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Research article

Behavioural responses of brown bears to helicopter capture

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Understanding the effects of capture and handling on wild animals is crucial in evaluating ethical practices in ecological research, and in avoiding biased conclusions from misinterpreting biologging data potentially affected by capture. The aim of this study was to assess the effects of helicopter capture on the behaviour of Scandinavian brown bears by comparing the expression of specific behavioural states between captured bears in spring and bears of a control group that were not captured during the same time period. We identified three different behavioural states: stationary, walking/foraging and transit. Our study revealed that captured bears were more stationary for up to four days after capture compared to bears of the control group, depending on their reproductive state. We found higher doses of the immobilizing drug, as well as abdominal surgery, to negatively impact the bears' movement after capture, highlighting the importance of careful consideration of drug doses and invasive procedures during wildlife capture. This study advances our understanding of the impact of helicopter capture and surgery on the movement of brown bears and helps to refine capture and handling protocols to ensure well-being and welfare during wildlife capture.

Keywords: behavioural classification, capture effects, chemical immobilization, field surgery, *Ursus arctos*

Introduction

Even though non-invasive methods for collecting data from wild animals (for example hair and faecal samples, or camera trapping) are developing rapidly, capture remains an important tool in wildlife research. In some cases, capture is the only available method to gather morphometric data, to sample tissue, or to deploy loggers to address specific research questions, management strategies and/or conservation initiatives (Thiemann et al. 2013, Brivio et al. 2015). Capturing wildlife can be achieved through

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a variety of methods, e.g. physical restraining (such as box, cage or foot hold traps) (Shury 2014) and pursuit (chasing from helicopter or car) (Jung et al. 2019). Necessary sedation can be carried out using a remote drug delivery system (darting and chemical immobilization), for example from a helicopter, at a bait site (Gittleman 2019) or via ground-stalking (Boesch et al. 2011). As well as collecting morphological measurements and samples, equipping wildlife with tracking or biologging devices is often the primary motivation for scientists and managers to capture wild animals (Wikelski and Cooke 2006, Chmura et al. 2018). Movement data are essential to further our understanding of elusive, wide-ranging or low-density species. Radio or very high frequency (VHF) telemetry and global positioning system (GPS) technology are the most widely used tracking systems and remotely provide detailed information on animal behaviour and movement (Latham et al. 2015).

Even though capture and deployment of tracking system devices are standard practices in wildlife ecology, these activities may compromise the animal's welfare, behaviour or fitness and could even lead to fatal outcomes (Cattet et al. 2008, Saraux et al. 2011, Arnemo et al. 2018, Bodey et al. 2018, Field et al. 2019, Petrusková et al. 2021). This form of intervention will always be a stressful event for wild animals (Wilson and McMahon 2006) and a harm–benefit analysis (Brønstad et al. 2016), including the evaluation of the 3Rs (refine, reduce, replace) (Lindsjö et al. 2016), is necessary. Stress is mediated through the activation of the hypothamalmic–pituitary–adrenal (HPA) axis and the consequent release of glucocorticoids. The HPA axis and its hormone excretion are influenced by the circadian clock and the disregulation of one of them can impact the other (Nader et al. 2010, Takahashi et al. 2013). Capture-related stress has been proposed to potentially impact circadian organization in wildlife (Brogi et al. 2019) and a comprehensive study of 42 terrestrial mammal species has found evidence of significant behavioural changes following a capture and collaring event in 70% of the investigated species. Herbivores generally increased their displacement and showed varying activity, while omnivores and carnivores decreased activity and displacement; however, pronounced inter- and intraspecific variation was evident (Stiegler et al. 2024). Hence, a thorough investigation of the effects of capture is required to minimize negative impacts on research animals and to obtain minimally biased and valid research data. One basic assumption in wildlife research is that the captured and tagged individuals are representative of the population and that their behaviour and physiology is comparable with that of unmarked individuals (Cooke 2008), an assumption that is rarely tested (Vandenabeele et al. 2011). A meta-analysis of the power to detect device effects in avian tracking literature, for example, found considerable variation in the statistical power of the included studies, as well as evidence for over- and underestimation of detected effects of device deployment (Cleasby et al. 2021). While any capture and tagging event has immediate effects on the study animal it is important to understand the duration of these effects and to quantify to which extent this is impacting the animal (Cattet et al. 2003, Powell and Proulx 2003, Cleasby et al. 2021).

To accurately quantify the effect of a disturbance event on animal behaviour, disturbed and captured individuals should ideally be compared to undisturbed individuals. Information on the behaviour of undisturbed animals – that is, individuals not captured and not tagged – is, however, limited in wildlife settings, especially for elusive and wide-ranging species. Therefore, useful comparisons between truly uncaptured and undisturbed individuals and captured individuals are difficult to derive. Studies conducted under captive conditions can give insights into the effects of device attachment, for example, since behavioural observations are more easily obtained. As an example, a study of long-tailed ducks *Clanula hyemalis* found pronounced differences in activity budgets, time spent in water and maintenance behaviour between individuals equipped with a radiotransmitter versus a control group without such a device. Advances in avian research facilitated the comparison of the survival of unmarked and unhandled male tree pipits *Anthus trivialis* with previously marked and handled individuals via the use of individual acoustic monitoring (Petrusková et al. 2021). Such detailed and unbiased observations are difficult for elusive and less vocally active wildlife such as mammals. As a consequence, studies evaluating the effects of capture and tagging focus on temporal changes in post-disturbance behaviour on an individual level, or compare behaviours to those animals that are tagged but not otherwise knowingly disturbed. For example, a study on Alpine ibex *Capra ibex* has found reduced activity for two days as a response to capture (Brivio et al. 2015), whereas moose *Alces alces* in northern Sweden showed increased movement for up to five days post-capture and a decreased probability of resting (Neumann et al. 2011, Græsli et al. 2023).

Evaluating the effects of capture and tagging on specific types of behaviour has received limited attention in wildlife but has been explored in white sharks *Carcharodon carcharias*, for example (Grainger et al. 2022). The main focus has traditionally been on the use of movement rates, and several studies have demonstrated modifications in movement patterns in bears. Brown bears *Ursus arctos* in Sweden, for example, reduced movement after being approached by a helicopter (Støen et al. 2010). Reduced movement could also be observed as a response to capture in grizzly bears *Ursus arctos horribilis* and black bears *U. a. americanus*, when the effect lasted for 3–6 weeks (Cattet et al. 2008). The capture of subadult brown bears during hibernation had long-lasting effects on the bears' physiological parameters as well as behaviour, as capture increased heart rates and body temperatures towards non-hibernating levels for 3 weeks and reduced movement rates for several months after den exit (Evans et al. 2016b, Thiel et al. 2023). Thiel et al. (2023) reported that bears have been shown to reduce their movement for up to 14 days in response to capture by darting from a helicopter and invasive muscle biopsy in summer. Darting from a helicopter is the preferred capture method for brown bears in Scandinavia during their active season (Arnemo and Evans 2017, Kreeger et al. 2023), and the majority of bears are captured during spring, shortly after den exit (Arnemo and Evans 2017). Shooting distance during a helicopter capture is ideally < 10 m, requiring bears to be chased into an open area in the landscape for the final pursuit (Arnemo and Evans 2017). Therefore, the characteristics of this capture method imply that it induces fear, a physiological stressor which initiates fleeing behaviours, a form of physical stress (Arnemo and Evans 2017, Kreeger et al. 2023). Both types of stressors can cause short-term effects, such as increased heart rate, resting, shifting activity patterns and increasing concealment (Kreeger et al. 2023). During spring, brown bears undergo a physiological and behavioural transition phase from hibernating to active (Evans et al. 2016a), which is characterized by a gradual increase in activity and in both diel and ultradian rhythms (Evans et al. 2016a, Thiel et al. 2022). Disturbance during this transition period may have pronounced impact on the bears' behaviour due to their depleted energy reserves post-hibernation (López-Alfaro et al. 2013). Behavioural observations of grizzly bears in Yukon, Canada, have shown that bears spend an average of 34.1% displaying inactive/resting behaviour in spring and the rest of the time feeding and foraging (MacHutchon 2001). However, we currently lack understanding about the extent to which capture and darting from a helicopter affects adult brown bear behaviour in Scandinavia during this critical transition period in spring.

