text{kg}^{-1} \cdot \text{h}^{-0.75}$] calculated from heart rate using the equation by (Renecker & Hudson 1985) and sample size (n) for seven observed behaviors in seven captive moose. Values are given as median \pm standard deviation.

Behavior	Metric	Fall	Spring	Late summer
Lying	ODBA	0.007 \pm 0.01	0.010 \pm 0.03	0.019 \pm 0.06
	HR	30 \pm 6.35	35 \pm 7.33	53 \pm 6.15
	EE	12.52 \pm 4.79	14.50 \pm 4.25	26.48 \pm 7.40
	n	932	4550	4002
Ruminating	ODBA	0.028 \pm 0.02	0.024 \pm 0.02	0.040 \pm 0.02
	HR	33 \pm 4.44	34 \pm 7.83	55 \pm 6.20
	EE	13.99 \pm 2.19	14.37 \pm 4.49	28.18 \pm 7.12
	n	819	1197	3426
Alert	ODBA	0.010 \pm 0.06	0.025 \pm 0.08	0.024 \pm 0.04
	HR	35.5 \pm 1.71	46.5 \pm 6.62	60 \pm 9.81
	EE	15.10 \pm 0.87	19.79 \pm 4.67	31.46 \pm 14.14
	n	4	18	42
Standing	ODBA	0.049 \pm 0.21	0.038 \pm 0.08	0.054 \pm 0.14
	HR	36 \pm 12.48	42 \pm 11.58	62 \pm 12.97
	EE	15.16 \pm 15.46	17.70 \pm 25.29	33.78 \pm 31.51
	n	260	1436	854
Foraging	ODBA	0.129 \pm 0.08	0.118 \pm 0.05	0.177 \pm 0.07
	HR	40 \pm 8.01	49 \pm 10.62	66 \pm 10.05
	EE	17.61 \pm 10.03	22.06 \pm 16.65	39.89 \pm 19.53
	n	1014	682	2093
Walking	ODBA	0.180 \pm 0.10	0.217 \pm 0.13	0.235 \pm 0.19
	HR	39 \pm 11.57	47 \pm 11.98	68.5 \pm 14.18
	EE	16.68 \pm 10.90	20.10 \pm 13.02	43.12 \pm 33.43
	n	132	253	436
Running	ODBA	0.794 \pm 0.72	0.994 \pm NA	1.294 \pm 0.38
	HR	79.5 \pm 23.25	59 \pm NA	72 \pm 12.73
	EE	69.72 \pm 46.24	28.09 \pm NA	44.97 \pm 17.28
	n	4	1	2

Paper II: Energy expenditure model

Table 4: Age, weight [kg], heart rate [bpm] (median \pm SD) and heart rate normalized by weight (Norm. HR) [bpm/kg^{0.25}] (median \pm SD) for seven captive moose with implanted heart rate loggers. One additional logger was implanted in another moose but could not be recovered. Summer data combines data from both early and late summer where available (for Sky, only data from late summer was available). Spring weight was calculated as mean of weights in spring 2021 and 2022, summer weight was calculated as mean of spring and fall weights.

Individual	Age in 2021 [yr]	Metric	Season		
			Fall	Spring	Summer
Roxanne	12	Weight	501	447	465
		HR	31 \pm 7	29 \pm 7	52 \pm 14
		Norm. HR	147 \pm 32	133 \pm 33	241 \pm 64
Minnie	13	Weight	464	403	423
		HR	36 \pm 6	37 \pm 7	59 \pm 10
		Norm. HR	167 \pm 28	166 \pm 32	268 \pm 45
Stella	12	Weight	533	497	509
		HR	36 \pm 8	46 \pm 9	54 \pm 10
		Norm. HR	173 \pm 37	217 \pm 43	256 \pm 47
Sky	9	Weight	486	NA	452
		HR	34 \pm 7	NA	58 \pm 10
		Norm. HR	160 \pm 32	NA	267 \pm 46
Babe	2	Weight	408	339	362
		HR	29 \pm 7	39 \pm 9	59 \pm 10
		Norm. HR	130 \pm 32	167 \pm 41	257 \pm 43
Wilma	9	Weight	529	485	500
		HR	29 \pm 11	34 \pm 9	50 \pm 9
		Norm. HR	139 \pm 52	160 \pm 40	236 \pm 43
Shiner	9	Weight	560	491	514
		HR	30 \pm 7	34 \pm 7	53 \pm 8
		Norm. HR	146 \pm 35	160 \pm 32	252 \pm 36

Table 5: Comparison of overall dynamic body acceleration and heart rate during different behaviors with high values of overall dynamic body acceleration recorded in spring, summer and fall in seven captive female moose using collar-mounted tri-axial accelerometers and implanted heart rate loggers.

Behavior	ODBA [g]			HR [bpm]	Sample size
	Min	Median	Max	Median	
Head shaking	0.01	0.19	1.20	58	18
Body shaking	0.16	0.20	2.16	63.5	6
Scratching	0.06	0.40	3.29	59.5	12
Running	0.25	1.02	1.84	74	7

Paper II: Energy expenditure model

Predicting energy expenditure from heart rate data

To compare our behavioral data with those from Renecker & Hudson (1989), we calculated the energy expenditure in Renecker & Hudson (1989) recorded during ruminating as mean of the energy expenditure during ruminating while standing and while bedded, if both behaviors were recorded. If only one ruminating behavior was recorded by Renecker & Hudson (1989), we

used that value as energy expenditure during ruminating. We calculated energy expenditure recorded by Renecker & Hudson (1989) during foraging as mean of the energy expenditure during browsing low, medium and high. We compared our energy expenditure during standing and lying to the behaviors “standing alert” and “lying alert” in Renecker & Hudson (1989), and investigated the energy expenditure during the behavior alert separately.

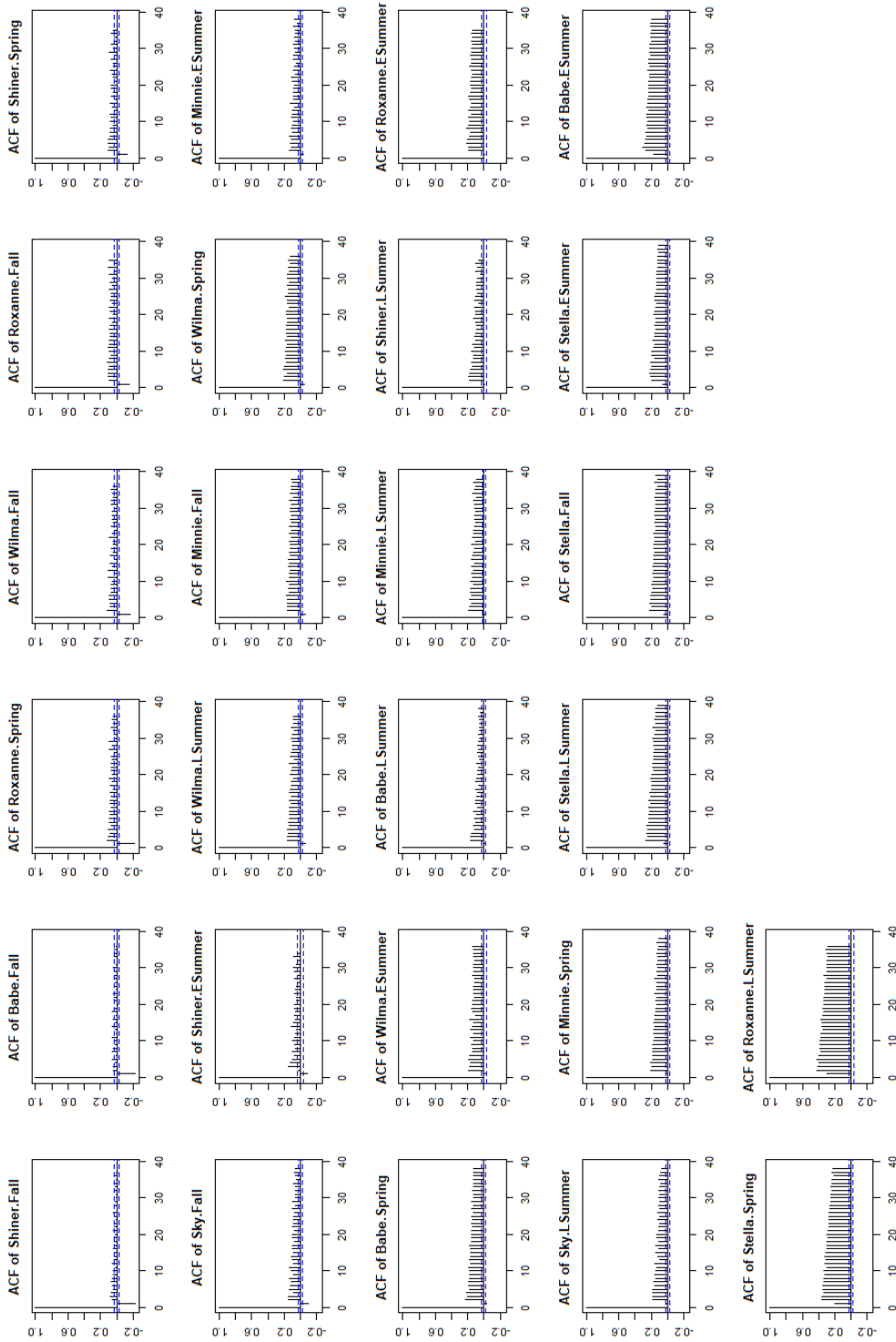
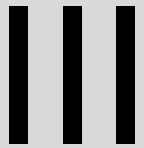


