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RESEARCH

Thermal and behavioural responses of moose to chemical immobilisation from a helicopter

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Abstract

Instrumentation and sample collection for wildlife research and management may require chemical immobilisation of animals, which may entail physiological and behavioural effects on them. It is therefore important to evaluate the immobilisation protocols to reduce the risk of mortality and morbidity of the handled animals and their populations. Using a multi-sensor approach, we assessed the short-term (< 10 days) thermal and behavioural responses of 10 adult female moose (*Alces alces*) equipped with ruminal temperature loggers and GPS collars with accelerometers to helicopter-based chemical immobilisations. We investigated the body temperature (T_b), movement rates, and resting time before, during, and after recapture. Chemical immobilisations on average increased maximum T_b by 0.71 °C during the capture day, and imposed longer travel distances during the capture day and the two following days (3.8 and 1.8 km, respectively), compared to a 10-day reference period before the immobilisation. The probability of resting was 5–6% lower on the capture day and the two following days compared to the reference period, and females with offspring had a higher probability of resting than females without. Maximum T_b, movement rate, and resting time returned to pre-capture levels on an individual level 2 h, 3 days, and 3 days after the immobilisation, respectively. Chemical immobilisation of moose from a helicopter increases the energy expenditure deduced through movement and T_b rise lasting for hours to days. Ecological and physiological studies aimed at inferring general patterns may encounter bias if including sensor and tracking data from tagged animals without accounting for potential post-capture effects.

Keywords *Alces alces* · Biologging · Body temperature · Capture · Movement · Thermoregulation

Introduction

Studying wildlife in their natural environment is important for understanding the behaviour and ecology of the species, for population management, for species conservation, and for understanding the role of wildlife in disease transmission. Studying free-ranging animals often requires capturing and chemical immobilisation of individual animals for instrumentation with biologging device(s), sample collection, and health examination (Kreeger and Arnemo 2018). Capturing of wild animals has raised concerns about animal welfare, and it is therefore important to evaluate the impact of capture and handling on both the individual and population level (JWD Wildlife Welfare Supplement Editorial Board 2016). Chemical immobilisation of free-ranging wildlife will always include the risk of adverse effects and mortality even in healthy animals, and mortality rates have traditionally been used to describe the negative impacts of wildlife capture (Hampton and Arnemo 2022; Kreeger and Arnemo 2018). In recent years, however, more studies have focused on the non-lethal adverse effects, including short-term physiological and behavioural effects on the individual animal and long-term impacts on both the individual and the population (Cattet et al. 2008; Hampton and Arnemo 2022; Trondrud

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et al. 2022). All stages of the immobilisation procedure could influence the animal both physiologically and behaviourally, and it is often not possible to distinguish which part of the capture process it comes from. To minimise the stress and risk of adverse effects of captures, it is important to follow established guidelines and procedures, use the right type and amount of drugs, minimise the handling time, and evaluate and refine the protocol if needed (Kreeger and Arnemo 2018).

Helicopters are often used when capturing remote populations of free-ranging large mammals, and several studies have documented physiological and behavioural effects of aerial disturbance on wildlife (Frid and Dill 2002; Stankowich 2008). These effects are likely linked to the distance between the aircraft and the animal, and the animal's previous exposure to aircraft (Andersen et al. 1996; Calef et al. 1976; MacArthur et al. 1982; Stankowich 2008; Valkenburg and Davis 1985). Increased activity and movement, hyperthermia, decreased forage intake, increased metabolic rate, and moving into more rugged terrain are examples of responses documented in ungulates including moose (*Alces alces*) (Brambilla and Brivio 2018; Jung et al. 2019; Neumann et al. 2011; Northrup et al. 2014; Stockwell et al. 1991; Støen et al. 2010; Thompson et al. 2020). Hyperthermia, defined as a rectal temperature ≥ 2 °C above the normal rectal temperature, is cause for concern (Kreeger and Arnemo 2018). Severe hyperthermia could be life-threatening due to cytotoxicity, and even short periods with high temperatures can be dangerous, depending on other stress factors (Lepock 2003).

Apart from the animal's condition, it is important to minimise the chase time when capturing animals from a helicopter and to consider the weather and snow conditions. Snow is an important limiting factor for ungulates living in the northern hemisphere, and moving in deep snow is energy-consuming, especially for smaller individuals like moose calves (Fancy and White 1985; Lundmark and Ball 2008; Neumann et al. 2010; Richard et al. 2014). Mental stress, pathologic lesions like abomasal haemorrhage, and degenerative muscular lesions in addition to changes in blood constitutes were found in semi-domestic reindeer (*Rangifer tarandus tarandus*) herded with a helicopter, and the severity of the effects was correlated to the distance of the drive (Rehbinder et al. 1982). Extreme physical exertion related to chasing and/or immobilisation can result in capture myopathy, a condition characterised by metabolic acidosis, muscle necrosis, and myoglobinuria with a high mortality rate (Breed et al. 2019). Death can occur during a stressful event or up to several days or weeks after (Breed et al. 2019). Capture myopathy is well known related to capture of several wildlife species including moose (Arnemo et al. 2006; Breed et al. 2019; Haigh et al. 1977). Opioid-based immobilisation may increase the risk of capture myopathy due to side effects like respiratory depression and poor muscle relaxation, combined with hypoxemia (Breed et al. 2019; Kreeger and Arnemo 2018).

The preferred technique for capturing free-ranging moose includes chemical immobilisation from a helicopter with a potent opioid agonist such as etorphine, thiafentanil, or carfentanil alone or in combination with sedatives like xylazine (Kreeger and Arnemo 2018). We capture moose in early winter prior to late gestation of moose in terms of avoiding chemical immobilisation in the last part of the pregnancy. Winter is best to avoid drowning after the ice becomes unstable, and because it is easier to find darted moose on a snow-covered ground (Arnemo et al. 2003). Because moose are a hunted species, it is also important to ensure that the withdrawal time of the anaesthetics used should not overlap with the moose hunt (Arnemo et al. 2003). In Scandinavia, a CO_2-driven drug delivery system is preferred and etorphine has been the drug of choice, either alone or in combination with xylazine and sometimes acepromazine (Evans et al. 2012; Lian et al. 2014). The capture-related mortality rate in moose in Scandinavia is extremely low (0.7%, $n = 2816$) (Arnemo et al. 2006). Several studies have in recent years evaluated non-lethal adverse effects of chemical immobilisations of moose, including physiological (Barros et al. 2018; Evans et al. 2012; Haga et al. 2009; Lian et al. 2014; Thompson et al. 2020) and behavioural effects (Neumann et al. 2011; Thompson et al. 2020). The physiological and behavioural impact of stressful situations on wildlife caused by human activity are important to assess, especially during winter when moose are hypometabolic and suffer from low food availability and harsh winter climate (Græsli et al. 2020b).

