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Master thesis

Short-term effects of capture on movement of free-ranging Scandinavian brown bears

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Table of contents

Abstract

Research of free-ranging wildlife often involves capture and chemical immobilization of animals. Such an invasive and stressful procedure may cause alterations in the animals' physiology and behavior. Thus, evaluating the effects of capture and handling can improve our understanding on the impact that these cause on both the welfare of wildlife and the quality of collected data.

This study aimed to evaluate the effects of capture on movement of Scandinavian brown bears (*Ursus arctos*). I used generalized additive mixed effect models to examine movement rates of 55 GPS-collared individuals during 91 capture events immediately after the capture and during the following 10 days. Most apparent effects were short-term, with individuals experiencing low movement rates the hours after the capture and returning to a stable movement rate 4 days after the capture. Moreover, the movement patterns of the 24 family groups differed from solitary bears. Family members showed higher movement rates immediately after capture followed by two periods of depression on the movement rates around 48 and 120 hours after capture. Additionally, higher movement rates were observed when ambient temperature was between 0 – 10 ºC and dropped as ambient temperatures increased. Bears travelled longer distances per hour during light and twilight conditions than during the night.

Further research is warranted to investigate the effect of additional variables on the post-capture movement patterns of the brown bear. However, based on the results of my study I suggest that data from at least the 4 following days after a capture event should be excluded when analyzing data from brown bears.

Introduction

Collecting data using both non-invasive and invasive sampling techniques from free-ranging animals is required for research, management and to support the conservation of wildlife. Much can be learned from non-invasive techniques where the capture of the individuals is not required, such as collecting hair or feces (Afonso et al., 2016). These types of genetic sampling can be used, for example, to study demographic characteristics such as population abundance (Sawaya et al., 2012; Roques et al., 2014), species and individual identification and diet analyses (Waits & Paetkau, 2005). However, some critical information can only be collected by capturing and immobilizing individuals. For example, techniques including global positioning system (GPS) collars or bio-logging and very high frequency (VHF) implants have become common in the field of animal ecology during the last decades (Cagnacci et al., 2010). Although many benefits can be obtained from the data collected by capturing free-ranging wildlife, captures may directly or indirectly affect the animal welfare, potentially causing physical injury (Muñoz-Igualada et al., 2008; Elbroch et al., 2013) or changes in their physiology and behavior (Cattet et al., 2008; Wilson, 2011; Evans, Singh, Fuchs, et al., 2016; Graf et al., 2016). Moreover, capture-related effects may accumulate over time and influence life history parameters, for example reproductive success, survival (Arnemo et al., 2006; Casady & Allen, 2013; Casas et al., 2015; Arnemo et al., 2018) or body condition (Cattet et al., 2008).

GPS technology has allowed investigation of the movement patterns of species after capture events (Graf et al., 2016; Thiemann et al., 2013; Brogi et al., 2019). Advances in this technology include reduced size and weight of equipment decreasing the observed impact on tagged animals in general (Golabek et al., 2008). Nevertheless, the capture and handling procedure can be stressful for the animal (Fletcher & Boonstra, 2006; Omsjoe et al., 2009; Esteruelas et al., 2016; Thompson et al., 2020) resulting in changes in movement rates, space use or reduced activity (Morellet et al., 2009; Northrup et al., 2014; Rachlow et al., 2014; Brivio et al., 2015; Broell et al., 2016; Brogi et al., 2019). Hence, the evaluation of the behavioral effects of capture, chemical immobilization and handling can improve our understanding on the impact of these research activities on wildlife health. Such assessments can also improve capture techniques and contribute to minimize negative effects of future research captures. Moreover, we will be able to use this knowledge to better manage the data obtained from the free ranging wildlife and improve precision of analyses and inferences (Dechen Quinn et al., 2012).

This work is part of an ongoing long-term study on the ecology of the brown bear (*Ursus arctos*) in Scandinavia: the Scandinavian Brown Bear Research Project (SBBRP). A total of approximately 2350 captures have been carried out in the SBBRP for several research purposes and projects, i.e. with an average of 60-70 bears captured each year. The project aims to monitor individual bears during their entire life thus creating pedigrees of the study population. Consequently, it provides a scientific basis for the management of the brown bear in Sweden and Norway and allows to share information about brown bears with the general public.

In Scandinavia, helicopters have been widely used to efficiently capture free-ranging large carnivores and ungulates (Arnemo & Evans, 2017; Kreeger & Arnemo, 2018); however, helicopter overflights might disturb individuals without signs of habituation (Côté et al., 2013; Brambilla & Brivio, 2018). The effects on the post-capture movement of helicopter-based captures have been studied previously in bison (*Bison bison*) (Jung et al., 2019), moose (*Alces alces*) (Neumann et al., 2011) and mule deer (*Odocoileus hemionus)* (Northrup et al., 2014). These studies reported minimal effects when chasing times were minimized and the individuals were handled at the capture site (Jacques et al., 2009; Northrup et al., 2014).