In this study we evaluated to what extent and for how long the behaviour of Scandinavian brown bears is affected by capture from a helicopter and sedation via darting. We compared bears that were captured in spring to bears of a control group, which had previously been equipped with GPS collars but were not captured during the same time period. Our first objective was to evaluate for how long the bears were affected in their normal behaviour, and we hypothesised that:

1. captured bears initially show altered behaviour and biological rhythms compared to bears of the control group but that captured bears return to normal behaviour and rhythmicity within 10 days post-capture. We predicted that
    1.1. captured bears would have a higher probability of expressing stationary behaviour as well as
    1.2. that the expression of different behavioural states will be more arrhythmic post-capture. Our second objective was to evaluate which capture-related variables impact the bears' recovery rate, and predicted that
2. the time it takes bears to displace 1000 m from the recovery site will be impacted by the
    2.1. immobilizing and
    2.2. top-up drug doses they received; if they had
    2.3. abdominal surgery or a
    2.4. tooth extraction performed on them; and the
    2.5. duration of the chase pre-capture as well as the
    2.6. time they were immobilized; and
    2.7. how many times they had been captured previously.

Material and methods

We included a total of 107 brown bears (68 females, 39 males, 4–24 years of age, in 234 individual bear-years) from the Scandinavian Brown Bear Research Project (SBBRP) (Table 1) population in south–central Sweden (61°N, 15°E, Fig. 1), an area which is dominated by coniferous forest (Moe et al. 2007) and low human density with 2.6–15.8 inhabitants km^{-2} (Statistics Sweden 2024). The mean ambient temperatures from April to July in the study area range from 4.0 to 15.4°C (Thiel et al. 2022).

Captured bears

The bears were captured (Table 1) in April and May 2003–2022 by immobilizing them by darting from a helicopter according to established protocols (Arnemo et al. 2007, 2011, Arnemo and Evans 2017). Total time of pursuit, including time of initial observation and alternating intensive and extensive pursuit, was kept < 30 min and the capture effort was aborted if pursuit > 30 min (Arnemo and Evans 2017). Once the bear was anaesthetized, it was either transported to a designated marking location within its home range via helicopter or was processed at the location where the anaesthesia took effect. Blood was sampled from the jugular vein, and hair and faecal samples as well as morphological measurements and body mass were taken from each bear. Some individuals were sampled for urine and milk. Offspring of marked adult females were followed from birth and captured as yearlings (at ~16 months of age); for bears of unknown age, one premolar was extracted to determine the age based on the annuli of a cross-section of its root (Harshyne et al. 1998). All bears were fitted with a GPS collar (Vectronic Aerospace GmbH, Berlin), which was programmed to record GPS positions every 60 min and dual-axis acceleration sensors to monitor

Table 1. Overview of sample sizes of individual bear years and the mean (minimum–maximum) age [years] of the bears per status and experimental group as well as the number of individual bears.

Status	Experimental group	Bear years	Age	Individual bears
Female with cubs of the year	Control group	64	11 (5–23)	38
Female with cubs of the year	Capture	19	8 (4–19)	18
Female with yearlings	Capture	32	13 (5–24)	23
Solitary female	Control group	6	9 (5–16)	6
Solitary female	Capture	33	6 (5–14)	25
Solitary male	Control group	4	6 (5–9)	3
Solitary male	Capture	76	9 (5–21)	39

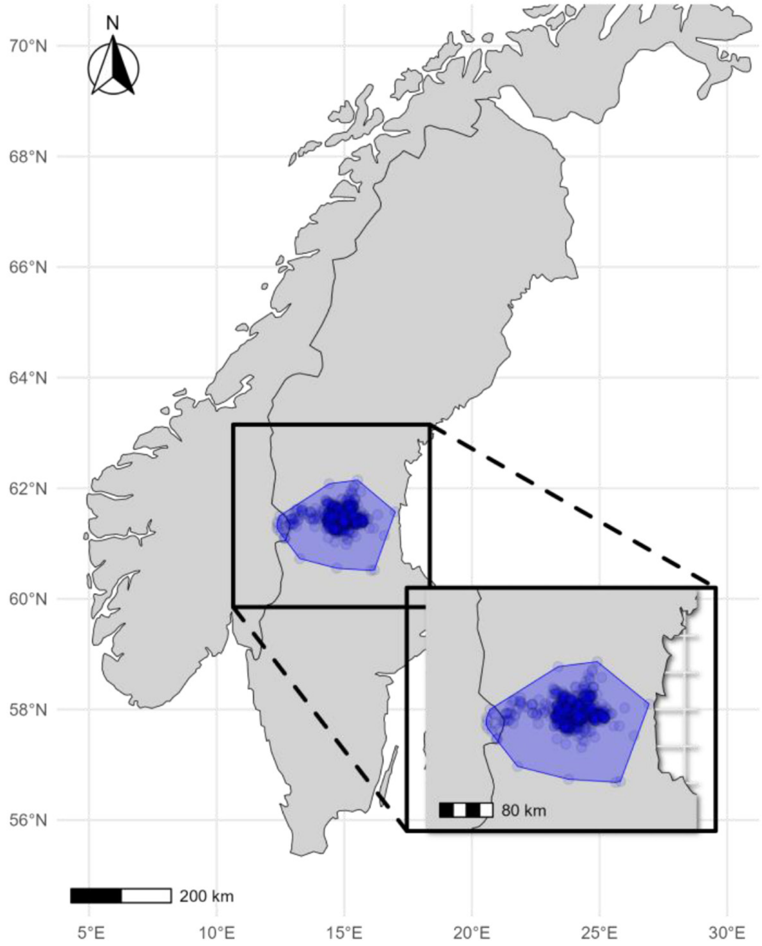

Figure 1. Capture locations of the captured individuals used in this study as blue dots and blue polygon around the capture locations to indicate the study area.

activity levels every 5 min (Supporting information). Some bears (53 out of 107 bears, i.e. 76 out of 234 individual bear years (38 male, 38 female bear years, age range 4–24 years)) underwent abdominal surgery to have a VHF transmitter (Telonics Inc, Mesa, AZ, USA, serial number IMP-400-2, 95 g or ATS Inc, Isanti, MN, USA, serial number M1250B, 100 g) and/or an abdominally implanted temperature logger (DST Centi, 15 × 46 mm, 19 g, Star-Oddi, Garðabær, Iceland) inserted or removed. After all sampling and surgical procedures were finished, the bear was either left in the shade in a remote area in the forest close to the marking location, or transported by helicopter back to the location where it was captured, or to a different location within its home range. Additional Ketmaine was given to ensure appropriate sedation throughout the transportation. Atipamezole (Antisedan®, Orion Pharma Animal Health) was administered to antagonize the effects of medetomidine. Female bears that were accompanied by dependent offspring, i.e. cubs of the year (without the capture of the offspring) were placed back on the tracks of their offspring to facilitate quick reunion of the family group. Details of capture-related variables can be found in Table 2–3. All captures and surgeries were approved by the Swedish Board of Agriculture and Ethical Committee on Animal research, Norwegian Food Safety Authority, as well as the Swedish and Norwegian environmental protection agencies. A list of all permits can be found in the Supporting information.

Drug and capture-protocol related information

All bears were darted from a helicopter with a remote drug delivery system (Dan Inject®) with a combination of medetomidine (Domitor®, Orion Pharma Animal Health, Espoo, Finland) and tiletamine-zolazepam (Zoletil®, Virbac, Carros, France [ZT]). Ketamine (1–2 mg kg^{-1}) was administered, if necessary, in the case of a prolonged procedure or signs of spontaneous recovery (Arnemo and Evans 2017). All bears were administered supplemental oxygen; ears and eyes were covered with a blindfold; and eye gel was administered to the cornea to avoid drying (Arnemo and Evans 2017). In the case of a tooth extraction, a local anaesthetic (Bupvicaine (Marcain®, Aspen Nordic, Ireland)) was administered. Prior to surgery, meloxicam (Metacam®, Boehringer Ingelheim Vetmedica GmBH, Germany) was administered (0.2–0.4 mg kg^{-1}) subcutaneously as analgesic. Details on surgical procedures can be found in Arnemo and Evans (2017). All VHF implants and temperature loggers were sterilized with ethylene oxide gas (Anaprolene AN74i 80 L, Andersen Europe, Kortrijk, Belgium) prior to implantation. Only the doses of ZT and Ketamine were included as relevant drug-related capture information. ZT is used as the primary immobiliant but is irreversible and long-lasting. Medetomidine was added to the dart at a fixed ratio with ZT, making the dose of Medetomidine inherently correlated to the dose of ZT. Ketamine was used as a top-off; this is irreversible, but has a short half-life (Plumb 2018), whereas medetomidine potentiates the effects of ZT and is a reversible sedative (Shury 2007).