Remote monitoring via biologging devices has made it possible to obtain physiological and behavioural data from free-ranging animals under non-disturbed conditions for an extended period of time (> 1 year) (Rutz and Hays 2009). Obtained data can be used to establish baseline values against which physiological and behavioural effects of potentially stressful situations can be evaluated (McLaren et al. 2007). Body temperature, heart rate, movement rate, and time spent feeding and resting are examples of data obtained by biologging devices used to measure stress in different wildlife species, including moose (Baskin et al. 2004; Ericsson et al. 2015; Græsli et al. 2020a; Neumann et al. 2011; Sand et al. 2016). A multi-sensor approach (combination of different types of biologgers) has increased the possibilities for more fine-scaled studies of the interplay between the physiological and behavioural processes of animals. This is especially relevant as there are examples of animals with pronounced physiological responses in the absence of behavioural changes in relation to human activity (Ditmer et al. 2015).

In this study, we used a combination of global positioning system (GPS) collars and biologging devices obtaining

T_b to investigate the thermal and behavioural responses of moose to chemical immobilisation from a helicopter using the drug combination of etorphine and xylazine (hereafter immobilisation). The first objective was to determine how moose are thermally and behaviourally affected by the immobilisation over a short-term time frame (< 10 days). We also wanted to determine if company of offspring influenced the responses, as movement in deep snow likely is more energy-consuming for the smaller-bodied calves than larger-bodied adults, and could thereby affect the behaviour of the mother (Fancy and White 1985; Lundmark and Ball 2008; Neumann et al. 2010). Based on previous studies (Neumann et al. 2011; Thompson et al. 2020), and using individual-based analyses, we tested the following predictions: (P1) maximum T_b will be higher, (P2) the total daily Euclidean distance travelled will be longer, and (P3) the probability of resting will be lower during the day of the immobilisation compared to a 10-day pre-capture reference period and the 10 days after the approach. The second objective was to determine how long the moose are behaviourally and thermally affected by the immobilisation event. This is important in an animal welfare context, but also to determine how long to expect the data to be biased due to the capture. Based on previous studies, we expected the thermal and behavioural parameters to be affected for hours to several days after the immobilisation event (Neumann et al. 2011; Thompson et al. 2020). The third objective was to determine if the behavioural and thermal parameters from the period between days 11 and 20 after immobilisation would match the reference period before the immobilisation (days − 10 to − 1), as shown in female bison (Jung et al. 2019). If so, this would allow us to recommend using behavioural and thermal data from days 11 to 20 after immobilisation as a reference period in later studies when data from before the immobilisation are not available.

Materials and methods

Study area

The study was conducted on the northern coast of Sweden, in the county of Västerbotten in the Nordmaling and Umeå municipalities (63°N). The study area is characterised by boreal forests, dominated by Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birches (*Betula pendula* and *Betula pubescens*). The elevation level in the area the moose were located in during the study period ranges from 18 to 178 m.a.s.l (mean ± SD; 78 ± 26 m.a.s.l). The snow depth at a weather station (78 m.a.s.l) in the study area ranged from 0.66 to 0.90 m in February 2018, with a mean snow depth of 0.78 m (SMHI 2019).

Study animals and immobilisation procedure

We recaptured 10 female moose in February 2018 (12 February–16 February) to download biologger data during an ongoing project (Græsli et al. 2020a). The moose were already equipped with GPS Plus collars (Vectronic Aerospace GmbH, Berlin, Germany), and ruminal temperature and mortality implant transmitters (MIT; Vectronic Aerospace GmbH, Berlin, Germany) during immobilisation in February 2017. We immobilised the moose according to an earlier described procedure (Evans et al. 2012; Græsli et al. 2020b; Lian et al. 2014), from a helicopter using a CO_2 powered rifle (DANiNJECT, Kolding, Denmark) with a drug combination slightly modified from previous work to 4.5 mg etorphine (Captivon® 98 Etorphine HCl, 9.8 mg/mL, Wildlife Pharmaceuticals (Pty) Ltd., White River, South Africa) and 50 mg xylazine (Xylased® 500 mg, Bioveta, Ivanovice na Hané, Czech Republic). For each moose, we recorded chasing time (time from observation to successful darting), induction time (time from darting to recumbency), immobilisation time (time from recumbency to administration of reversal), and recovery time (time from administration of reversal to standing) during immobilisation. We also noted if the moose were accompanied by a calf or not. The degree of immobilisation was classified as level 1 (light stage of sedation with the moose raising up and laying down again), level 2 (sedated but alert moose trying to raise up), level 3 (immobilised moose, not able to raise up, raised head, responding to stimuli and intact reflexes), level 4 (completely immobilised moose, slightly or not responding to stimuli, depressed reflexes, and unable to lift the head), and level 5 (unconscious moose with absent reflexes). We evaluated the degree of immobilisation at approach and once more during the immobilisation. We measured rectal temperature (with a digital clinical thermometer, AccuTemp express; Jahpron, Bodø, Norway, accuracy according to the manufacturer ± 0.1 °C) and respiratory rate (counting thoracic elevations) as soon as possible after recumbency. We classified the T_b as hypothermia ($T_b \geq 2$ °C under the normal temperature), normothermia (normal temperature ± 2 °C), and hyperthermia ($T_b \geq 2$ °C above the normal temperature) (Kreeger and Arnemo 2018). Normal temperature was defined as the mean T_b measured by the MIT during a reference period before the captures. We administered intranasal oxygen at a flow rate of 2–4 L/min to the moose during the immobilisation (Lian et al. 2014). Pregnancy status was determined by rectal palpation (Solberg et al. 2003). The moose underwent surgical removal of a subcutaneous heart rate logger (DST centi-HRT; Star Oddi, Gardabaer, Iceland) used in another study (for details, see