Figure 6: Residual autocorrelation in the generalized additive mixed model of moose heart rate.



Do you mind? Behavioral responses of moose to experimental disturbance and implications for energy expenditure

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Abstract

Disturbances from human activities can impact wildlife and elicit changes in behavior, movement, and physiology. Disturbance effects on individuals can result in population-level impacts if resulting changes in behavior and physiology cause negative energy balance or reduced recruitment. Therefore, knowledge of wildlife responses to disturbances is important for species and ecosystem management and conservation. A keystone species of boreal forests, moose are exposed to a variety of disturbances from human activities including forestry practices, hunting and recreational activities. Here we conducted a behavioral response study on wild moose bearing GPS-accelerometer collars to quantify the effect of simulated recreational activities (hiking and snowshoeing) on moose behavior and energy expenditure. We systematically approached nine collared moose in Innlandet county, Norway, and Värmland county, Sweden, during summer and hunting season in 2021 and during winter 2021/2022, in mornings and afternoons. Using an existing machine learning model, we predicted one of seven common moose behaviors for each three-second accelerometer data interval during the approaches. Using an existing model together with a published equation, we predicted heart rate and corresponding energy expenditure during the approaches from the accelerometer data. To investigate detailed temporal variation in the disturbance response, we calculated the change in behavior and energy expenditure during different time intervals during the approach relative to control periods on the day preceding the approach. In 48 trials we approached the moose to a distance between 17-266 m (we defined the minimum distance to the moose during an approach as contact distance). Locomotor activity was increased particularly during the first ten minutes following contact, coinciding with increased energy expenditure and decreased foraging and ruminating behavior. Foraging activity recovered to levels comparable to the controls ca. 2 hours following the approach. We observed seasonal variation in the disturbance response; moose responded to close approaches with a stronger flight response in summer and winter compared to fall. In winter, locomotor activity increased earlier and lasted longer, and contact distances were longer. We suggest that the prominence of hunting activity with baying dogs in the study area may be responsible for the muted flight response to close approaches during the hunting season, and that increased range of detection during winter approaches may have resulted in longer contact distances. We demonstrate negative effects of disturbances from simulated recreational activities on the energy budget of moose (increase in energy expenditure and decrease in foraging activity) on an unprecedented level of detail. Our results can inform bioenergetic models to improve our understanding of disturbance effects on individual moose with implications for the wider population.

Introduction

Increasing encroachment of humans on wildlife is a growing concern for species management and conservation (Stankowich 2008, Ciuti et al. 2012). Human activity can be perceived by animals as predation risk (Frid & Dill 2002), contributing to the landscape of fear – spatio-temporal variation in perceived predation risk – which wild animals navigate (Brown et al. 1999, Laundre et al. 2010, Gaynor et al. 2019). This effect of human activity on wildlife was demonstrated by expanded movement ranges across a diverse range of taxa during large-scale restrictions of human activity resulting from lockdowns during the COVID-19 pandemic in 2020 (Bates et al. 2021, Tucker et al. 2023). Risk effects are costs incurred by animals responding to perceived predation risk (Creel & Christianson 2008), for example by changing their behavior (Creel et al. 2009), habitat use (Heithaus et al. 2009) and energy expenditure (Papastamatiou et al. 2023). Risk effects acting on individuals can have implications for the size and structure of the wider population (Lima 1998, Frid & Dill 2002). For example, reduced energy intake through a reduction in foraging activity (Creel et al. 2009), reduced parental provisioning (Dudeck et al. 2018) or increased energy expenditure (through increase in vigilance or predator avoidance) (Ciuti et al. 2012) can result in reduced recruitment (Hik 1995, Creel et al. 2007, LaManna & Martin 2016, Gallagher et al. 2021, Allen et al. 2022), emphasizing the importance of considering risk effects in wildlife management (Perona et al. 2019, Mumme et al. 2023).

Traditionally, studies investigating the effects of disturbances on individuals often focused on changes in movement, for example temporary increase in movement following a disturbance (Græsli et al. 2020a) or displacement from home ranges (Faille et al. 2010). However, occurrence of spatial displacement might depend on

availability and connectivity to suitable alternative habitat, and thus, a lack of movement response to disturbance does not necessarily indicate a lack of response to disturbance (Gill et al. 2001, Frid & Dill 2002). Alternatively, disturbances can result in subtle changes to behavior and physiology that may not be detectable from location data alone (Andersen et al. 1996, Gill et al. 2001), such as interruption of foraging behavior (Goldbogen et al. 2013) and changes in heart rate (MacArthur et al. 1982, Moraes et al. 2021, Williams et al. 2022).

Moose (*Alces alces*) are a good example species for studying the effects of disturbance on wildlife. They are a keystone species in boreal forests (Molvar et al. 1993, Snaith & Beazley 2002). In Scandinavia, which hosts some of the highest moose densities worldwide (Timmermann & Rodgers 2005), population levels are heavily managed in attempts to strike a balance between minimizing browsing damage to commercial forest plantations and maximizing yield during the moose hunt (Storaas et al. 2001, Timmermann & Rodgers 2005). Annually, ca. 25% of the Scandinavian population is harvested (Ericsson & Wallin 1996, 2001, Solberg et al. 1999). Activities that can disturb moose, including hunting attempts of which usually half are unsuccessful (Heberlein 2000, Græsli et al. 2020a), timber harvest and silvicultural practices, wildlife viewing, berry and mushroom picking, hiking and skiing are of high socio-economic importance throughout much of the moose distributional range (Lavsund et al. 2003, Timmermann & Rodgers 2005, LeBlanc et al. 2011, Milner et al. 2013, Helseth et al. 2022). Globally, some moose populations have experienced declining recruitment and population health (Monteith et al. 2015, Timmermann & Rodgers 2017, Weiskopf et al. 2019), and recent research suggests that risk effects may compound other stressors including

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thermal stress and increased parasite loads (Spong et al. 2020, Fohringer et al. 2022).

Here, we use existing models (Kirchner et al. 2023) (Paper II) to analyze the fine-scale behavioral and energetic response of individual wild collared female moose in Norway to experimental disturbances simulating human recreational activities during three different seasons (summer, hunting season and winter). We analyzed continuously recorded high-frequency tri-axial accelerometer data in combination with GPS data to quantify changes in behavior and energy expenditure before and after the disturbance compared to a control day. We quantified the disturbance response in relation to distance to the disturbance source and investigated seasonal and diurnal variation. We expected that the disturbance would result in increased energy expenditure and decreased foraging activity, and that the disturbance response would be stronger during the hunting season compared to the other seasons.

Methods

Study area

We conducted our study in the Northern Finnskogen area on the border of Innlandet county (Norway) and Värmland county (Sweden) (Figure 1). This area is characterized by stands of Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*) interspersed with deciduous species (mainly birch (*Betula pubescens*) and aspen (*Populus tremula*)) and wetlands, and heavily influenced by commercial logging and forestry practices (Zimmermann et al. 2014, Wam et al. 2021). Moose in this area are highly managed with an annual harvest between September 25 and December 30 during which approximately 25% of the population are taken (Ericsson & Wallin 1996, 2001, Solberg et al. 1999, Zimmermann et al. 2015). Hunting occurs

mainly with baying dogs (Græsli et al. 2020a). Wolves (*Canis lupus*) and brown bears (*Ursus arctos*) are present and prey mainly on moose calves (Ausilio et al. 2023).