For other species, short-term effects on movement and activity did not exceed two weeks: 2 days in Alpine ibex (*Capra ibex*) (Brivio et al., 2015), 10 days for wild boars (*Sus scrofa*) (Brogi et al., 2019), while white-tailed deer (*Odocoileus virginianus*) needed up to 14 days to recover (Dechen Quinn et al., 2012). However, in ursid species, a broader variation of the recovery period has been observed. Polar bears (*Ursus maritimus*) showed normal movement and activity levels within 5 days after capture (Rode et al., 2015; Thiemann et al., 2013). In contrast, Cattet et al. (2008) observed an immediate depression of the movement rate of grizzly bears (*Ursus arctos horribilis*) after the capture but it took an average of 28 days and a maximum of 53 days for black bears (*Ursus americanus*) to reach normal daily movement rates.

The long-term SBBRP has an extensive capture program of Scandinavian brown bears of over 30 years. Consequently, this thesis aims to investigate the short-term movement pattern during the days after the capture among a sample of free-ranging

Scandinavian brown bears. I hypothesized that bears will show signs of exhaustion after a stressful helicopter-based capture. Therefore, (1) I predict that brown bears would exhibit a depression of movement rate for a period of *n* days after the capture. Moreover, (2) I expect that the movement post capture is influenced by intrinsic factors such as sex and social status, and also, (3) it may vary due to environmental factors, such as ambient temperature and light conditions. Finally, because the brown bears in the study population of the SBBRP have been repeatedly captured during their whole life, (4) I predict that the movement patterns of individuals will be impacted differently, depending on how many times they have been captured before.

Material and methods

Study area

The data for the present study was collected in south-central Sweden, an area located in Dalarna and Gävleborg counties at 61ºN, 15ºE (Figure 1).

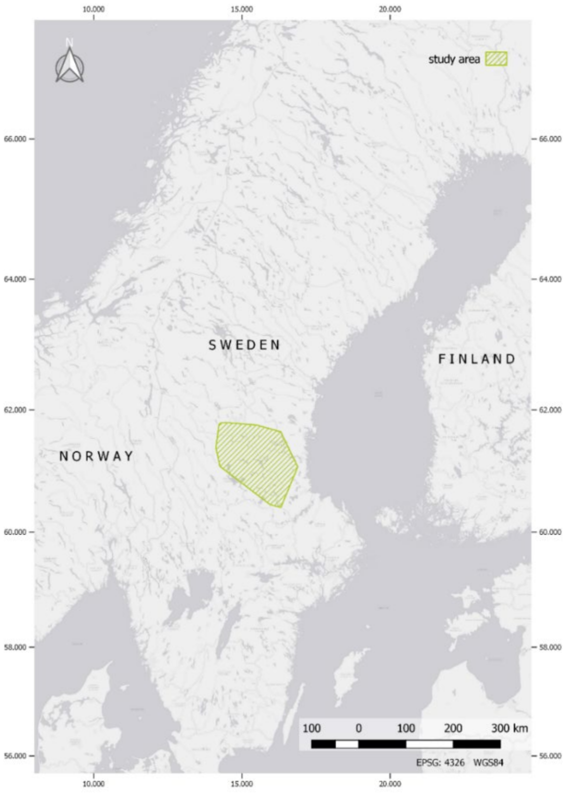

Figure 1. *Brown bear study area (in green) in Scandinavia from 2010 to 2018.*

The study area has a hilly landscape with lakes and bogs but most of it is dominated by an intensively managed coniferous forest; composed of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) with elevations ranging from 200 m to 1000 m above sea level. Regardless of the low human density (10.3– 15.9 habitants per km^2 in 2019) (Statistics Sweden, 2019) an intense network of gravel roads is found in the area (Ordiz et al., 2014). The study area has a continental climate with cold winters with a mean daily ambient temperature range from -7ºC in January and short, warm summers up to 15ºC in July. Snow cover lasts from end of October until late April. The annual precipitation averages 500 – 1000 mm (Swedish Meteorological and Hydrological Institute).

Data collection

In this study, the movement patterns of GPS-collared bears were analyzed from 2010 to 2018. Captures were carried out by the SBBRP in early spring and summer following the established biomedical protocol (Arnemo & Evans, 2017). The bears were located from a helicopter and immobilized using a remote drug delivery (Dan-Inject®, Børkop, Denmark) with a dose of medetomidine (Domitor, Orion Pharma Animal Health, Turku, Finland) and tiletamine-zolazepam (Zoletil, Virbac, Carros, France) adjusted to the bear body mass. Atipamezol (Antisedan, Orion Pharma Animal Health) was used as a reversal drug to counteract the anesthetic effects (5 mg per mg of medetomidine). The total time of pursuit never exceeded 30 minutes and intensive chasing was kept at a minimum (< 3 min) to avoid stress and physiological side-effects during immobilization. Females with yearling offspring were captured and, in these cases, the capture procedure was to first immobilize the yearlings and then the mother afterwards. The family group was handled at the same time, in the same location and they were given the antidote together. The animals were positioned in lateral recumbency with the mouth and the head low relative to the body to prevent the aspiration of saliva or vomits. During the handling, body temperature, heart rate and respiratory rate were monitored to prevent hyperthermia, hypothermia or insufficient ventilation. The eyes were covered and eye gel was applied to the cornea to prevent from drying. For more details on the capture procedures and drug doses refer to Arnemo and Evans (2017).