Græsli et al. 2020b) during the immobilisation. We administered a local anaesthetic, bupivacaine (Marcaine 5 mg/mL, AstraZeneca, Cambridge, UK) at a total dose of 5.0 mg/moose prior to the surgery. We also gave the moose a subcutaneous injection of analgesics, meloxicam (Metacam, Boehringer Ingelheim Vetmedica GmBH, Ingelheim am Rhein, Germany) at a dose of 0.5 mg/kg. When finished with the handling procedure during immobilisation, we reversed etorphine with 50 mg naltrexone (Naltrexonhydroklorid vet. APL 50 mg/mL; Apotek Produktion och Laboratorier, Kungens Kurva, Sweden) and xylazine with 5 mg atipamezole (Antisedan®, 5 mg/mL; Orion Pharma Animal Health, Turku, Finland) intramuscularly. We performed visual field checks in the spring to investigate the post-natal survivorship a few days after the estimated calving date (calving date was based on GPS clustering) (Neumann et al. 2020).

The project was approved by the Regional Animal Ethics Committee for Northern Sweden in Umeå (Dnr A14-15, A3-16, A28-17) and was conducted following Swedish laws concerning animal research ethics. Experienced field personnel, pilots, and veterinarians carried out captures and handling, and all personnel were trained and certified according to the standards of the Swedish Animal Welfare Agency and the Swedish Board of Agriculture.

Biologgers, programming, and data collection

The collars used in this study included a GPS receiver, an accelerometer sensor, a mortality sensor, an ambient temperature recorder, a very high frequency (VHF) transmitter, and a Global System for Mobile (GSM) communication modem (Vectronic Aerospace 2021). In addition, each collar was linked to the MIT sensor in the rumen of the moose (Vectronic Aerospace 2022). The GPS was scheduled to record positions at 3-h intervals during the duration of this study, and together with the most recent ambient and ruminal temperature, those readings were sent using the GSM network to a WRAM (Wireless Remote Animal Movement) database for storage (Dettki et al. 2014). The MITs recorded the ruminal temperature at 5-min intervals with an accuracy of ± 0.1 °C, and they have a resolution of ± 0.001 °C (Herberg et al. 2018; Vectronic Aerospace 2022). The acceleration sensor integrated in the collar measured activity over two axes (*X* and *Y*) as back-forward and left–right movement on a scale from 0 to 255 at 6 to 8 Hz, with 0 representing no activity and 255 the highest activity. It stored average values over 5-min recording intervals, and the overall activity is presented as the sum of the activity data on both axes, ranging from 0 to 510 (Gervasi et al. 2006). During recaptures in February 2019, the collars were changed and data recorded by the retrieved collars including MIT data were manually downloaded and sent to the WRAM database (Dettki et al. 2004).

Data preparation and analyses

To determine the thermal and behavioural effects of helicopter-based chemical immobilisations on moose, we tested for changes in the following variables: maximum T_b [°C], Euclidean distance travelled [m/day], and probability of resting [between 0 and 1, where 0 indicates impossibility of resting and 1 indicates certainty]. The explanatory variables included were as follows: days since immobilisation (categorical variable) using daily values of all variables from the capture day (during) and days 1–10 post-capture (days 1–10), and one average value from days − 10 to − 1 pre-capture (before); company of calf (factor with two levels; with/without calf). We used the 10 days before the day we started with the captures in the area as the 'before' category (reference period) (2–11 February), as the helicopter activity in the area might influence the moose behaviour and physiology (Stankowich 2008; Støen et al. 2010). Six of the females had a calf at heel during the immobilisation.

For movement data, we calculated the Euclidean distance between consecutive GPS positions using the AdehabitatLT package (Calenge 2006), to then calculate the total distance travelled per day (m). We modelled maximum T_b and total distance travelled per day (response variables) using gamma-distributed generalised linear models with identity link function from the lme4 package (Bates et al. 2015). Due to low sample size issues, we were unable to include the moose ID as a random structure. We used ACF (autocorrelation function) plots to check for autocorrelation and found it negligible (Supplementary Information 1). We based our model selection for all response variables on Akaike's information criterion corrected for a small sample size (AICc). Model selection was carried out with the function ICtab from the bbmle package (Bolker and R Core Team 2017), and we selected the most parsimonious and highest-ranked model within $\Delta\text{AICc} \leq 2$.

To assess the potential impact of captures on moose time allocation, we classified behaviour into (1) inactive (i.e. resting) and (2) active by fitting a hidden Markov model (HMM) to the observed activity data (summed acceleration of *X*- and *Y*-axes, recorded at 5-min intervals). HMMs assume that the observed patterns in movement or activity data are driven by a 'hidden' underlying finite state sequence. These states are interpretable as proxies for animals' behavioural modes which cannot be observed directly (Langrock et al. 2012; Patterson et al. 2009). We modelled activity using a state-dependent gamma distribution. As the observed activity data did not exhibit large individual variation, we did not explicitly account for variation between individual moose in the HMM. The HMM was fitted via numerical likelihood maximisation using the 'momentuHMM' package in R (McClintock and Michelot 2018), testing 30 sets of random starting values to avoid local likelihood maxima. Each observation was then decoded (into 'inactive' or 'active') by applying the Viterbi algorithm, which identifies the most likely state sequence given by the model. The inactive state was characterised by very low activity levels (mean summed *X*- and *Y*-acceleration of 1.52 (SD = 0.65, zeromass = 0.98)), and the active state by higher activity levels (mean = 43.88, SD = 38.44, zeromass = 0.01).

Based on the results of the HMM-based behaviour classification, we then ran a generalised linear model with a binomial family distribution (Binomial Regression Model) with the proportion of the day allocated to resting versus active behaviour as the response variable and performed model selection following the same approach as for T_b and movement. We back-transformed the log-odds values returned by the highest-ranked binomial model using the emmeans-function in the R-package emmeans (Lenth et al. 2019).

To calculate the number of days it took for each response variable and for each moose to return to the pre-capture levels, we calculated the upper and lower 95% confidence intervals of the pre-capture mean (hourly mean for T_b and daily mean for movement and resting time) of all response variables for each individual. Then, we determined for each individual if the daily (movement and resting time) or hourly (maximum T_b) mean values after the immobilisation fell within the confidence interval of the pre-capture level. We thereby calculated the time since immobilisation it took for each moose to fall within the 95% confidence interval. We assumed that the variables were at the levels of the reference period once the values fell within the confidence intervals.