Collar deployment

We deployed Vertex Plus GPS-accelerometer collars (Vectronic Aerospace GmbH, Berlin, Germany) on nine wild female moose in Innlandet county in Norway between January and March 2021. The moose were immobilized with a CO₂-powered rifle (Dan-Inject, Børkop, Denmark) from a helicopter using a combination of 50 mg xylazine (Rompun Dry Substance, Bayer AG, Leverkusen, Germany) and 4.5 mg etorphine (Etorphine HCl 9.8 ml/ml, Vericode Veterinary products, Novartis Animal Health UK Ltd, Litlington, United Kingdom) and reversed with 50 mg naltrexone (Naltrexonhydroklorid vet. APL 50 gm/ml; Apotek Produktion och Laboratorier, Kungens Kurva, Sweden) (Evans et al. 2012, Lian et al. 2014, Græsli et al. 2020b). The collars were programmed to record one GPS position every hour and transmit packages of seven positions via the GSM network over the course of the deployment. They continuously recorded tri-axial accelerometer data at 32 Hz.

Experimental disturbances

Experimental disturbances were conducted by a human observer approaching the moose in summer (July 19-26) and fall (October 18-29) 2021, and in winter (January 18 - February 7) 2022. During an approach, the observer followed the approach route based on the last known position of the moose transmitted via the GSM network and recorded their GPS position every second using a handheld GPS unit (GPSMAP 64s, Garmin, Southampton, U.K.). The approach route started at the observer start position approximately 1 km away from the last known position, passed this position at a 50 m distance (the passing position) and continued another 500 m to the observer end position (Eriksen et al.

2022). The straight-line approach route was followed as closely as possible, at normal hiking speed, on foot or snowshoes. The observer took notes of moose sightings (if any) and the overall environmental conditions at the three fixed positions along approach route (observer start position, passing position, observer end position) but aimed to minimize the duration of stops. When leaving the area, the observer took care to minimize repeated disturbance of the moose by avoiding approaching moose positions which had been transmitted during the approach whenever possible. We re-programmed the GPS schedule of the collars for the approach day to transmit GPS positions every 10 min for 4 hours prior to the approach period, every 1 min during a two-hour approach period, and every 10 min for two hours afterwards. We re-programmed the collars with the same GPS schedule as the control day on the day prior to the approach, to act as control. Each moose was approached twice per season, once in the morning (10:00-12:00) and once in the afternoon (15:00-17:00).

Data preparation and analysis

We retrieved the collars (during re-captures in April 2022 or via remote drop command issued to the collar, which was then collected in the field) and downloaded the GPS and accelerometer data from the collars and processed them for analysis in R Studio (v.2023.6.1.524) (Posit team 2023) running R (v.4.3.1) (R Core Team 2023). To match the temporal resolution of the observer's GPS data, we fitted a continuous time movement model to the moose GPS data during the approach to predict the moose positions every second (crawl package v.2.3.0) (Johnson et al. 2008). We then calculated the distance between the moose and the observer every second, to identify the shortest distance during the approach, which we defined as contact distance (wildlifeDI package v.0.5.0, adehabitatLT package v.0.3.27) (Calenge 2006, Long et al. 2022). To assess the validity of

these estimated contact distances, we quantified their difference relative to contact distances calculated only from the 1-minute GPS locations. Using an existing behavioral classification model (Kirchner et al. 2023), we then classified the behavior of the focal moose from the accelerometer data at three-second intervals throughout the approaches. To apply the behavioral classification model, we visually inspected and, if necessary, adjusted the orientation of the accelerometer axes to match that required for model input. We then calculated predictor variables from the accelerometer data summarized in three-second intervals as input for a random forest model predicting one of seven behaviors (lying with the head down/tucked, lying with the head up, ruminating, standing, foraging, walking, or running) for each interval (Kirchner et al. 2023). To evaluate changes in moose heart rate relative to contact distance, we calculated overall dynamic body acceleration (ODBA) from four-second running means calculated over each accelerometer axis (Wilson et al. 2006) and applied an existing generalized additive mixed model to predict heart rate from the median values of ODBA for every four-second interval as described in Paper II. We calculated energy expenditure in every four-second interval from the corresponding heart rate prediction using Equations 1 and 2 (Renecker & Hudson 1985), assuming a weight of 300 kg for all moose in all seasons (Milner et al. 2013).

$$\text{Equation 1: } \textit{norm.HR} = \frac{HR}{M^{-0.25}}$$

$$\text{Equation 2: } \textit{Metabolic rate} = 4.655 \times e^{0.0071 \times \textit{norm.HR}}$$

We summed the energy expenditure calculated for each four-second heart rate prediction interval to calculate energy expenditure in different time bins before and after contact (before contact: 60-30 min, 30-10 min, 10-0 min, after contact: 0-10 min, 10-30 min, 30-60 min, 1-

2 hours, 2-3 hours, 3-6 hours, 6-12 hours, 12-24 hours). This allowed us to investigate fine-scale variation in energy expenditure at different times before, during and after contact. We calculated energy expenditure in the different time bins for the approach and control day, and calculated the difference in energy expenditure during each time bin between the approach and control (Neumann et al. 2010a). For these same time bins, we also summarized the behavioral predictions from the three-second behavioral prediction intervals to calculate the proportion of time engaged in each behavior relative to the control period, standardized by bin length.

Results

We conducted 50 approach trials on nine individual moose (Figure 1). In 48 trials, the observer approached the moose to a between 17 and 266 m. In two approaches, observer never came closer than 600 m to the moose; we did not consider these approaches successful and excluded them from further analysis. Across all seasons, the most conspicuous changes in behavior in the first 10 min after contact were a distinct increase in locomotor activity (walking and running), particularly in the mornings, and a decrease in foraging and ruminating (Figure 2). This trend abated during the first hour, concurrent with an increase in standing; foraging

activity remained depressed until ca. two hours after contact, particularly in the fall. In winter, locomotor activity increased 30 min prior to contact and remained elevated for at least one hour after contact, particularly in the mornings.

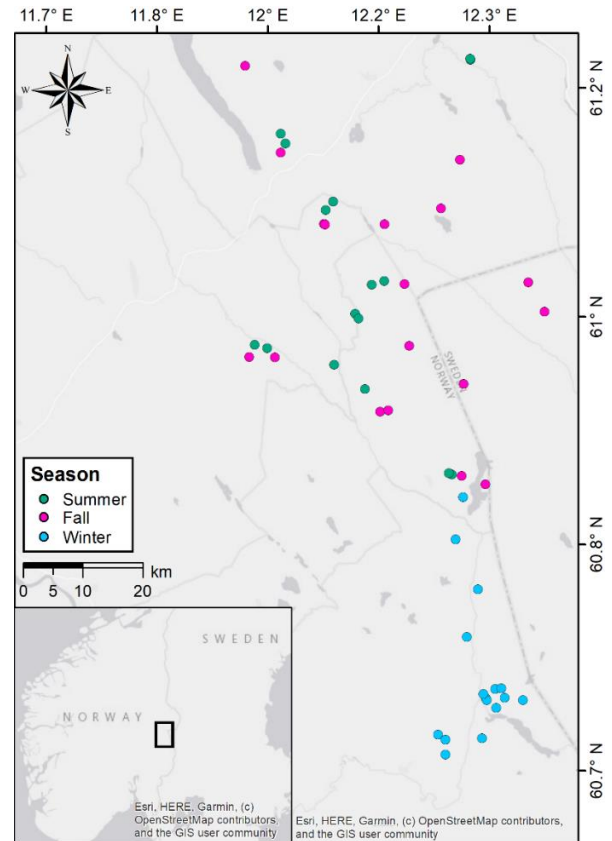


Figure 1: Location of the study area on the southern border of Norway and Sweden. Passing positions of 50 experimental approaches conducted on collared moose are color-coded by season.