Control group

According to the SBBRP's policy, bears are not routinely captured annually, provided that the GPS collar is functioning and that its battery is likely to continue to function until the subsequent year. In the case of malfunctioning of the GPS collar, the VHF receiver on the collar or the implanted VHF transmitter can be used to locate the bear so the collar can be changed. Bears that were previously captured – but not during April or May – the following year (did not encounter any direct capture disturbance, 47 individuals) were used as the control group in this study to illustrate the bears' normal, undisturbed behaviour patterns in spring. For these bears we simulated dummy capture dates and times, following approximately the same distribution of the capture dates and times of the bears that were actually captured in April and May, to account for the bears' seasonality in behaviour and physiology (Evans et al. 2016a, Supporting information).

Bear status group

The brown bears' behaviour and physiology is highly impacted by their age and life history stage (Bogdanović et al. 2021), which is why we separated bears into different status groups:

1) adult female bears with cubs of the year (i.e. females accompanied by cubs that were born in winter the same year);
2) adult female bears with yearlings (i.e. females accompanied by cubs that were born in the winter the previous year);
3) adult solitary females (i.e. females, not accompanied by offspring and ≥ 5 years of age); and
4) adult solitary males (i.e. males ≥ 5 years of age).

An overview of the number of individuals and detailed information on the individuals can be found in Table 1.

The reproductive status was assessed via aerial monitoring from a helicopter or airplane and based on activity or body temperature profiles (Friebe et al. 2014, Lemière et al. 2022). In family groups, we only tested the effect of capture on the adult female, as the behaviour of her cubs post-capture is correlated with their mother's (Gardner et al. 2014). Female bears with yearlings were usually captured in spring because the project's monitoring objective was to follow females and their offspring (Table 1) and was therefore lacking a control group.

Table 2. Overview of capture information on bears included in the models to predict displacement time with mean (minimum–maximum). Discrepancies in sample size to the capture versus control group levels arise due to exclusion of individuals with unknown body mass. Top-up Ketamine was administered in 27 out of 92 captures (30%).

Status	Capture day	Chase duration	ZT (mg/kg)	Time immobilised (min)	Ketamine (mg/kg)	No. of previous captures	No surgery	Surgery	No tooth extraction	Tooth extraction
Female with cubs of the year	125 (102–142)	6 (3–12)	4.06 (2.72–6.25)	59.4 (20–127)	0.58 (0–2.33)	4.75 (3–8)	6	4	10	0
Female with yearlings	121 (104–142)	10 (2–27)	3.79 (1.76–8.33)	101.93 (19–170)	1.07 (0–5.71)	7.12 (3–15)	16	11	26	1
Solitary female	116 (99–143)	6 (3–18)	4.13 (2.55–9.04)	82.64 (9–125)	1.02 (0–6.18)	4.81 (1–8)	11	17	27	1
Solitary male	111 (98–150)	10 (1–29)	4.79 (1.64–8.58)	106.48 (37–176)	0.99 (0–7.6)	4.54 (1–12)	23	31	44	10

Table 3.Explanation of variables included in the analysis to predict 1000 m displacement time from the recovery site. All continuous variables were included as a non-linear effect.

Predictor	Explanation
Hour	Numeric. Time/Hour of day (0–23).
Helicopter chase duration	Numeric. Time difference [in minutes] between first visual observation of the bear (or start of the chase, depending on helicopter protocol completeness/time stamp availability) until it lay down (i.e. sedation started to take effect)
ZT	Numeric. Dose of the irreversible immobilizing drug (tiletamine-zolazepam) in the dart(s) received by the bear [mg kg^{-1}]. If it received several darts, the total of all darts was used as the total dose
Time immobilized	Numeric. Time difference [in minutes] from the time of darting (first successful hit) and antagonist administration
Surgery	Factor Yes/No. Was abdominal surgery undertaken for VHF transmitter implantation and/or body temperature logger inserted/removed?
Tooth extraction	Factor Yes/No. Was premolar extracted for age determination during the capture?
Ketamine	Numeric. Total dose of supplementary Ketamine it received during anaesthesia [mg kg^{-1}].
Number of previous captures	Numeric. Capture history: 1 = first capture of a specific bear, 2 = second capture, etc.

Data analysis

Detailed information on the data preparation can be found in the Supporting information. A conceptual graphical illustration of the workflow and analytical approach used to quantify the effects of capture on movement behaviour in Scandinavian brown bears can be found in Fig. 2.

Latent behavioural state estimation

We used a non-parametric Bayesian mixture model for movement from the ‘bayesmove’ package ver. 0.2.1 (Cullen et al. 2022, Valle et al. 2022) to estimate latent behavioural states based on *step length* (distance [m] moved within 1 h), *turning angle* and *activity* (Supporting information). The model requires the variables to be discretized into bins, with the selection of the number of bins representing the continuous distribution of the variable by using as few bins as necessary (Cullen et al. 2022). The discretization process was done separately for all status groups, due to their behavioural differences, which are reflected into movement (Bogdanović et al. 2021). Detailed information on the discretization process can be found in the Supporting information. These three discretized variables were analysed using the M3 method of the package ‘bayesmove’ ver. 0.2.1 (Cullen et al. 2022, Valle et al. 2022), in which observations are clustered into an unknown number of discrete latent behavioural states. By specifying the maximum number of possible behavioural states and using a penalizing Bayesian prior, the model estimates the most likely number of states and assigns these states to the observations (Cullen et al. 2022, Valle et al. 2022). We ran a model for each status group and used 20 000 Markov chain Monte Carlo (MCMC) iterations with 1/3 of the total MCMC iterations as a warm-up. Previous research on different bear species has distinguished three distinct behavioural states (encamped/resting, foraging, longer/directed movement) based on movement data by using hidden Markov models (HMMs) (Karelus et al. 2019, Zeller et al. 2019, Togunov et al. 2022, Mumford et al. 2024), which is why we set the maximum number of possible states to three. Observations were labelled as ‘unclassified’ if < 75% of all posterior estimates belonged to a single state and this state was not included in futher analyses (Cullen et al. 2023). This was done to ensure high certainty of the behavioural state assignments. The hyperparameter α was set to 0.1 and we evaluated model convergence by evaluating the log likelihood trace plots.

Statistical analysis on the effects of capture

Capture versus control group

Behavioural states

We used GAMs in a Bayesian framework with the R package ‘brms’ (Bürkner 2017) to assess whether captured and control group bears differed in their probability to express a specific behaviour in the 10 days following the capture/dummy capture event. We modelled the behavioural states that were defined for each GPS relocation of solitary males, solitary females and females with cubs of the year with a categorical family (i.e. multinomial response) and a logit link function over the time after capture (Time since antidote, TsA, in hours), ultimately resulting in probabilities that a specific behaviour is expressed over time. We included the time after capture with an interaction for capture category (captured versus control group) and included the time of day (i.e. hour of the day) to account for daily activity patterns (Ordiz et al. 2014, Bogdanović et al. 2021, Thiel et al. 2022). We also accounted for the day of the year of capture to account for seasonal variation in behaviour (Ordiz et al. 2014, Evans et al. 2016a, Bogdanović et al. 2021, Thiel et al. 2023). We included the individual bear ID and year as group-level effects, used three MCMC chains and a total of 5000 MCMC iterations, of which 2000 were used as a warmup and set the thinning parameter to 10. We used weakly informative priors of normal(0, 3) for all coefficients and default priors for all other model parameters. Model convergence and stability were checked visually as well as by evaluating that Rhat values did not exceed 1.01 (Vehtari et al. 2017). We defined significant differences between captured and control group bears when the 95% credible intervals of one group were not overlapping with the median of the posterior distribution of the other group.