To determine if we could use data from the period between days 11 and 20 after the immobilisation as a proxy for pre-capture levels of activity, T_b, and movement data, we tested the parameters for normality, and thereafter used *t*-tests on the data from days 11 to 20 after the immobilisation and compared it to the pre-capture data.

All the data were prepared and analysed using R version 4.0.5 (R Core Team 2021), and p-values < 0.05 were considered significant.

Results

All moose were immobilised with one dart, resulting in a moderate degree of immobilisation (9 out of 10 moose showed level 3 degree of immobilisation, whilst one moose went from 2 to 3 during the immobilisation), with the moose lying in sternal recumbency with the head raised. No capture-related mortalities or morbidities occurred, and all moose were alive 1 year after the immobilisation. This was the second time each of these moose had been immobilised. All pregnant moose still sending data in the spring of 2018 ($n = 7$) were in the company of newborn calves a few days after the calving. Time variables recorded during immobilisation are summarised in Table 1. We had to exclude one of the moose from the movement analysis due to missing data points on the day of the immobilisation. Nine moose were included in the analysis of the activity and T_b data, as we lost contact with one moose before we were able to download the data.

The most parsimonious and highest-ranked model for T_b included day since immobilisation only, and for daily travel distance and probability of resting the additive effect of day since immobilisation and having a calf (Table 2). When chemically immobilised from a helicopter, the moose increased their T_b, activity, and daily movement rate on the day of the capture (Table 3). A graphical presentation of the T_b and activity for one representative individual is given in Fig. 1 (for the rest of the moose, please see Supplementary Information 2). We observed a significantly higher maximum T_b during the day of the immobilisation compared to the period before the immobilisation (0.71 °C (SE 0.11 °C, p-value < 0.001)) (Table 3; Fig. 2). The mean T_b during the reference period defined as the normal T_b was 38.02 ± 0.02 °C (mean ± SE). Two moose had $T_b \geq 2$ °C above the normal T_b (hyperthermia) during the day of the immobilisations with 40.09 °C and 40.23 °C as their highest measured body temperatures; the rest of the moose ($n = 7$) were normothermic with the highest measured body temperatures ranging from 38.55 to 38.99 °C. For all moose except one, the rectal measured temperature was higher than the ruminal measured temperature (Supplementary Information 3). Daily Euclidean distance travelled was significantly higher during the day of the immobilisation (3800 m (SE 1354 m, p-value 0.006)), and day 1 (1799 m (SE 783 m, p-value 0.024)) and day 2 (1822 m (SE 789 m, p-value 0.023)) after the immobilisation compared to the period before the immobilisation (Table 3; Fig. 3). An animation of the movement of the moose and the helicopter during the days of capture is available as an online resource (Supplementary Information 4). Moose in company of a calf had a

Table 1 Time variables reported as mean and standard error (SE) associated with helicopter-based chemical immobilisation of female moose ($n = 10$) immobilised with a combination of etorphine and xylazine, February 2018, Sweden

Variable	Units	Mean ± SE	Minimum–Maximum
Chasing time	Minutes	7.3 ± 1.5	1.0–14.0
Induction time	Minutes	6.3 ± 1.2	2.0–13.0
Immobilisation time	Minutes	65.1 ± 3.1	52.0–80.3
Recovery time	Minutes	2.9 ± 0.2	2.2–4.3
Total time	Minutes	81.6 ± 3.8	68.6–101.0

Chasing time: time from observation of the moose to successful darting

Induction time: time from darting to recumbency

Immobilisation time: time from recumbency to administration of reversal

Recovery time: time from reversal to the moose was standing

Total time: time from observation to the moose was standing

Table 2 Log-likelihood (logLik and ΔlogLik), Akaike's information criterion corrected for small sample size (AICc and ΔAICc), number of parameters (n), and model weight (weight) for the linear model combinations evaluating maximum body temperature, movement (distance travelled), and resting behaviour (probability of resting) of female moose ($n = 10$) chemically immobilised from a helicopter, February 2018, Sweden

Model combinations	logLik	AICc	ΔlogLik	ΔAICc	n	Weight
Body temperature [°C]						
Days since immobilisation	15.7	−1.5	34.8	0.0	14	0.62
Days since immobilisation + company calf	16.5	−0.5	35.6	1.0	15	0.38
Days since immobilisation * company calf	17.6	30.7	36.7	32.2	26	< 0.001
Null model	−19.1	42.3	0.0	43.8	3	< 0.001
Company calf	−18.6	43.5	0.4	45.1	4	< 0.001
Movement [m/day]						
Days since immobilisation + company calf	−875.2	1782.9	30.2	0.0	15	0.981
Days since immobilisation	−880.5	1790.8	24.9	7.9	14	0.019
Days since immobilisation * company calf	−870.7	1807.2	34.7	24.3	26	< 0.001
Company calf	−904.2	1814.7	1.1	31.8	4	< 0.001
Null model	−905.4	1814.9	0.0	31.9	3	< 0.001
Probability of resting						
Days since immobilisation + company calf	−712.0	1453.9	85.5	0.0	14	0.86
Days since immobilisation * company calf	−697.5	1457.5	100.0	3.6	25	0.14
Company calf	−756.4	1517.0	41.1	63.1	3	< 0.001
Days since immobilisation	−753.2	1533.7	44.3	79.8	13	< 0.001
Null model	−797.5	1597.1	0.0	143.1	2	< 0.001

significantly lower daily travel distance compared to moose without an accompanying calf (−598 m (SE 237 m), p-value 0.013). The probability of resting was significantly lower (5–6% lower) on the immobilisation day, day 1, and day 2 (p-values < 0.001) after the immobilisation compared to the reference period (Tables 4 and 5; Fig. 4). Moose in company of offspring had a significantly higher probability of resting than moose without (5% higher, p-value < 0.001).