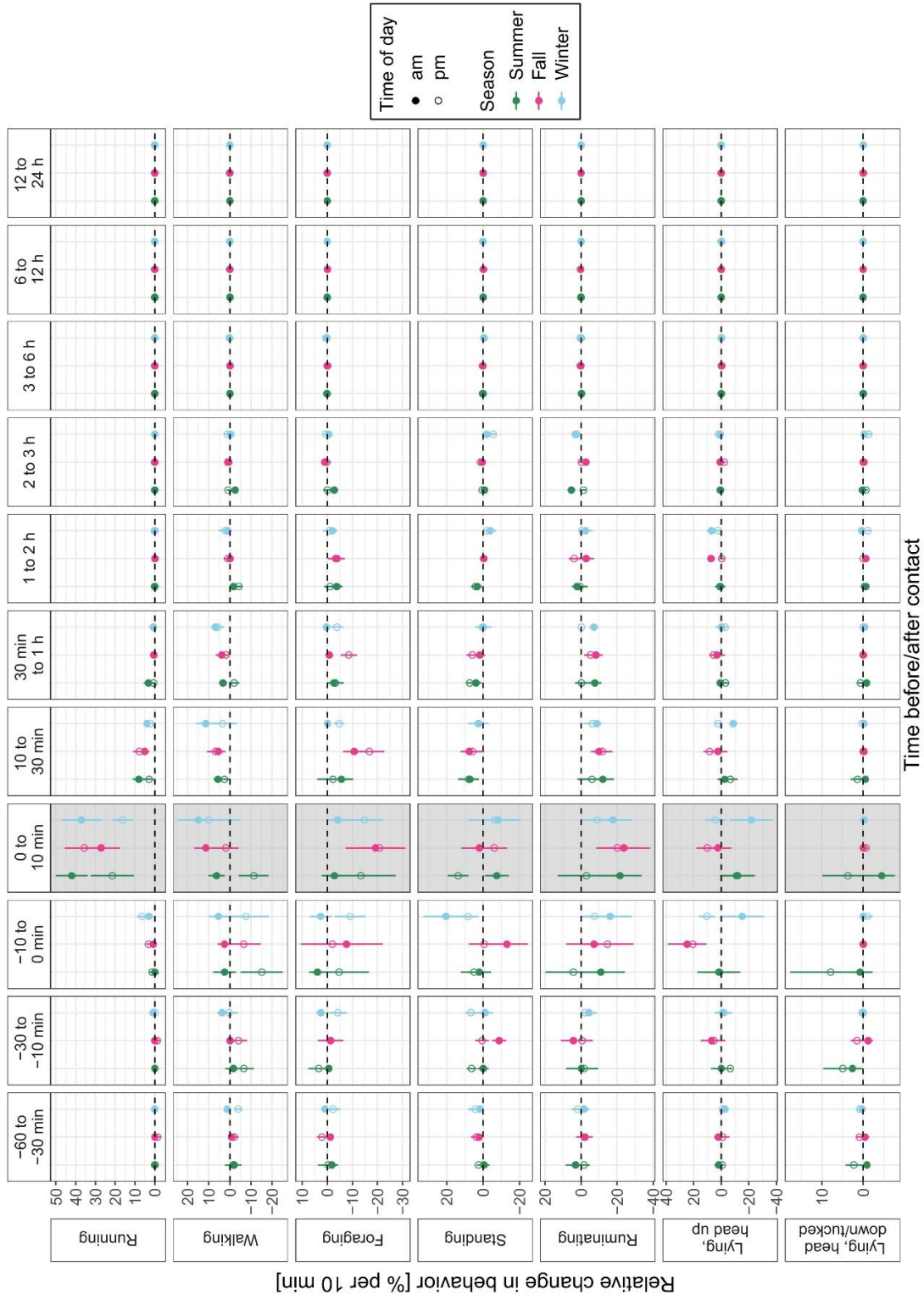


Figure 2: Mean and standard error of the proportion of each behavior predicted from accelerometer data for different time bins before and after contact to observer during experimental approaches on wild collared moose. Each time bin compares the data from the approach to the control period during the same time of day the day before. The data is split by season and time of day during the approach.

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This is corroborated by the longer contact distances in winter (mean \pm standard deviation: 163 ± 43 m) compared to the other seasons (summer: 101 ± 64 m, fall: 110 ± 47 m). We found large seasonal variation in the disturbance response that was at least partly related to contact distance (Figure 3): The closer the contact, the stronger the flight response in summer and to a lesser degree also in winter. In fall, we observed the opposite: The closer the contact, the lower the proportion of running

behavior. This is reflected in the large proportion of predictions of running for a summer approach with a contact distance of 52 m (Figure 4), and the large proportion of running, walking and standing for a summer approach with a contact distance of 113 m (Figure 5). In contrast, for a fall approach with a contact distance of 40 m, we predicted a low proportion of running behavior and much higher proportion of stationary behaviors (Figure 6).

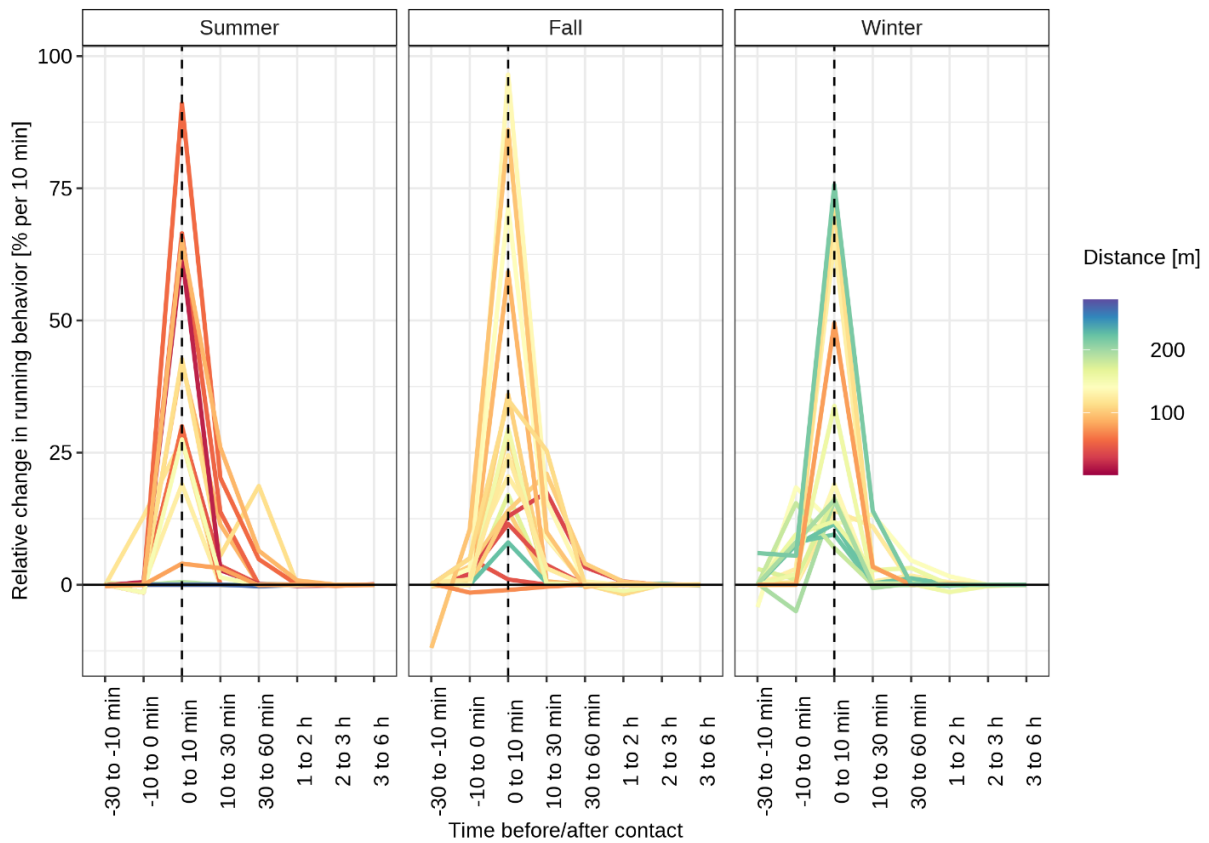


Figure 3: Proportion of running behavior predicted from accelerometer data on wild collared moose during different time bins before and after contact during experimental approaches relative to the control period on the same time of day the day before.