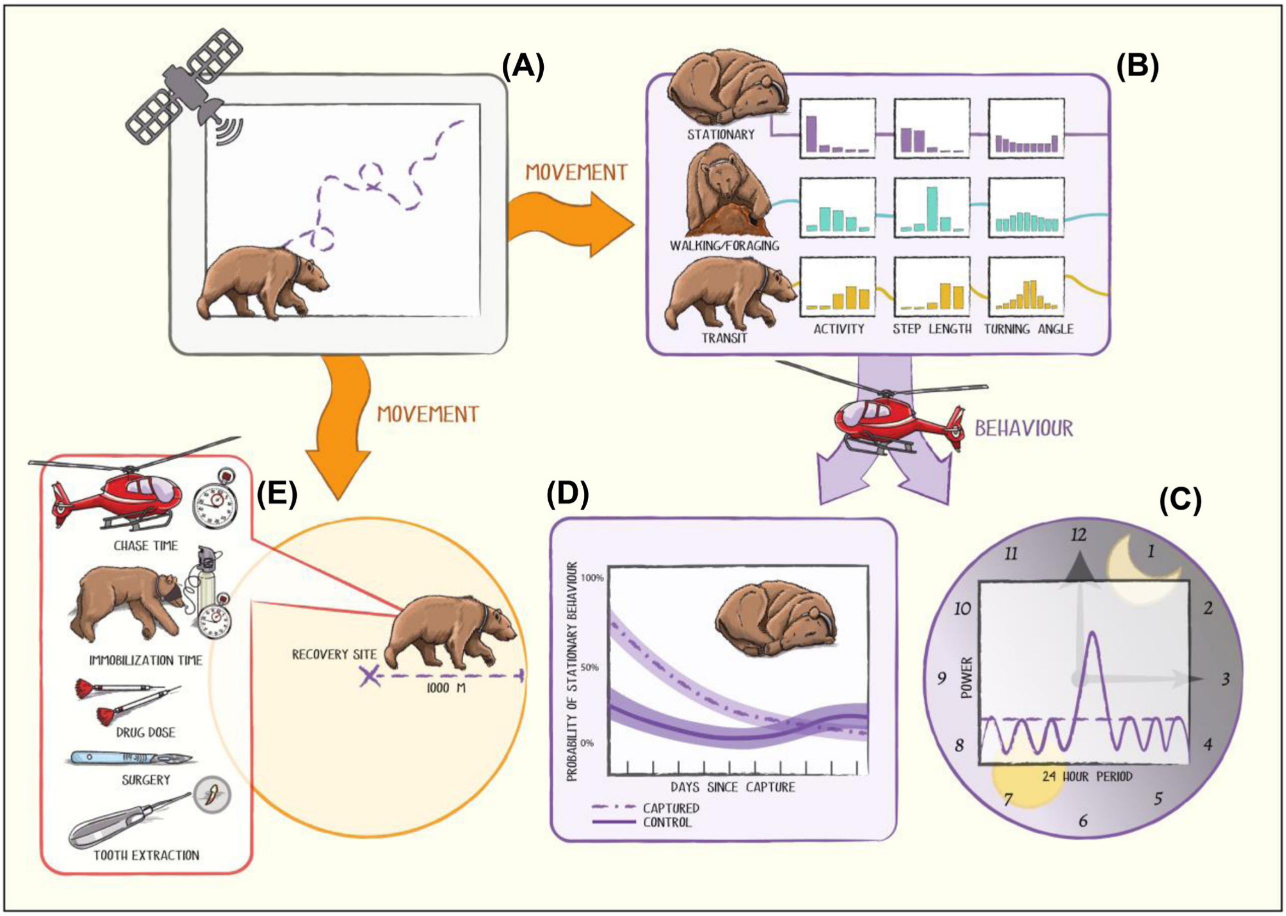

Figure 2. Graphical illustration of the workflow of the analytical approach and statistical methods used. Movement data (A) were collected from GPS-collared free-ranging brown bears, scheduled to take GPS positions with a 1-h positioning interval and activity data every 5 min. The GPS-collar derived metrics activity, step length and turning angle were used for a non-parametric bayesian mixture model to classify three different types of behaviours (stationary, walking/foraging and transit). We then used these behaviours and Bayesian generalized additive mixed models (GAMs) to evaluate the effects of helicopter capture on the (C) rhythmicity of these behaviours and (D) probability that a behaviour is shown 10 days after capture by comparing captured bears to a control group. Finally, we used Bayesian GAMs to (E) quantify which capture-related variables impact the time it takes captured bears to move 1000 m away from the recovery site after the reversal drug was administered. Graphical illustration: Juliana Spahr of SciVisual.com.

Rhythmicity in behavioural state occupancy

Capture-related stress has been proposed to impact circadian organization in wildlife through the influence of stress on the HPA axis and its impact on the circadian clock (Brogi et al. 2019). To test if and for how long biological rhythms were influenced by a capture event we used Lomb–Scargle periodogram (LSP) analysis from the R package 'lomb' (Ruf 1999) to test for periodicity in the expression of behavioural states derived from non-parametric Bayesian mixture models depending on the bear status group and capture category. To reliably detect biological rhythms it is recommended to perform analysis on at least ten periods (in our case days) (Sokolove and Bushell 1978). To account for this, we set up a moving window of 10 days (van Beest et al. 2020), starting on the day of capture for each individual capture event (i.e. the first time window consists of the first 10 days after capture, the second window consists of days 1–11 after capture and so forth); analysed each time window individually; and searched for periodicities within each time window. We selected the highest peak detected by the LSP algorithm and characterized rhythms based on Thiel et al. (2022) and van Beest et al. (2020). We differentiated between ultradian (2–18 h) and diel (18–36 h) rhythms and included non-significant peaks as arrhythmic and created a categorical variable with these three factors (ultradian, diel, arrhythmic), which acted as the multilevel response variable for the subsequent analysis.

To test the probability that a bear showed an ultradian or diel rhythm or arrhythmicity in the days following a capture/dummy capture event, we set up multinomial logistic regressions, following the same approach as in the analysis for capture versus control group. This accounted for the day of the year of capture/dummy capture and included the individual bear ID and year as group level effects.

Impact of capture-related factors

We also investigated which capture-related factors influence the time it takes captured bears to displace 1000 m from the recovery site. Choice of the 1000 m threshold was based on a previous study of bears in the same study population. In that study the bears, when approached by humans on foot, moved on average 1173 m from the encounter site before settling again in densely vegetated habitat (Moen et al. 2012). We assumed that the previously experienced capture will be perceived as a disturbance and that the bears will respond to this disturbance by moving away from the recovery site, for example to find a different recovery site of their own choosing or to return to their natural behaviour. We used the time the bears reached 1000 m as a temporal indicator for their physical ability to walk a comparable distance, as they would have as a response to a different type of disturbance. We calculated the displacement (straight line distance) from the recovery site to each GPS position following the antidote administration. We then used the time corresponding to the first displacement value $\geq$ 1000 m as response variable. All numeric predictor variables were checked for correlations.

We set up a list of candidate models including the variables helicopter chase and immobilization duration, the dose of immobilizing drug (ZT) the bear received, the dose of Ketamine as top-up to prolong anaesthesia (27 out of 92 captures), the number of previous captures and if the bear had an abdominal surgery or a tooth extracted, in addition to the hour of day and bear status. Detailed definitions of the investigated capture-related factors can be found in Table 2–3. All continuous variables were included as a thin-plate regression spline with shrinkage.

We used the R package 'brms' (Bürkner 2017) and set up all models with a gamma family distribution and the log link function, a total of 5000 MCMC iterations with a warm-up of 1000 iterations over three MCMC chains and a thinning of 10, resulting in 1200 final posterior samples. All models included the individual bear ID and year as group level effects. Model diagnostics were checked as described above. We compared all models with leave-one-out (LOO) cross-validation to select the most accurate model (Vehtari et al. 2017). In case the theoretical expected log pointwise predictive density (elpd) < 4, we used stacking of predicted distributions to evaluate which of these models had the highest probability to be the most accurate (Yao et al. 2018).

Results

Latent behavioural state estimation

We identified three behavioural states based on step length, turning angle and activity, representing 'stationary' (low activity values, short step lengths and high turning angles (near $-\pi$ and π), purple, Fig. 3), 'walking/foraging' (medium activity and step lengths but a more uniform distribution of turning angles, turqouise, Fig. 3) and 'transit' (high activity and step lengths and lower turning angles, close to 0 π, yellow, Fig. 3). Depending on reproductive class, 13–18% of the data could not be classified (Supporting information).

Capture versus control group

Behavioural states

Captured solitary females and males were more stationary compared to bears of the control group for the first 36 h (1.5 days) and 94 h (3.9 days) after a capture/dummy capture event, respectively (Fig. 4A–B, Supporting information). One hour after antidote administration, captured solitary females and males had a 67 and 73% probability to be stationary. In contrast, females and males of the control group had a 40 and 30% probability to be stationary. Walking/foraging behaviour differed by 8 and 20% between captured and control group bears at 24 h after antidote administration, for solitary females and males, respectively (Fig. 4A–B). The probability of transit behaviour was only significantly different for solitary males. Captured females accompanied by cubs of the year did not differ in the expression of their behaviour from control group bears (Fig. 4C, Supporting information). The probability of stationary behaviour in general decreased with the day of the year of capture, while the probability of walking/foraging and transit behaviour increased for all reproductive classes (Supporting information). Bears were most stationary in the middle of the day and at midnight, with distinct activity peaks around crepuscular hours (Supporting information).