Hourly max T_b returned to pre-capture level 2 ± 1 h (mean ± SE (range 0–6 h)) after the immobilisation on an individual level (Supplementary Information 5). Daily travel distances were at pre-capture levels 3 ± 1 days (mean ± SE (range 1–6 days)) after immobilisation (Supplementary Information 5). We also documented two moose with movement rates at reference period levels the first day after capture, followed by elevated movement levels in the following 5 and 7 days, respectively. The time allocated to resting per day was at pre-capture level 3 ± 1 days (mean ± SE (range 0–9 days)) after immobilisation. The resting time per day was up to 6.6 h lower for one individual compared to the mean resting time of this moose in the reference period (10 h compared to 16.6 h) (Supplementary Information 5). Only one individual moose had a longer resting time after the immobilisation, with a 2.6-h longer resting time the first day after the immobilisation compared to the mean resting time in the reference period (19.4 h compared to 16.8 h).

Body temperature (max T_b), daily travel distance, and activity data from before and after immobilisation were all normally distributed, and the values from the pre-capture period did not significantly differ from those from days 11 to 20 after the immobilisation (maximum T_b: $t = -0.28$, p-value = 0.78; total travel distance: $t = 0.84$, p-value = 0.42; activity: $t = -0.64$, p-value = 0.53).

Discussion

This multi-sensor approach study, combining data from different biologging devices, provides detailed insight into the short-term (< 10 days) thermal and behavioural responses and the interplay amongst these responses of moose to helicopter-based chemical immobilisation. We observed notable changes in the responses during the day of the capture (T_b, movement, and resting), and the two following days (movement and resting) compared to a pre-capture reference period. We also documented large individual variations in both the intensity of the responses and the duration of the response.

As predicted (P1), the moose increased their T_b during the day of capture compared to the reference period. We documented two moose exhibiting capture-induced hyperthermia, with T_b exceeding 2 °C above the mean T_b in the reference period. The capture-induced hyperthermia is likely due to a combination of the helicopter chase and the drugs used (Kreeger and Arnemo 2018). Scandinavian moose in two other studies immobilised with the same drug combination were all normothermic (Evans et al. 2012; Lian et al. 2014), whilst rectal temperatures ≥ 40 °C were documented in Scandinavian moose captured with different capture methods and drug combinations (Barros et al. 2018; Haga et al. 2009; Rostal et al. 2012). The differences between the studies could be due to the length of the helicopter chase, differences in drugs and dosages, environmental conditions

Table 3 Model parameter estimates, standard errors (SE), t-values, and p-values for variables in the linear models evaluating body temperature (maximum) and movement (distance travelled) of female moose ($n=10$) chemically immobilised from a helicopter, February 2018, Sweden. Reference period (1–10 days before immobilisation) in the intercept

Model parameters	Estimate (β)	SE	t-value	Pr(> |t|)
Body temperature [°C]				
(Intercept)	38.50	0.07	520.47	< 0.001
Day 0 (immobilisation day)	0.71	0.11	6.69	< 0.001
Day 1	−0.08	0.10	−0.73	0.47
Day 2	−0.05	0.10	−0.51	0.61
Day 3	−0.06	0.10	−0.55	0.59
Day 4	−0.04	0.10	−0.39	0.70
Day 5	0.00	0.10	0.04	0.97
Day 6	0.09	0.10	0.81	0.42
Day 7	0.08	0.10	0.81	0.42
Day 8	0.08	0.10	0.74	0.46
Day 9	0.09	0.10	0.90	0.37
Day 10	0.07	0.10	0.69	0.49
Movement [m]				
(Intercept)	1240	299	4.1	< 0.001
Day 0 (immobilisation day)	3800	1354	2.8	0.006
Day 1	1799	783	2.3	0.024
Day 2	1822	789	2.3	0.023
Day 3	264	365	0.7	0.47
Day 4	227	356	0.6	0.53
Day 5	535	434	1.2	0.22
Day 6	392	397	1.0	0.33
Day 7	508	427	1.2	0.24
Day 8	−52	291	−0.2	0.86
Day 9	346	385	0.9	0.37
Day 10	−329	240	−1.4	0.17
Company calf: yes	−598	237	−2.5	0.013

like snow depth and ambient temperature, and the fact that continuous T_b measurements provide more detailed information compared to traditional rectal temperature measurements a few times during the capture. We also documented a difference between the rectal temperature and the ruminal temperature, with all except one rectal temperature being higher than the ruminal temperature. The difference was largest at the highest measured temperatures, indicating that the highest measured ruminal temperatures are too low and therefore not representative of the core T_b (rectal temperature). More research is needed to investigate the extent of the difference, and also if it could be linked to the accuracy of the measurements (Herberg et al. 2018). The accuracy of the ruminal temperature is likely influenced by the amount and consistency of the ruminal content, the location of the transmitter, and the duration of the core T_b elevations.

There was no evidence of febrile responses the first 10 days post-capture, as a result of the surgical removal of the subcutaneous biologger. Febrile responses after surgical implantation of biologgers are earlier documented in other ungulate species like free-ranging impala (*Aepyceros melampus*) and the greater kudu (*Tragelaphus strepsiceros)* (Hetem et al. 2008; Kamerman et al. 2001). Our results thus indicate that moose are thermally affected by the immobilisation for only a few hours. The average time from observation until the moose was standing after the immobilisation was < 90 min, and the T_b returned to pre-capture levels 2 h after the immobilisation was finished. This is in line with other reports for moose (Thompson et al. 2020). However, in the present study, the T_b remained stable when returning to pre-capture levels even with increased movement the following 2 days, which is contradictory to the findings by Thompson et al. (2020) which showed elevated T_b in the 48 h following the immobilisation. The differences between the studies could be due to differences in biologging devices (vaginal versus ruminal biologgers), anaesthetics used and dosages, capture protocol, environmental conditions, and other uncontrolled stressors.