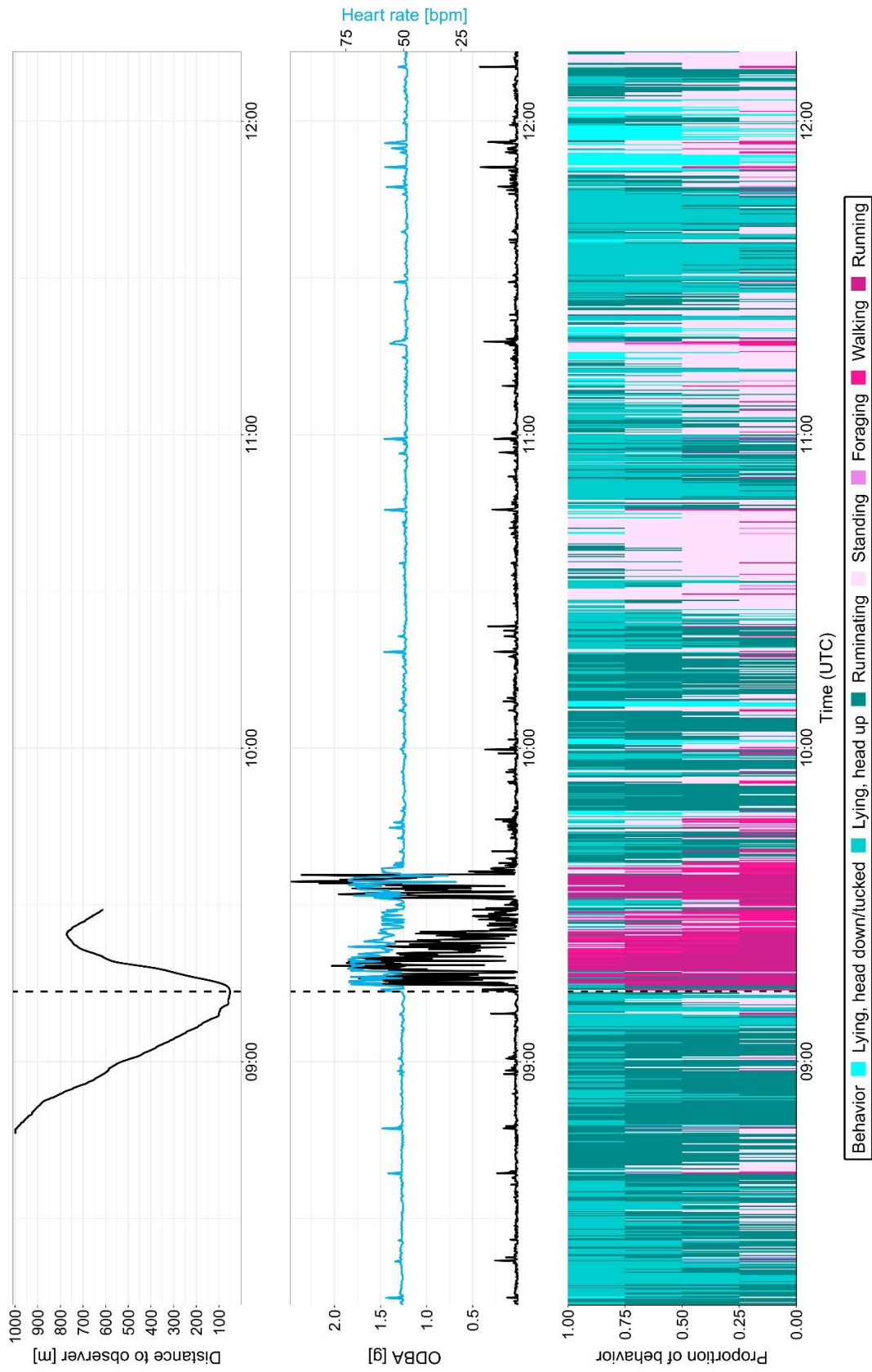


Figure 4: Moose-human contact distance during an experimental approach trial (top), overall dynamic body acceleration (ODBA) calculated from accelerometer data and heart rate predicted from ODBA (middle) and behavior predicted from accelerometer data (bottom) for one summer morning approach with a contact distance of 52 m. Vertical dashed line indicates time of minimum contact distance. Plot of contact distance ends when the observer reached the observer end position of the approach route.

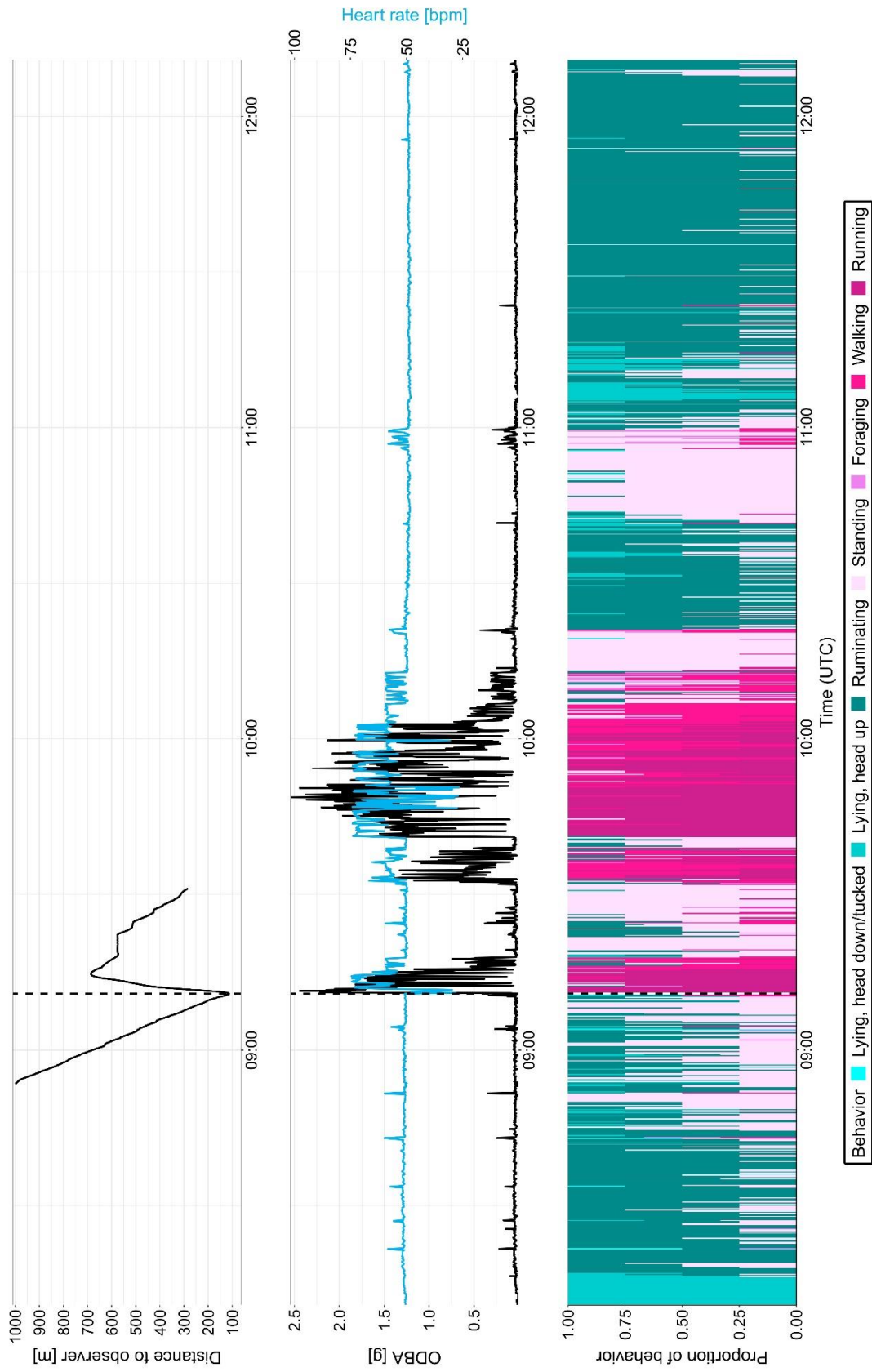


Figure 5: Moose-human contact distance during an experimental approach trial (top), overall dynamic body acceleration (ODBA) calculated from accelerometer data and heart rate predicted from ODBA (middle) and behavior predicted from accelerometer data (bottom) for one summer morning approach with a contact distance of 113 m. Vertical dashed line indicates time of minimum contact distance.