Rhythmicity in biological rhythms

Bears expressed diel, ultradian and arrhythmic behavioural rhythms for 22 ten-day-periods after capture in all status groups (Fig. 5, Supporting information) for all behaviours. All status groups showed a generally high probability to express diel rhythms (~24 h rhythmicity) in stationary behaviour with an increasing trend for females with cubs of the year (Fig. 5C). Ultradian rhythms (< 18 h rhythmicity) in stationary behaviour generally increased over the 22 ten-day-periods and arrhythmicity decreased, except for solitary females of the control group, which showed an increasing probability in arrhythmic stationary behaviour (Fig. 5A). Captured and control group bears followed similar trends over the 22 ten-day-periods in all three rhythms with little variation between the experimental groups (Fig. 5). Solitary females that expressed walking/foraging behaviour had the highest probability of being arrhythmic, whereas solitary males and females with cubs of the year expressed arrhythmic and diel probabilities to similar extents (Supporting information). For transit behaviour, females with cubs of the year had highest probabilities for arrhythmic behaviour, followed by solitary males and females (Supporting information). The experimental groups did not differ substantially from each other over time in any of the behaviours.

Impact of capture-related factors

We calculated 92 displacement episodes for 62 bears and used these to determine which capture-related factors influence the length of time a bear needed to leave the recovery site after a capture event. The ZT dose and abdominal surgery increased the 1000 m displacement time while the other predictors were not among the most accurate model (Supporting

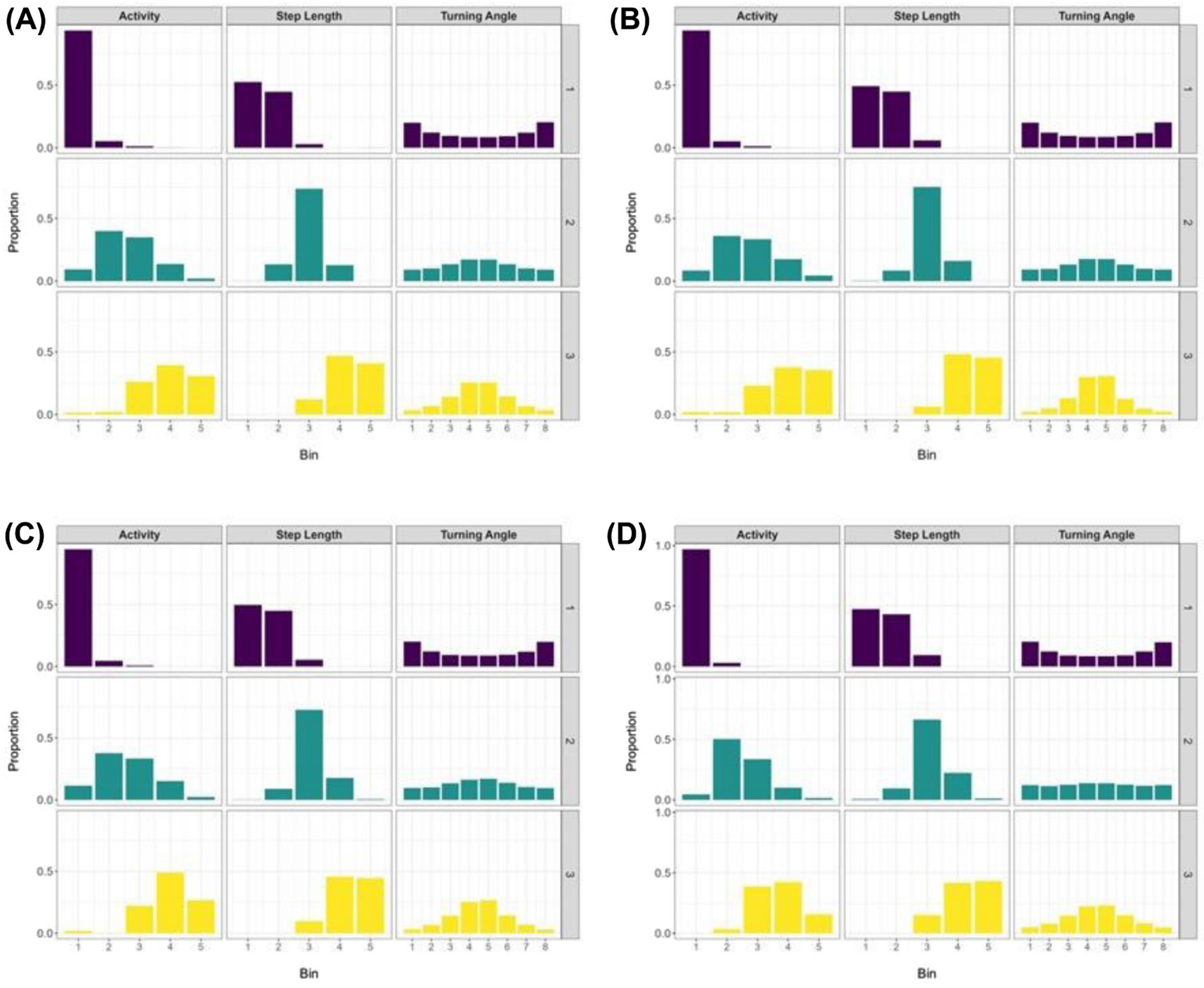

Figure 3. Discretized distributions for each behavioural state for (A) solitary females, (B) solitary males, (C) females with yearlings and (D) females with cubs of the year. State 1 representing stationary behaviour (purple), state 2 representing walking/foraging behaviour (turquoise) and state 3 representing directed, long-distance movement (transit, yellow).

information). The most accurate model predicted that an increase of one unit (mg kg^{-1}) ZT delayed the displacement time by 10.12%, i.e. 2.31 h (Fig. 6C, Supporting information). As an example, a solitary female that received 3 mg kg^{-1} ZT had moved 1000 m away from the capture site on average after 22.83 h (CI: 8.96–50.63 h), whereas a solitary female that received 7 mg kg^{-1} ZT reached that 1000 m threshold after 31.03 h (CI: 11.11–77.62 h). Abdominal surgery increased that time by an additional 32.53%, i.e. 6.6 h (Fig. 6B). Notably, the individual with the longest time until the 1000 m displacement threshold was reached (126.6 h, see Fig. 6C) was a solitary male, which was administered 4.6 mg kg^{-1} ZT and underwent surgery.

Discussion

Ensuring the welfare of captured animals in ecological research is paramount and stands in delicate balance with gaining insights into aspects such as species' biology, population dynamics, ecosystem health and ecophysiology. In this study we evaluated for how long brown bears in Scandinavia were behaviourally affected by helicopter capture and surgery in spring, and quantified the magnitude of the effect.

Latent behavioural state classification

We determined three latent behavioural states with the non-parametric Bayesian mixture model for movement (Valle et al. 2022), in line with previous literature on other bear species using hidden Markov models (Karelus et al. 2019, Zeller et al. 2019, Togunov et al. 2022, Mumford et al. 2024). Based on the characteristics of the movement parameters, the states can be interpreted as stationary (short step lengths, wide turning angles and low activity), walking/foraging (medium step lengths and activity levels and narrower turning angles) and transit behaviour (long step lengths, higher activity values and directed movement) (Zeller et al. 2019). Bears in our study showed a high percentage of stationary