As predicted (P2), the moose increased their movement during the day of capture. The daily travel distance during the day of the immobilisation was seven times longer than the daily travel distances during the reference period for females with calves, and four times longer for females without calves. The cost of the accompanying calves for the captured females is an important issue to evaluate. In the present study, we showed that females with offspring had lower movement rates and a higher probability of resting than females without. Movement in deep snow is more energy-consuming for calves due to their smaller size, lower breast height, and stride length compared to adult moose (Fancy and White 1985; Lundmark and Ball 2008). Increased movement is energy-consuming and requires increased food intake and/or resting time to compensate for the energy used. The GPS-fix rate in this study was 3 h; data with higher resolution would have given more detailed information about the movement behaviour in relation to immobilisation. The daily travel distances on days 1 and 2 post-capture were 1.8 km longer than the distance during the reference period. The increased movement in the first days after the immobilisation could be due to the moose changing habitat, moving from the area of the immobilisation (Neumann et al. 2011; Støen et al. 2010), or due to a generally increased vagility in relation to the captures. Female mule deer (*Odocoileus hemionus*), female bison (*Bison bison*), and female moose all showed short periods of elevated movements following recaptures, which is in contrast to male bison immobilised for the first time that reduced their movement and displacement rates following capture (Jung et al. 2019; Neumann et al. 2011; Northrup et al. 2014; Thompson et al. 2020). Overflights by the helicopter capturing other moose in

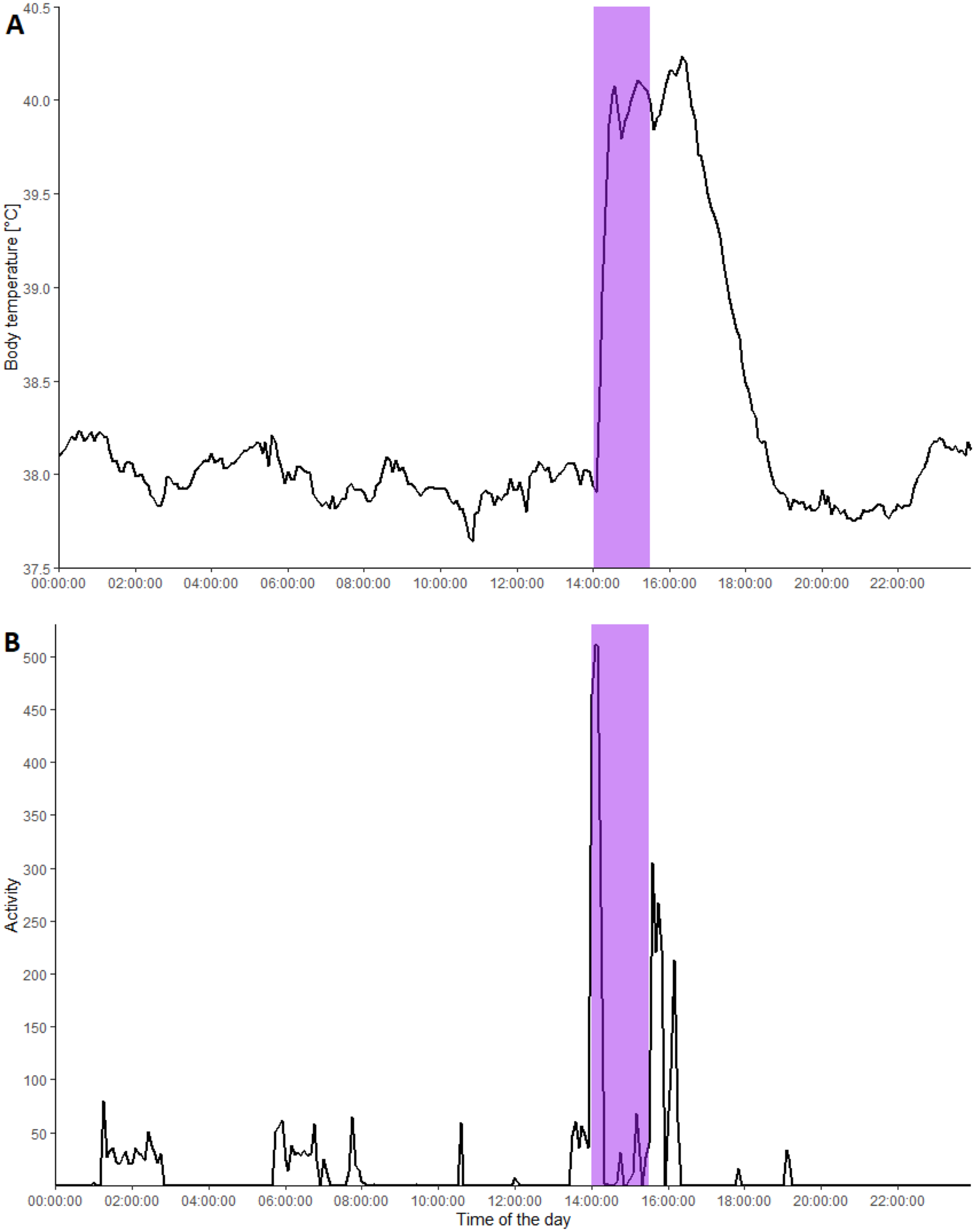
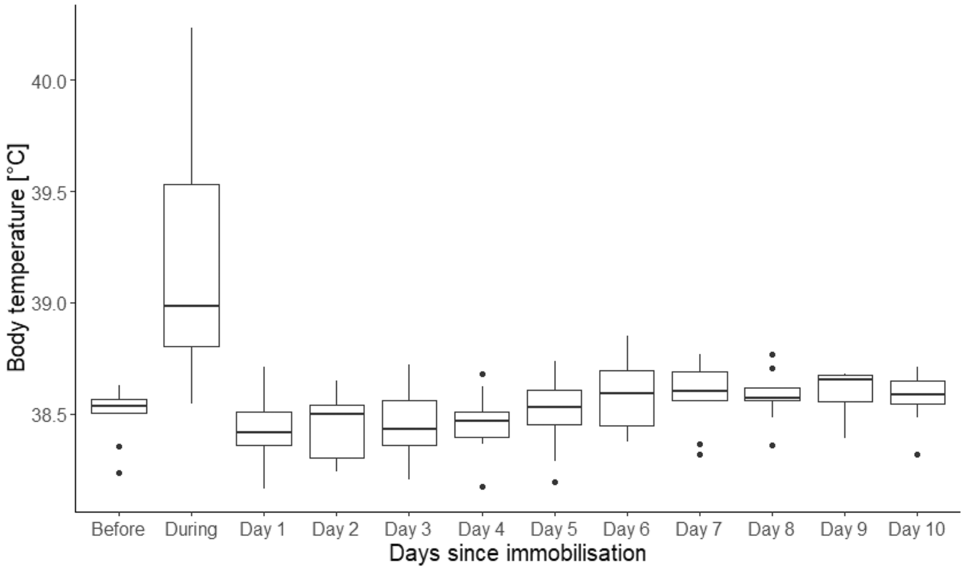