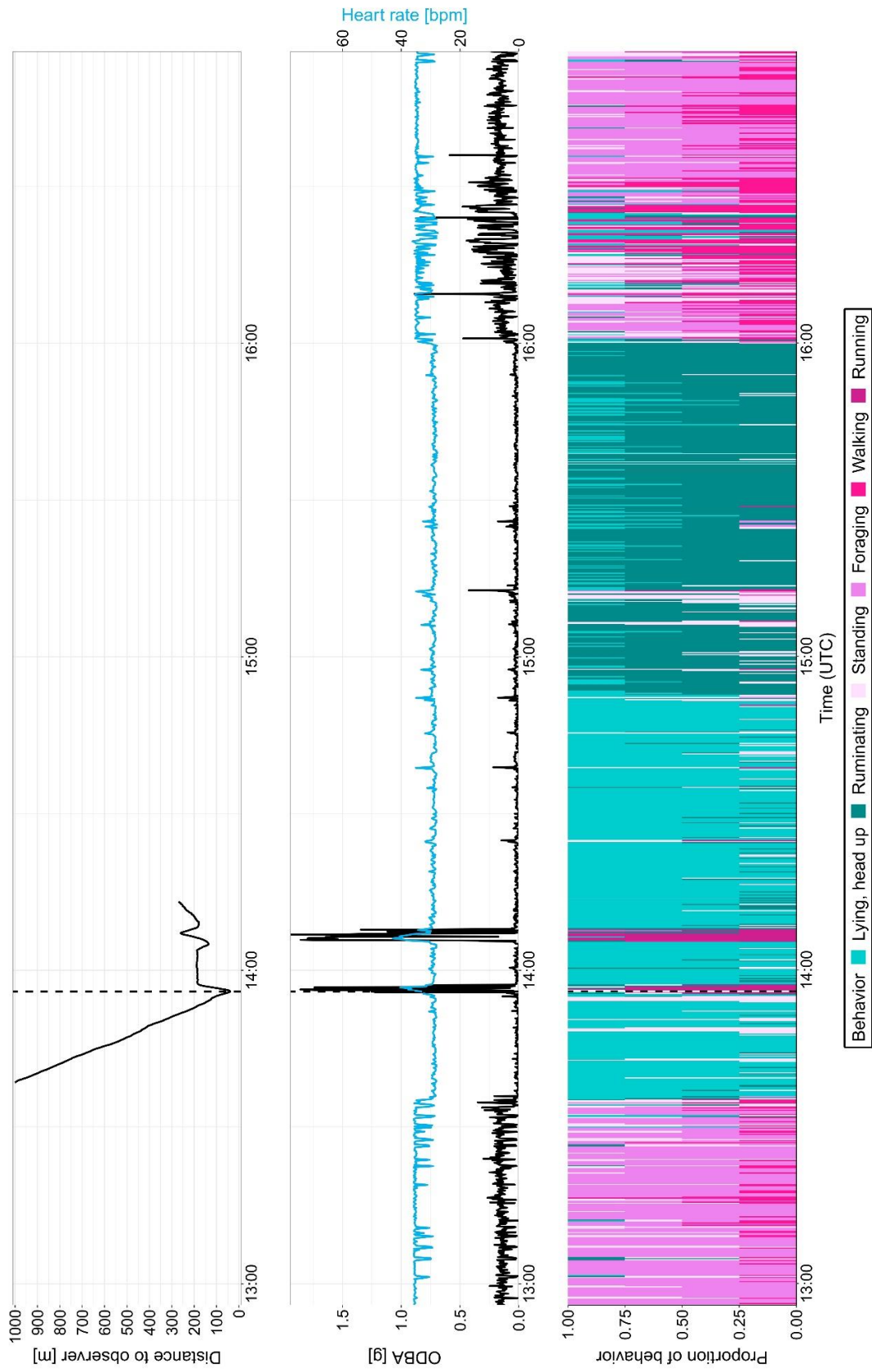


Figure 6: Moose-human contact distance during an experimental approach trial (top), overall dynamic body acceleration (ODBA) calculated from accelerometer data and heart rate predicted from ODBA (middle) and behavior predicted from accelerometer data (bottom) for one fall afternoon approach with a contact distance of 40 m. Vertical dashed line indicates time of minimum contact distance. Plot of contact distance ends when the observer reached the observer end position of the approach route.

The contact distances calculated from the moose GPS positions were 15 ± 23 m (mean \pm standard deviation) greater than those of the movement model (range of differences: 0-98 m). The greatest difference was determined for the approach with the shortest contact distance (17 m) where no GPS data was recorded for 10 min

during the contact phase of the approach. Overall, we recorded the highest increase in energy expenditure relative to the control during the first 10 min after contact during summer mornings, with an average increase of 25 % (from 5.2 to 6.5 $\text{kJkg}^{-1}\text{h}^{-1}$) (Figure 7).

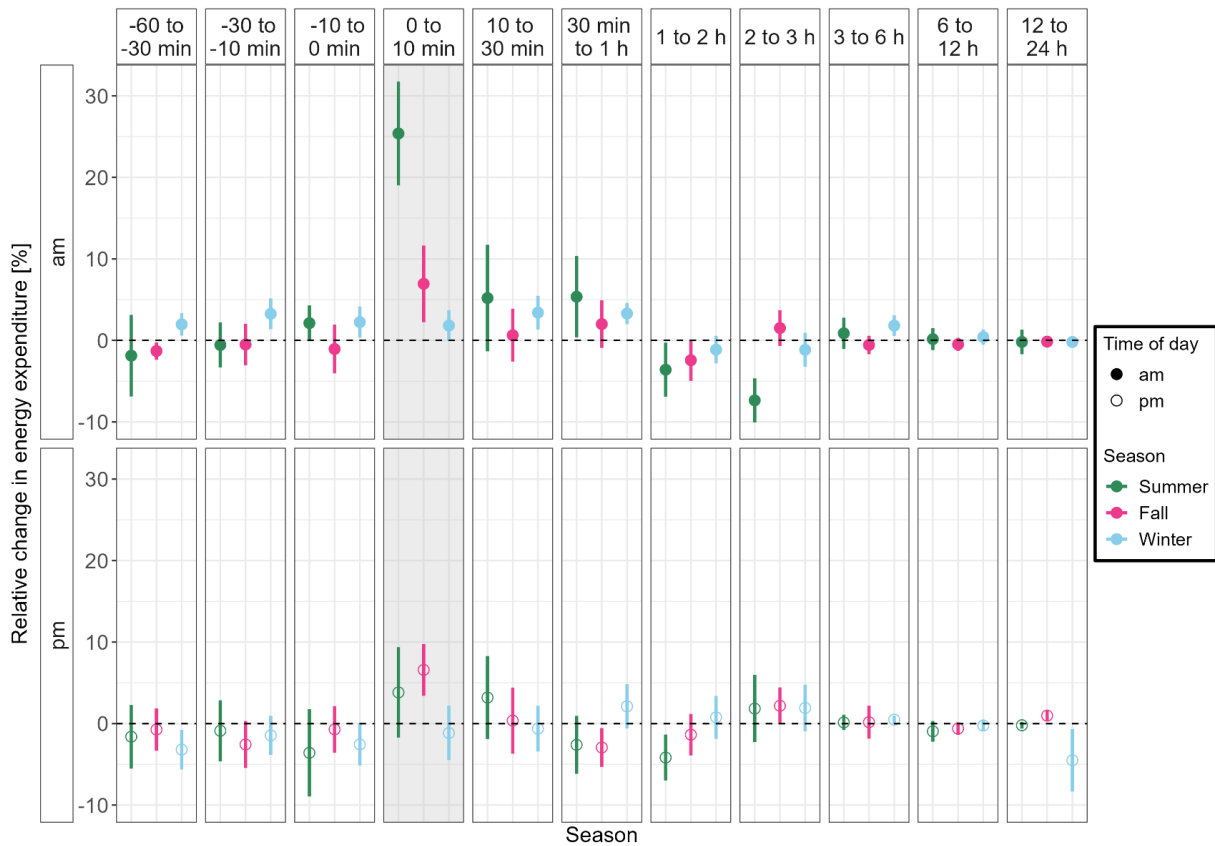


Figure 7: Change in energy expenditure calculated from overall dynamic body acceleration recorded during experimental disturbances on collared wild moose in Norway relative to the control period during the same time of day the day before. Time indicates time to/since minimum distance to the observer.