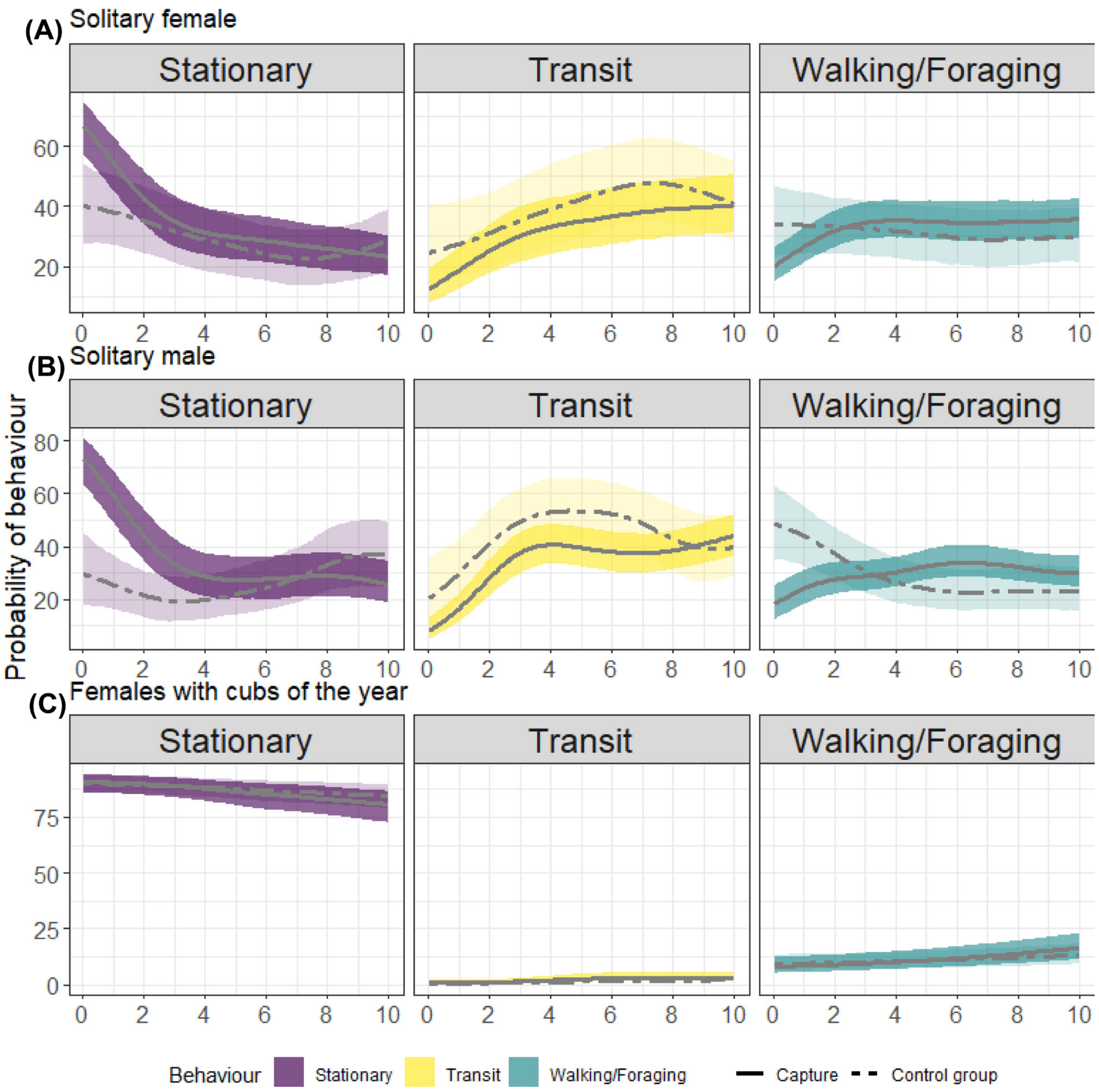

Figure 4. Predictions of the probability of behavioural state occupancies for solitary females (A), solitary males (B) and females with cubs of the year (C) for the 10 days after capture/dummy capture event. Predictions are standardised for day of the year 120 (average day of capture in the Scandinavian Brown Bear Research Project, SBBRP) and hour of the day 18 and show the median of the posterior distribution of the three behavioural states stationary (purple), walking/foraging (turqouise) and transit (yellow) with 95% credible intervals. Captured bears are shown with a solid line and bears of the control group with a dashed line.

behaviour, which was highest early in the year (shortly after den emergence), in line with low activity levels and high proportions of resting behaviour post-den emergence seen in grizzly bears *Ursus arctos horribilis* (McLellan and McLellan 2015, Mumford et al. 2024). The percentage of stationary behaviour, however, decreased towards late spring/summer, while transit behaviour increased (Supporting information), suggesting a dynamic adjustment period from hibernation state into active state (Evans et al. 2016a, Thiel et al. 2023). Bears may be particularly vulnerable to disturbances during this period owing to reduced or depleted energy reserves after hibernation (López-Alfaro et al. 2013).

Dynamic control group

Given that these captures are predominantly conducted in spring, shortly after den emergence, this dynamic adjustment period underlines the importance of incorporating a control group to evaluate potential effects of capture on brown bear behaviour. When evaluating how long it takes until bears return to baseline behaviour after being captured in spring,

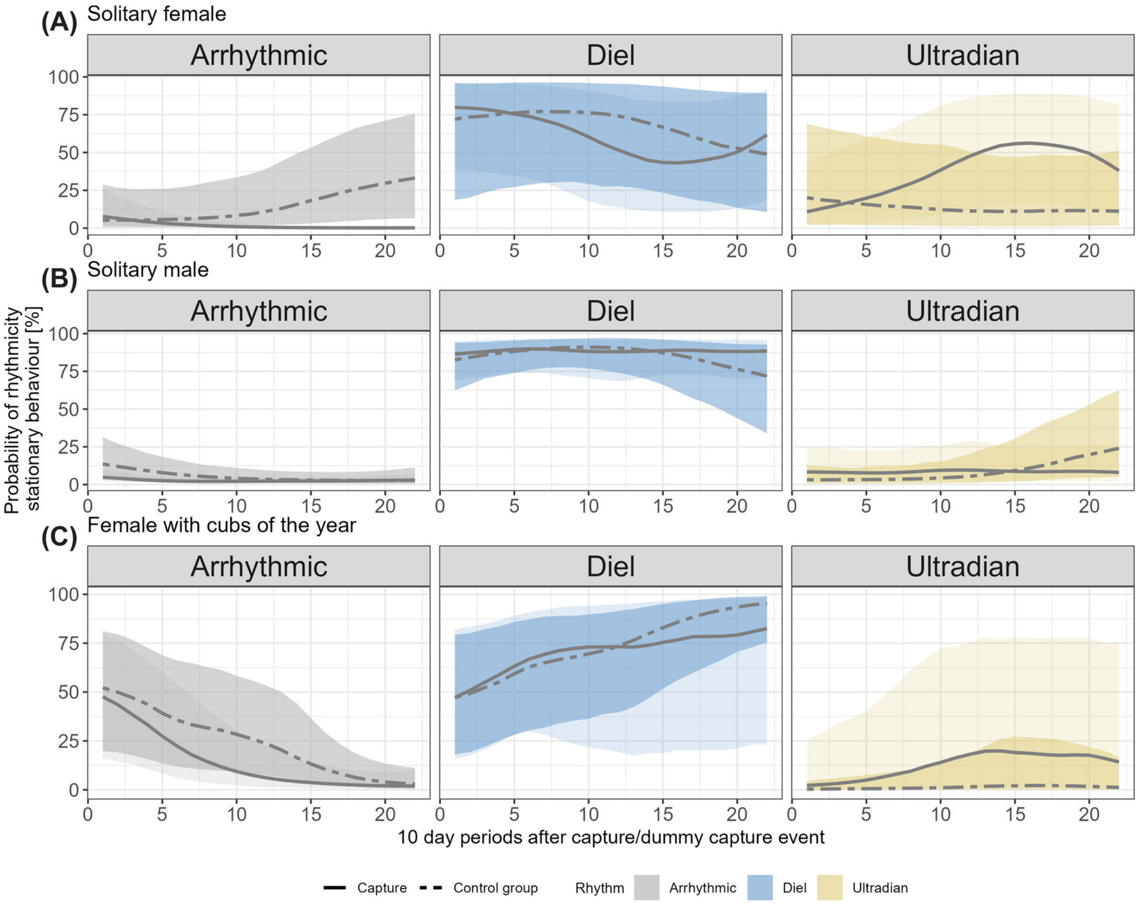

Figure 5. Predictions of the probability of rhythms of stationary behaviour of solitary females (A), solitary males (B) and females with cubs of the year (C) for the first 22 ten-day periods post capture/dummy capture event. Rhythms are expressed as the median of the posterior distribution of arrhythmic (grey), ultradian (yellow) and diel (blue) rhythms and 95% credible intervals. Captured bears are shown with a solid line and bears of the control group with a dashed line.

we cannot expect a stable plateau as baseline (as shown in wild boars *Sus scrofa* Brogi et al. 2019). Rather, we would expect a dynamic fluctuation of the three movement behaviours, reflecting changes in metabolism, activity rate and resource availability and distribution at this time of year (McLellan and McLellan 2015, Evans et al. 2016a, Ordiz et al. 2017). We want to mention the possibility of behaviour misclassifications of captured bears during the first hours of recovery due to the dissociated recovery from ZT. Bears and other wildlife are disorientated when recovering from ZT, resulting in uncoordinated head and body movement (ataxia) (Hampton et al. 2019, Kucharski and Kiełbowicz 2021). This can translate into slow and more undirected movement, a movement signature similar to walking/foraging.