Fig. 1 Graphical representation of body temperature [°C] (**A**) and activity (**B**) of a female moose (aa_ac_17_025) during the day of the immobilisation. The purple ribbon represents the duration of the immobilisation, i.e. the time from observation to the moose was standing. The y-axis on graph B represents the sum of the activity measurements over two axes (X and Y) on a scale from 0 to 510 (0–255 on each axis)

Fig. 2 Maximum body temperature [°C] associated with immobilisation (before: a 10-day reference period before the immobilisation, during: the day of the immobilisation, days 1–10: days 1–10 after the immobilisation)



the same area could also be a reason for the increased movement in the days following the immobilisation, especially in smaller study areas (as indicated by the animation included in Supplementary Information 4), as most of the study animals were located in the same area. On average, we demonstrated that the daily travel distance returned to baseline levels (i.e. pre-capture levels) 3 days after immobilisation, which is in line with earlier reports of moose and other ungulates (Jung et al. 2019; Neumann et al. 2011; Northrup et al. 2014; Thompson et al. 2020).

As predicted (P3), the probability of resting was significantly lower on the day of the immobilisation compared to the reference period. The probability of resting was also lower on the two following days compared to the reference period. The moose being more active after the immobilisation could be due to increased feeding behaviour to compensate for the energetic use in relation to the immobilisation, and continued exposure to helicopter overflights, and is likely linked to the increased movement the days after the immobilisation (Støen et al. 2010).

We documented large individual variations in the response to immobilisation. Maximum T_b ranged from 38.55 to 40.23 °C and returned to baseline values within the first day after the immobilisation. We, therefore, recommend omitting T_b data the day after the immobilisation. It took 3 days (mean) to return to pre-capture levels for movement and resting on an individual basis. This data should therefore be omitted for at least 3 days after immobilisation. One should though be aware that the data could be biased for several additional days for some individuals, as the maximum times it took for some moose to return to baseline levels were notably higher than the mean values (resting time 9 days and movement 6 days). Since the maximum T_b, movement, and activity data from days 11 to 20 after the immobilisation did not significantly differ from those during the pre-capture period, we can recommend using from days 11 to 20 after the immobilisation as a proxy for the reference period before the immobilisation in future analysis of moose biologging data.

Fig. 3 Daily Euclidean distance travelled [m/day] associated with immobilisation (before: a 10-day reference period before the immobilisation, during: the day of the immobilisation, days 1–10: days 1–10 after the immobilisation), for female moose with and without company of calves

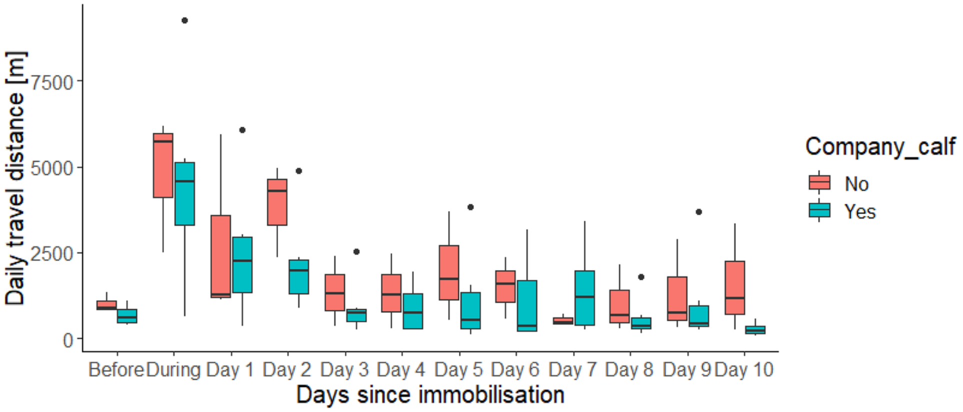


Table 4 Model parameter estimates, standard errors (SE), z-values, and p-values for variables in the binomial regression model evaluating resting behaviour of female moose ($n = 9$) chemically immobilised from a helicopter, February 2018, Sweden. Reference period (1–10 days before immobilisation) in the intercept

	Estimate	SE	*z*-value	Pr(> |z|)
(Intercept)	0.56589	0.04390	12.9	< 0.001
Day 0 (immobilisation day)	−0.20751	0.05856	−3.5	< 0.001
Day 1	−0.25984	0.05831	−4.5	< 0.001
Day 2	−0.23576	0.05839	−4.0	< 0.001
Day 3	−0.06943	0.05900	−1.2	0.24
Day 4	−0.11520	0.05880	−2.0	0.05
Day 5	0.01179	0.05938	0.2	0.84
Day 6	−0.05982	0.05905	−1.0	0.31
Day 7	−0.01276	0.05926	−0.2	0.83
Day 8	0.05522	0.05960	0.9	0.35
Day 9	0.03479	0.05948	0.6	0.56
Day 10	0.09242	0.05981	1.5	0.12
Company calf: yes	0.21870	0.02409	9.1	< 0.001

Moose display hypometabolism during winter, with lower T_b, heart rate, and activity in winter compared to summer (Græsli et al. 2020b). However, as moose are already suffering from limited resources and the harsh climate during winter, it is important to minimise the adverse effects of the immobilisation by evaluating its impact and improving the capture protocols. Our study demonstrated that chemical immobilisation of moose from a helicopter with the drug combination of 4.5 mg etorphine and 50 mg xylazine resulted in a safe and effective immobilisation of the moose, with no capture-related mortalities, all pregnant moose were observed with newborn offspring in the following spring, and all moose were still alive 1 year post-capture. A short chasing time and a quick and smooth induction are essential for the safety of the animals, decreasing the risk of morbidity, mortality, and losing track of the moose. The induction times (6.3 ± 1.2 min (mean ± SE)) were comparable to moose immobilised with a combination of etorphine, xylazine, and acepromazine (6.5 ± 2.5 min (mean ± SE)) (Evans et al. 2012). The induction times recorded were 2 and 4 min longer, respectively, than the induction times for Scandinavian moose immobilised with etorphine or thiafentanil as sole agents (Barros et al. 2018; Evans et al. 2012; Haga et al. 2009). To minimise the stress load of the capture, it is important to be effective and organised to decrease the duration of the anaesthesia (Kreeger and Arnemo 2018). In the present study, we had a long immobilisation time (65.1 ± 3.1 min (mean ± SE)) due to the handling