Energy expenditure relative to control days was generally highest during the first 0-30 min after contact, and higher and more persistent in mornings than afternoons, likely due to the increased locomotor activity. This circadian difference was most pronounced in the summer and least in the fall. In winter mornings, energy

expenditure relative to control days was higher from the hour before to the first hour after contact. The opposite occurred in winter afternoons, where energy expenditure was not elevated until 30 min to three hours after contact. This is likely explained by increased locomotor activity during winter morning

approaches before and just after contact, while in winter afternoons locomotor activity was less prominent but more persistent (Figure 2).

We compared our estimates of changes in energy expenditure during the first ten minutes and the first hour after contact (relative to the controls) to published values of moose energy expenditure during hiking, skiing and snowmobile approaches (Neumann et al. 2010 a, b). These published values were calculated from rates of movement between successive GPS positions using a general equation calculating energy expenditure during

terrestrial locomotion as a function of body mass and speed of movement (Taylor & Heglund 1982, Neumann et al. 2010 a, b) (Table 1). Relative increase in energy expenditure during the first hour after the approaches (relative to the controls) was much higher in these studies. However, the relative increase in energy expenditure we calculated for the first ten minutes after contact for summer approaches was comparable to the published values of energy expenditure for the first hour after summer hiking approaches (Neumann et al. 2010b).

Table 1: Energy expenditure calculated from predictions of heart rate from accelerometer data during first 10 min and first 60 min after contact for 48 approaches on wild collared moose (highlighted in grey) compared to results from other studies estimating energy expenditure from movement rates (Neumann et al. 2010b* a^). Moose silhouette from Colourbox.

Approach method	Season	Energy expenditure (mean ± SD) [kJkg ⁻¹ h ⁻¹]					
		0-10 min since contact			0-60 min since contact		
		Approach	Control	Relative increase [%]	Approach	Control	Relative increase [%]
Hike	Summer	6.0 ± 0.8	5.3 ± 0.5	14.6 ± 19.7	5.4 ± 0.6	5.2 ± 0.4	4.5 ± 13.0
Hike	Fall	3.1 ± 0.2	2.9 ± 0.2	6.8 ± 11.7	2.9 ± 0.2	2.9 ± 0.2	1.0 ± 8.2
Snowshoe	Winter	3.3 ± 0.1	3.3 ± 0.2	0.3 ± 7.5	3.4 ± 0.1	3.3 ± 0.2	1.8 ± 5.3
Hike*	Summer				4.3 ± 0.2	3.7 ± 0.1	16
Ski^	Winter				5.4 ± 0.5	3.6 ± 0.1	48
Snowmobile*	Winter				4.4 ± 0.1	3.7 ± 0.1	19



Discussion

Using a published model to predict behaviors from collar-borne accelerometer data (Kirchner et al. 2023), we detected behavioral responses in wild moose to experimental disturbances. Specifically, as expected, we observed an increase in locomotor activity and a decrease in foraging and ruminating. Our findings illustrate that moose perceived the approaching observer as a disturbance, and that the resulting response was energetically costly due to both an increase

in energy expenditure and a decrease in energy gain.

Among approaches, we found large variation in contact distances as well as changes in behavior and the rate of energy expenditure in response to contact. Such high variation is common in wildlife disturbance response studies and may be mediated by a combination of many factors that can be hard to tease apart, including perceived level of threat or type of perceived stimulus, seasonal variation in body condition and reproductive status, time of day, habitat, proximity to cover, behavior at time of

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disturbance, prior experience with disturbance and overall individual personality (Altmann 1958, MacArthur et al. 1982, Andersen et al. 1996, Goldbogen et al. 2013, Sih 2013).

Seasonal variation in disturbance response

We found strong seasonal variation in contact distance and behavior during the first 10 min after contact. In winter, contact distances were longer – likely because the onset of locomotor activity occurred earlier before contact, and moose ran less after contact. One explanation is that the snowshoeing observer was audible over longer distances, facilitating an earlier and therefore less intense disturbance response.

The range of contact distances in summer was comparable to that in fall; however, the behavioral responses to contact at the upper and lower end of this range were reversed between the seasons: At close contact distances, moose ran more in the summer and less in the fall. This is in contrast to our expectation of stronger disturbance responses in the fall. One explanation for intense response to close distances in summer is that approaches with a short range of detection (facilitated by for example, ground cover that muffled sound, no wind or the observer approaching from downwind of the moose) resulted in close approaches that startled the moose into running. Alternatively, close contact distances in summer may have resulted from heat-stressed moose avoiding increased activity levels from a response to the encroaching observer until they felt increasingly threatened and started to run. This notion is supported by a higher proportion of locomotor activity following contact in summer mornings compared to afternoons when temperature is usually higher and overall moose activity lower (Thompson et al. 2021). Alternatively, the moose may have avoided a flight response due to the presence of a young calf. Increasingly close contact may have allowed the cow to identify the species of intruder and

rule out fast-running natural predators targeting the calf, which eventually enabled flight together with the calf.

In fall, the moose ran when they detected an encroaching threat that was still far away, potentially because immediate flight increases their chance of escape from hunting activity with baying dogs (Sand et al. 2006, Græsli et al. 2020a). In contrast, when they did not detect the observer until the observer was near, their response was not to flee but to stay put, by either hiding so as to not reveal their location (Ericsson & Wallin 1996), or preparing to stand and fight (Ericsson et al. 2015). An alternative explanation for less running at close contact distances in the fall is that a human intruder (not accompanied by a dog) during the hunting season may have been perceived as less threatening compared to a dog or an intruder with a dog. In the hunting season, undisturbed habitat is likely rare (Ericsson & Wallin 1996), and initiating flight in response to a perceived low-level threat could potentially displace the moose into a higher-risk area with an active hunt (Baskin et al. 2004). Accordingly, an important consideration in the study of wildlife disturbance response is that wildlife may not leave an area of disturbance if no suitable alternative habitat is available (Gill et al. 2001, Frid & Dill 2002, Ericsson et al. 2015). Repeating approaches with a leashed dog accompanying the observer may reveal whether the mere presence of a dog induces flight in moose independent of contact distance and whether there are seasonal differences, ultimately elucidating the ability of moose to distinguish approaching intruders and adjust their behavioral response according to species of intruder and seasonal context. Longer depression of foraging and browsing activity following contact in fall may suggest increased (auditory) vigilance of moose that did not flee when approached (Lynch et al. 2013) but instead carefully monitored and continuously assessed the disturbance situation; however some authors

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suggested that (visual) vigilance is possible while ruminating (Fortin et al. 2004).

Comparison to other studies

Neumann et al. (2010b) calculated increased movement by female moose for 1-2 hours following hiking disturbance in the summer and snowmobile approaches in the winter; this is a longer flight duration than that estimated from our summer approaches based on the behavioral predictions. This discrepancy may stem from the comparatively coarse resolution of GPS positions (ca. two per hour) used for the calculation of displacement, which could lead to an overestimation of flight duration. From these movement rates, Neumann et al. (2010b) calculated a 16% (hiking) and 19% (snowmobile) increase in the rate of energy expenditure during the first hour after flight initiation compared to the control, using a general equation quantifying energetic costs of terrestrial locomotion depending on body mass and movement speed (Taylor & Heglund 1982). These estimates are much higher than our estimated rates of energy expenditure in the first hour after contact (5% increase in energy expenditure in summer and 2% in winter) (Table 1). Calculating the rate of energy expenditure from movement rates rather than movement speed assumes constant speed and straight-line movement between GPS positions. However, the speed of the moose likely varies over the course of their flight, and their flight path can be tortuous (Ericsson et al. 2015, Græsli et al. 2020a). Our fine-scale analysis of energy expenditure revealed variation in the rate of energy expenditure within the first hour of the flight, with higher initial rates suggesting higher movement speed in the first 10 min after contact. During this time, our calculated increase in the energy expenditure in the summer (15%) matches that calculated by Neumann et al. (2010b) for the first hour following an approach. However, it is possible that energy expenditure particularly during the intense locomotor activity

in the first 10 min after contact was even higher than what we calculated here. We suspect that our model predicting heart rate from ODBA introduced a systematic underestimation of heart rate and therefore energy expenditure at exactly the high range of ODBA values associated with fast locomotor activity (Paper II).