Capture versus control group

Behavioural states

We compared the probability of behaviours during the 10 days following a capture/dummy capture event in solitary females, males and females with cubs of the year. All status groups show the highest probability of stationary behaviour earlier in the year/shortly after den emergence, and show decreasing trends in this behaviour as the year continues, while the probabilities of walking/foraging and transit behaviour increase (Supporting information). Our first prediction, that bears show a higher probability of stationary behaviour, was supported. Captured solitary bears show a higher probability of stationary behaviour 1 h after capture compared to bears of the control group, and reach control group levels in stationary behaviour 1.5–3.9 days after capture. These results suggest that captured bears increase resting periods as a response to capture. During this recovery period, bears are impacted in their natural behaviour, such as the balance between resting and foraging. Consequently, captured bears rest more at the expense of other behaviours, which can affect resource acquisition and ultimately energy reserves. Captured females with cubs of the year did not, however, differ from bears of the control group. The high percentage and arrhythmicity in stationary behaviour in females with cubs of the year in general, especially after den emergence, may make it difficult to detect changes and/or differences between captured and control group bears. The behaviour of mothers

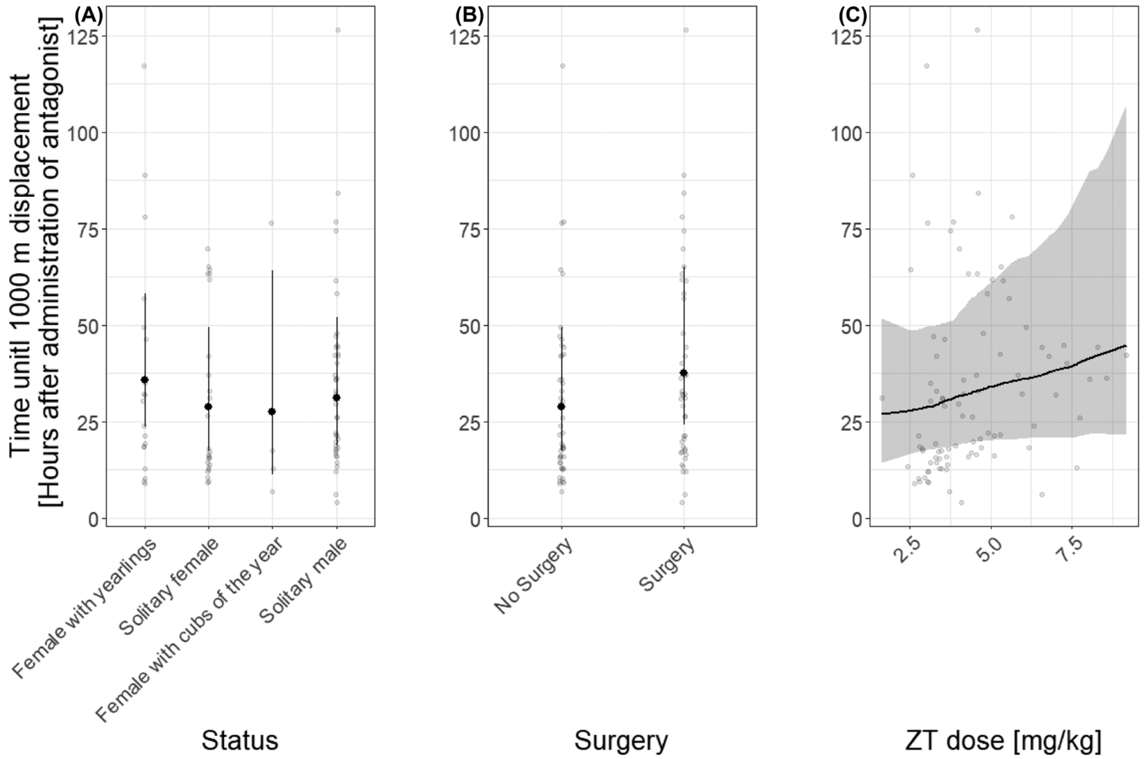

Figure 6. Predictions of the 1000 m displacement time from the capture site in relation to the status of the bear (A), abdominal surgery (B) and the dose of tiletamine-zolazepam (ZT/kg [mg]) (C) administered to the bear during the capture event. Predictions are presented as the median posterior distribution and the 95% credible intervals. Raw data are presented as hollow circles.

with cubs of the year is influenced by her offsprings' needs and mobility, i.e. the frequency of maternal nursing and the cubs' capability to move around in the landscape (Greenwald and Dabek 2003, Gartland et al. 2023), as well as the avoidance of infanticide by males during the mating season (Dahle and Swenson 2003, Gardner et al. 2014). Thus, the effects of capture might not be easily distinguishable from the natural behaviour of mothers with cubs of the year of the control group.

In line with a previous study on a subsample of bears of the same study population (Pi Serra 2020), we found recovery periods of 1.5–3.9 days. Studies on polar bears *Ursus maritimus* reported similar recovery rates, with 69 and 90% of bears reaching normal movement patterns after 3 and 5 days, respectively (Thiemann et al. 2013, Rode et al. 2014). Thiel et al. (2023), however, reported a recovery period of 14 days for subadult bears of the same study population of the SBBRP, captured at peak activity in summer and Cattet et al. (2008) found a recovery time of 3–6 weeks in black bears *Ursus americanus* and grizzly bears *Ursus arctos horribilis*. The use of different methodologies (behavioural states versus movement rates and the lack of a control group) and differences in age groups involved in the studies, as well as capture and sampling techniques and time of the year of capture (i.e. differences in baseline activity level) may be reasons for these discrepancies. A recent meta-analysis of 42 terrestrial mammal species found faster recoveries for species that inhibited areas with a high human footprint and associated this to adaptation to human disturbance (Stiegler et al. 2024). Human footprint in our study is low (Statistics Sweden 2024) but recovery rates of up to 6 days for omnivores and carnivores in the study by Stiegler et al. (2024) is in line with recovery rates of brown bears in our study. The results of our study suggest excluding a period of 1.5–3.9 days from data analysis on Scandinavian brown bears if fine-scaled movement in spring is the focus of the study question. This is, however, depending on reproductive state but can help to avoid any bias arising from capture effects. Even though the potential effect of capture may vary in magnitude and depend on species and capture method, it should be taken into consideration by any research project drawing conclusions from captured individuals.

Rhythmicity in behavioural states

Brown bears in our study exhibited a high flexibility in behavioural rhythms, expressed in the presence of diel and ultradian rhythms as well as arrhythmic behaviour. This is in line with the findings of Thiel et al. (2022), who investigated rhythmicity in activity in brown bears of the same study population during the transition phase from hibernation into active phase, but specifically excluded a period of two weeks after capture.

Contrary to Thiel et al. (2022), we found that solitary females and females accompanied by cubs of the year showed profound differences in the probability of expressing arrhythmic stationary behaviour. However, sample sizes and the metric investigated (behavioural states versus activity levels derived from collar accelerometer) differ between the studies. In this study, females with cubs of the year exhibited a higher probability of stationary behaviour compared to solitary females in the start of the 22 ten-day-periods. Despite this, both status groups followed a decreasing trend in the probability for arrhythmic stationary behaviour over time, a pattern observed for both captured and control group bears. Studies under laboratory conditions have found free-running activity rhythms of female rats who had free access to their pups for nursing, highlighting the arrhythmicity in nursing behaviours of females with dependent offspring (Caba and González-Mariscal 2009). Ware et al. (2020) reported higher proportions of arrythmic activity in free-ranging polar bears in spring and for denning females with cubs of the year, and related this lack of rhythmicity to a masking effect of feeding schedules and offspring activity. Polar bear cubs have been shown to spend 20% of the day nursing, and this behaviour increased with the age of the cub (Greenwald and Dabek 2003, Gartland et al. 2023). Black bears in North America have been reported to engage in 64 nursing sessions within a 24-h day period while still in the den (Rogers et al. 2020). Frequent but potentially arrhythmic nursing activities and limitation of movement by the cubs impacts the rhythmicity in the behaviour of females accompanied by dependent cubs. Dahle and Swenson (2003), however, postulated that it is not only the reduced mobility of the offspring that influences the movement pattern of the mother, but also the incentive of the mother to avoid encounters with adult males and therefore reduce the probability of infanticide. Female grizzly bears in Alaska that had lost their cubs have been found to use more habitat patches and stay in individual habitat patches for shorter time periods than female grizzly bears who are still accompanied by cubs (Gardner et al. 2014).