Table 5 Probability, standard errors (SE), degrees of freedom (df), and 95% confidence interval of resting behaviour associated with immobilisation (before: a 10-day reference period prior to the immobilisation, during: the day of the immobilisation, days 1–10: days 1–10 after the immobilisation) based on binomial regression models for female moose ($n = 9$) with and without company of calves, February 2018, Sweden

Capture category	Probability	SE	*df*	95% Confidence interval
Company calf: no				
Before	0.6378	0.0101	Inf	0.6177–0.6574
During	0.5886	0.0104	Inf	0.5681–0.6088
Day 1	0.5759	0.0104	Inf	0.5554–0.5962
Day 2	0.5818	0.0104	Inf	0.5613–0.6020
Day 3	0.6216	0.0102	Inf	0.6014–0.6415
Day 4	0.6108	0.0103	Inf	0.5905–0.6307
Day 5	0.6405	0.0101	Inf	0.6205–0.6601
Day 6	0.6239	0.0102	Inf	0.6037–0.6437
Day 7	0.6349	0.0102	Inf	0.6147–0.6545
Day 8	0.6505	0.0101	Inf	0.6305–0.6699
Day 9	0.6458	0.0101	Inf	0.6258–0.6653
Day 10	0.6589	0.0100	Inf	0.6390–0.6782
Company calf: yes				
Before	0.6867	0.0093	Inf	0.6681–0.7047
During	0.6404	0.0097	Inf	0.6211–0.6593
Day 1	0.6283	0.0098	Inf	0.6089–0.6473
Day 2	0.6339	0.0098	Inf	0.6145–0.6528
Day 3	0.6715	0.0095	Inf	0.6527–0.6898
Day 4	0.6614	0.0096	Inf	0.6424–0.6798
Day 5	0.6892	0.0093	Inf	0.6707–0.7072
Day 6	0.6737	0.0095	Inf	0.6549–0.6919
Day 7	0.6839	0.0094	Inf	0.6653–0.7020
Day 8	0.6984	0.0092	Inf	0.6800–0.7162
Day 9	0.6941	0.0093	Inf	0.6757–0.7120
Day 10	0.7062	0.0091	Inf	0.6880–0.7238

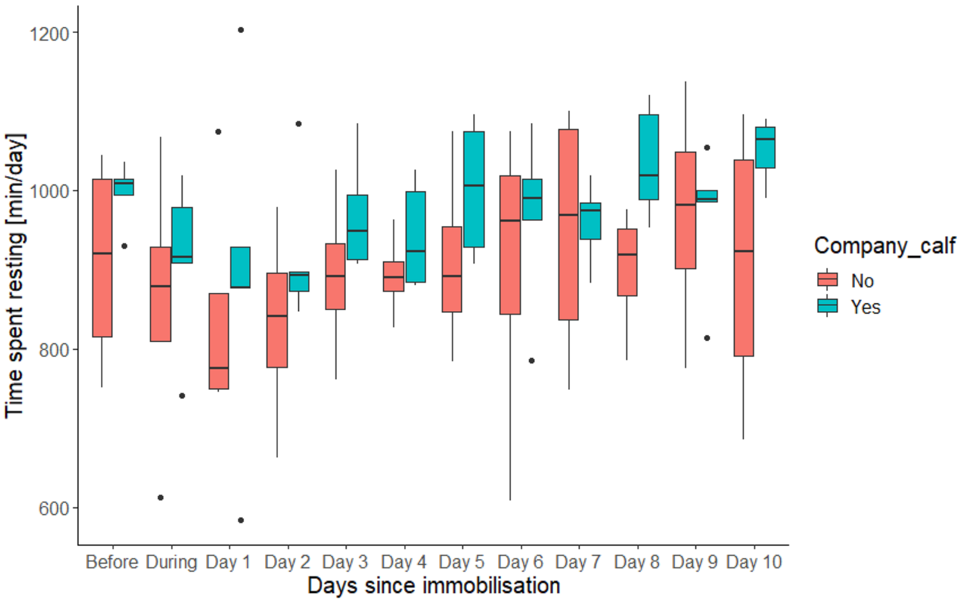


Fig. 4 Time allocated to resting per day [min/day] associated with immobilisation (before: a 10-day reference period before the immobilisation, during: the day of the immobilisation, days 1–10: days 1–10 after the immobilisation), for female moose with and without company of calves

of the sensors (i.e. surgical removal of biologging devices and data download). We can therefore not rule out that the immobilisation time might have affected the recovery and post-capture responses of our study animals.

However, the overall impact of chemical immobilisation is difficult to determine, and one needs to evaluate both immediate (hours to days) and more long-term (months to years) behavioural and physiological effects to conclude. Examples of long-term effects of stressful situations include changes in body condition, calf survival rates, immune suppression, and habitat changes on an individual level, which could impact population dynamics due to reduced survival and reproductive rates (McLaren et al. 2007; Moberg 2000). The literature on the long-term effects of immobilisation in free-ranging ungulates is limited with inconsistent conclusions (Larsen and Gauthier 1989; Omsjoe et al. 2009; Trondrud et al. 2022). A follow-up to the present study to evaluate long-term effects could be to look at the post-natal survivorship and slaughter weights of calves born in the spring after the immobilisation, as well as the reproductive rates of the females in the following years and their slaughter weights. The main issues when working with data from free-ranging animals are first to have a control group to compare the results to, and second that other biological and environmental factors in addition to other stressful situations during the year could influence the results.

Conclusion

In summary, we demonstrated short-term (< 10 days) behavioural and thermal responses of moose to chemical immobilisation from a helicopter with increased energy expenditure lasting for hours to days after the immobilisation. To avoid biased results in future analysis of newly immobilised moose, we recommend omitting T_b data for at least 1 day and resting time and movement data for at least 3 days after the immobilisation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10344-023-01673-3.

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Data availability The datasets generated during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval All procedures performed in this study involving captures and handling of animals were conducted following Swedish laws concerning animal research ethics. The project was approved by the

Regional Animal Ethics Committee for Northern Sweden in Umeå (Dnr A14-15, A3-16, A28-17).

Competing interests The authors declare no competing interests.

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