Despite these uncertainties around our estimates, the average rate of energy expenditure of our winter controls is only 0.3 kJkg⁻¹h⁻¹ less than that of the controls estimated by Neumann et al. (2010a). Different moose weights used in the calculations may have contributed to these differences (Neumann et al. (2010a) used an estimated weight of 390 kg). Calculating energy expenditure using the general equation for terrestrial locomotion does not consider seasonal variation in metabolism. Hence, this equation may be more useful for quantifying the variation in the rate of energy expenditure among treatments, than for quantifying the absolute energy expenditure in a given time or resulting from a given treatment. In contrast, our estimates of the rates of energy expenditure during the controls vary among seasons as expected for moose with seasonal hypometabolism (Renecker & Hudson 1989, Græsli et al. 2020b).

We distinguished contact distance from the flight initiation distance (FID) quantified in other studies (Græsli et al. 2020a, Versluijs et al. 2022) to avoid both the implication that every approach elicited a flight response, and the assumption that the time of contact coincided with the onset of flight. An increase in distance to the observer moving along the approach route could stem from either flight of the moose or solely from the movement of the observer, and flight could be initiated before or after the time of minimum distance to the moving observer. However, we considered these metrics comparable as they quantify the closest proximity of the observer

permitted by the approached animal. Our average contact distance in the winter was only 3 m greater than the average flight initiation distance of female moose approached by an off-trail backcountry-skiing observer (Neumann et al. 2010a), validating the accuracy of our estimates and suggesting an ecological relevance of these contact distances.

In the study by Neumann et al. (2010a), the skiing approaches and subsequent tracking of the focal moose elicited a flight response resulting in increased spatial displacement during the first three hours after contact, from which a 48 % increase in the rate of energy expenditure in the first hour was calculated. This much higher response compared to the approaches on snowmobiles (Neumann et al. 2010b) and our snowshoeing approaches likely resulted from the tracking that was conducted after the initial skiing approach (Neumann et al. 2010a). Movement directionality is an important predictor of ungulate flight response, and the persistent tracking may have more closely resembled a predatory pursuit than our comparatively transient disturbance (Stankowich 2008, Neumann et al. 2010a, Harris et al. 2014). Similarly, tracking duration is an important determinant in behavioral response of moose to pursuit by baying dogs (Ericsson et al. 2015, Græsli et al. 2020a). Accordingly, our observations suggest that, within the same approach route, an accidental repeated approach of the focal moose after initial contact seemed to trigger another strong running response even when it may have occurred at greater distances (Figure 5), although we did not collect observer positions sufficiently long after the end of the approach route to quantify contact distances after the observer reached the observer end position.

Sources of uncertainty

Our behavioral classification model was not trained to predict vigilance behavior. We expect that at least some moose were alert during parts of the approaches, and that the behavior during these times was classified as inactive behavior with a posture that resembled that assumed by vigilant moose - standing or lying with the head held high. As shown during model testing, these two behaviors were also occasionally confused for each other (Kirchner et al. 2023). Behavioral classification models based on accelerometer data may confuse behaviors with similar accelerometer signatures, particularly when they involve little body movement (Graf et al. 2015, Fehlmann et al. 2017).

Our quantification of energy expenditure from body acceleration is limited to changes in energy expenditure resulting from changes in physical activity. In addition to physical activity, metabolic factors such as temperature (Thompson et al. 2020) and non-metabolic factors such as excitability (e.g., alertness, stress) (MacArthur et al. 1982, Franzmann et al. 1984, Brouwer et al. 2018) affect heart rate and energy expenditure. Because our information about energy expenditure was limited to body acceleration, we may have underestimated total energy expenditure during the approaches.

By quantifying the disturbance effect as change relative to the behavior and energy expenditure the day before the approach, we are assuming that the moose were not disturbed during the control periods. By linking the approach to energy expenditure over the course of 24 hours after the approach, we are also assuming that the moose experienced no further disturbance during this time. However, these assumptions might be naïve, since recreational activities are likely common in the study area, particularly during the hunting season in the fall. In fact, we observed berry pickers during one of our

approaches, heard dogs barking during several approaches, and noticed cues of recent hunting activity (gunshots, footprints imprinted in the bog and flags marking the hunting area) prior to or during two other approaches. Furthermore, several approaches were conducted in the vicinity of cabins, houses and active logging operations, where moose are likely to encounter human activity. Especially in the winter, several moose were within close proximity of each other, and the approach on one day might have affected the control for a moose on another day.

In addition to improving the accelerometer-based model of energy expenditure, future studies could compare this method to other methods quantifying energy expenditure. For example, a time budget derived from accelerometer- or GPS- based behavioral predictions (Ditmer et al. 2018, Kirchner et al. 2023) could be combined with behavior-specific estimates of energy expenditure (Jeanniard-du-Dot et al. 2017). This would also enable an assessment of the effect of anaerobic exercise during intense flight on the heart-rate based estimation of energy expenditure, which assumes a physiological steady state and therefore no anaerobic metabolism (Green 2011). Neumann et al. (2010a) based their calculations of energy expenditure during moose approaches and tracking on a general equation quantifying the energetic costs of terrestrial locomotion depending on body mass and movement speed (Taylor & Heglund 1982). Applying this method to a path reconstructed from ca. 30 min GPS positions as in Neumann et al. (2010a) assumes a constant speed during each 30 min path segment and does not consider path tortuosity, which may characterize the flight path of moose (Ericsson et al. 2015, Græsli et al. 2020a). Using our more frequent GPS positions combined with the continuous-time movement model would allow for a more realistic reconstruction of flight path, movement distance

and speed, and could improve the resulting estimates of energy expenditure. A comparison of our estimations of flight duration from increased proportion of locomotor behaviors compared to control would benefit from a comparison of movement distances calculated from the GPS data and movement model.

Conclusions

We used fine-scale GPS and accelerometer data and existing models to investigate on an unprecedented level of detail the behavioral responses of moose to experimental disturbances mimicking common recreational activities. Our data clearly demonstrated a negative effect of the disturbance on the energy budget of the moose through an increase in locomotor activity and decreased foraging and ruminating behavior. We showed that moose perceive human recreational activity as threat that contributes to their landscape of fear and has corresponding risk effects. Our detailed analysis revealed spatio-temporal variation in the disturbance response that has important implications for models of moose energy budgets. Our analysis can improve parameter estimates in bioenergetic models aiming to quantify the impact of repeat disturbances and cumulative impacts of disturbances and climatic changes on the energy budget of individual moose and how these may translate to population-level consequences.

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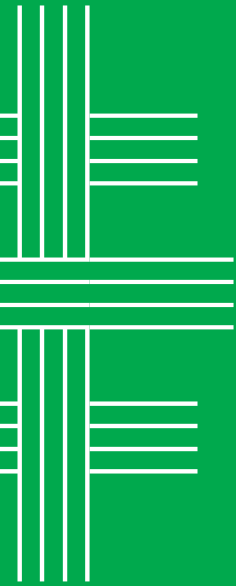
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Understanding the effects of anthropogenic disturbances on wildlife can improve management and conservation efforts. In this thesis, I used data from animal-borne accelerometers and heart rate loggers collected in captive moose to develop models predicting behavior and energy expenditure from accelerometer data. I applied these models to accelerometer data from collared wild moose subjected to experimental disturbances from a hiking or snowshoeing observer.

Overall, locomotor activity and energy expenditure of the approached moose were elevated particularly in the first ten minutes following disturbance, compared to control periods. Foraging activity was reduced during the first two hours following disturbance. I observed seasonal variation in 1) the intensity and 2) the onset of flight, relative to the distance to the disturbance stimulus, suggesting 1) seasonal variation in the perception of threat and 2) variation in the detectability of the disturbance stimulus.

The models and disturbance study presented here improve our understanding of anthropogenic disturbance effects on the energy budget of individual moose. Because compromised individual energy budgets can affect the wider population, my thesis is an important contribution to the efforts to evaluate population-level consequences of disturbances in moose.