Effects of capture on rhythmicity in behavioural states

Rhythmicity of the analysed behaviours did not differ substantially between the experimental groups and therefore contradicts our prediction 1.2) that differences in arrhythmic behaviour would be a result of the capture event. A lack of changes in activity rhythms in response to capture was also observed in wild boar captured with ZT or ZT-xylazine (ZTX) (Brogi et al. 2019). Biological rhythms are highly entrained by external zeitgebers, such as photoperiod and other environmental conditions (Bradshaw and Holzapfel 2007, Thiel et al. 2022). Shortly after den exit, bears in Scandinavia experience not only an increase in day lengths but also the transition into the start of the mating season. Additionally, they express a highly flexible foraging strategy with a combination of predating on moose calves (Rauset et al. 2012) as well as foraging for insects and berries (Stenset et al. 2016) and utilizing bait and slaughter remains (Steyaert et al. 2014). A combination of these conditions might mask the effects of capture, such that captured bears might not exhibit changes in the rhythmicity or timing of certain behaviours, but instead reduce the intensity and type of behaviour they engage in, as seen in the results addressing the behavioural state probability.

Impact of capture-related variables

The 1000 m displacement time from the capture site was most influenced by the dose of ZT the bears received during the capture event and by abdominal surgery, which supports parts of our second prediction (2.1, 2.3). We found that an increase of 1 mg kg^{-1} ZT and abdominal surgery will delay the bears' 1000 m displacement by ~2.3 and ~6.6 h, respectively. These findings are in line with a study on grizzly and black bears (Radandt 2009) who found that bears immobilized with ZTX recovered faster (after ~5 days) than bears immobilized with only ZT (after ~8 days), and attributed this faster recovery to the lower dose of total ZT in the ZTX combination. Similarly, longer recovery times with increasing doses of ZT have also been found in wolves *Canis lupus* (Kreeger et al. 1990). Both studies involved a range of ZT doses overlapping with those in our study. This can be explained by the half-life of elimination rate constant of ZT. A study of polar bears darted with ZT from a helicopter found average half-lives of ZT ranging from 1.2 to 1.8 h (Semple et al. 2000). No relationship between ZT dose and recovery time could be found in a different study of polar bears (Thiemann et al. 2013), which, however, involved average ZT doses that were two to three times higher than those used in our study. ZT is considered a safe drug for brown bear immobilization with a wide safety margin, but long recoveries are a known side effect (Kreeger et al. 1990) and, even though brown bears may tolerate high doses, our study shows that a dose reduction can have positive effects on their recovery times. Occasional high doses in our study often resulted from the need to administer a second dart, either due to imperfect administration (fatty or subcutaneous tissue); underdosing after misjudgement of the body mass; or, and likely the most prevalent, increased individual stress levels and associated decreased response to the administered drugs. Additionally, the metabolic seasonality in brown bears requires higher doses at peak activity, while during hibernation doses can be reduced by 75% (Evans et al. 2012). During spring, the metabolism of bears is in an increasing phase with variation between individuals (Evans et al. 2016a) and consequently varying responses to anaesthetics.

In addition to the effect of ZT dose, surgery affects bears in a similar way by increasing the 1000 m displacement time significantly. This may be explained by the elevated post-operative pain and discomfort that the animals experience. The abdominal surgeries performed in our study had the purpose of inserting or removing a VHF implant or biologger and were also accompanied by the administration of analgesics. The duration of the effect of surgery, however, lasted for a shorter period than that described in Thiel et al. (2023). This might be for a combination of factors, including both studies being performed at different times of the year and with associated different baseline activity levels (Evans et al. 2016a, Ordiz et al. 2017, Bogdanović et al. 2021, Thiel et al. 2022) between spring and summer and the possibility that repeated muscle biopsies have a more prolonged impact on post-capture behaviour with potentially long-lasting effects from the capture earlier in winter the same year (Thiel et al. 2023). Nevertheless, we conclude that post-operative analgesia may not have been adequate in the bears that underwent surgery. These bears showed a delayed 1000 m displacement from the recovery site compared to bears that did not undergo surgery, and this difference is likely to be explained by pain and discomfort (Anil et al. 2002, Fiorello et al. 2016). Evaluating the effect of abdominal surgery on free-ranging brown bears presents significant challenges due to the difficulty to observe them in their natural environment. While some studies have focused on mortality rates (Mulcahy and Esler 1999, Arnemo et al. 2018), the morbidity arising from the adverse effects of surgery, which may manifest in altered behaviour, has not been thoroughly studied (Thiel et al. 2023).

Notably, the immobilization duration was not among the most accurate models. This is surprising, as with prolonged immobilization ZT is continuously metabolized, potentially reducing its effect by the time the antidote is administered. A study on humans found that duration of pain perception had little influence on how adversely the subjects experienced the procedure but was instead determined by the discomfort at the worst and final moments (Kahneman et al. 1993). This shows that discomfort perception is not always a straightforward process and is highly impacted by subjective experience; this may contribute to the reasons why immobilization duration is not selected in the statistical model selection. We observed limited variability in the variable chase duration in our data set, suggesting the effectiveness of the capture team. Additionally, the median chase time in our study was 7 min, which is well below the maximum pursuit time recommended for helicopter chases of wildlife and appears to be an efficient strategy for minimizing stress on animals during capture events (Arnemo and Evans 2017). Our study was also biased towards bears that did not have a premolar extracted because most bears have been followed from birth and therefore their age is known. However, we cannot rule out the possibility that tooth extraction may have had an impact on the bears' recovery time, but was undetectable in our data set. Malayan sun bears *Helarctos malayanus* that underwent a dental extraction under anaesthesia showed reduced activity one week post-operatively, despite the administration of the non-steroidal anti-inflammatory meloxicam, indicating that the bears still experienced pain (Fleming and Burn 2014). Tooth extraction was not identified as one of the important variables in our study, potentially because of small sample sizes, but also because we used a local anaesthetic at the tooth extraction site. Neither the number of previous captures nor Ketamine dose were among the most accurate models, indicating that previous experience with capture does not impact the bears' recovery times and that Ketamine, because of its short-acting properties, was most likely metabolized by the time the bears regained conciousness. The individuals that showed the most delayed departure time from the capture site may have been impacted by factors additional to the ZT dose and surgery. Age has been shown to have an impact on recovery times in geriatric dogs and cats being at risk for prolonged recovery times from anaesthesia (Hughes 2008, Baetge and Matthews 2012). Measuring the extent of pain and discomfort that the bears may have perceived in association with the whole capture event (including helicopter chase, darting, sampling and surgery) and identifying key contributors is a difficult task under field conditions, and a combination of all capture-related factors may impact the quality and time it takes for the bears to recover from a capture event. Notably, we must consider the potential impact of general pain (Jirkof 2017) resulting from the impact and placement of the dart, as well as the exhaustion incurred during the chase phase, particularly for bears administered higher doses of ZT, as these individuals were more likely to have received multiple darts, potentially prolonging the overall duration of capture and chase. These additional and potentially at least partly interrelated factors warrant careful consideration, as their interplay may have profound effects on recovery rates. Another interesting avenue may be to explore the spatial component in the recovery from capture, focusing on habitat selection post-capture.

Conclusions

This study aimed to critically evaluate the impact of capture practises in wildlife research on the welfare of Scandinavian brown bears. Our findings indicate that bears showed changes in activity budgets, such as increased stationary behaviour, for up to four days following a capture event. Additionally, the immobilizing drug dose and surgical procedures substantially affected post-capture movement. The results of this study highlight that helicopter capture and surgery have a measurable short-term impact on bear behaviour and movement. The inclusion of a control group in this study was crucial in understanding the extent of the effects of capture on brown bear behaviour and in enabling us to make recommendations on data censoring. To enhance the reliability and ethical standards of capture-related research, it is essential to carefully manage drug dosages. Alternatives to the current drug protocol may be explored to facilitate the reduction of ZT and improve recovery from anaesthesia. Furthermore, the invasiveness of any planned procedures, such as surgery, should be considered and critically evaluated. These measures ultimately contribute to the well-being of wildlife populations involved in ecological research.

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Author contributions

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Transparent peer review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/wlb3.01416.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5281/zenodo.13939579 (Thiel et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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