The bears were equipped with a GPS-GSM neck collar with a VHF transmitter included (VECTRONIC Aerospace GMbH, Berlin, Germany). The collars were programmed to record a position every 1 minute up to three hours depending on the individual research projects. Dependent on the weight of the bear, the collar varied from 520 to 1570 g, representing a maximum of 2% of the animal weight (Arnemo & Evans, 2017; Ordiz et al., 2012). The GPS receivers from the collars are estimated to have an accuracy within 5 m in mixed forest with foliation and 13.8 m in coniferous forests (Stache et al., 2012). Within the long-term research project (SBBRP), the capture-related mortality rate is the lowest among Scandinavian large carnivores (0.9%, N = 1079) and none of the deaths were related to the collar (Arnemo et al., 2006). The Ethical Committee on Animal Experiments in Uppsala, Sweden and the Swedish Environmental Protection Agency (application numbers C18/15) approved all animal captures and handling.

Data preparation

The data-set used in the present study is based on GPS positions and included information about sex, age, family captures and life history (previous captures) thanks to the long-term individual-based monitoring program carried out by the SBBRP. All statistical analyses were done in R-studio using the 4.0.0 R's version (Team, 2019; Team, 2013)

GPS positions of 55 brown bears (29 females and 26 males) and a total of 91 captures within 2010 and 2018 were analyzed. Fixes with impossible coordinates or far from the study area were visually identified and removed from the raw data using QGIS 3.12 Bucaresti software (QGIS.org, 2020). Moreover, GPS positions with horizontal dilution of precision (HDOP) values of ≥ 5 and ≤ 4 available satellites were also removed from the analysis for more accurate locations (Lewis et al., 2007). Data up to two weeks after the capture was selected to test the effect over time. Due to lack of data fixes on a very fine scale, 1-hour intervals were chosen over a period of 10 days immediately after capture. Missing relocations (6.6% of the total) were linearly interpolated using the "*na.approx*" function of the "*zoo*" R-package (Zeileis et al., 2020). GPS position were used to construct movement patterns by calculating the Euclidean distance traveled between consecutive positions with the R-package "*adehabitatLT"* (Calenge, 2006).

Explanatory variables

Hours since capture were calculated as the difference between the time of every GPS fix and the time the antidot was given per each bear and capture. The ambient temperature was obtained from the Swedish Meteorological and Hydrological Institute for Hamra's weather station (14.75ºE, 61.76ºN) which represented the average climatic conditions within the bears' home ranges. Sunrise, sunset, dusk, dawn times were calculated for the study area with the R-package "*geosphere*" (Hijmans, 2012). These times were determined according to the civil twilight definition, when the sun is between 6 and 0 degrees below the horizon. Furthermore, a photoperiod was defined as: "Light", the time between sunrise and sunset, "Twilight" the time between dawn-sunrise and sunset-dusk and “Dark” between dusk and dawn. Day length was defined as hours of light per day and was calculated at the specific latitude of the study area. Captures were differentiated as family capture (F, *n* = 24), when bears were captured together (i.e. mother with cubs) or solitary (S, *n* = 67), when captured alone. In addition, a status variable was determined accounting for sex differences; “Solitary females” (*n* = 34), “Solitary males” (*n* = 32) and “Family” (*n* = 24) since I expected the whole family group to move as a unit.

Variable name	***Variable type***	***Definition***
dist	Continuous	Distance in meters, rounded
h_since_c	Continuous	Hours after capture, from 0 to 255
temp	Continuous	Hourly air temperature in degrees Celsius (ºC)
day_length	Continuous	Hours of daylight for every day
photoperiod	Categorical	Light conditions: "Light", "Twilight" or "Dark"
fam_sol	Categorical	Family capture (F) or Solitary (S)
n_captures	Continuous	The times the bear has been captured previously
status	Categorical	“Family”, “Solitary female”, “Solitary male”

Table 1. *Summary of the response and explanatory variables used in the generalized additive mixed model to determine the factors influencing the movement patterns post-capture for brown bears in Scandinavia.*

Statistical analysis

Generalized additive mixed models (GAMM) were fitted to investigate the variation of the brown bears’ movement patterns during the following days after the capture. A GAM model relates a univariate response variable y to some predictor variables x_i. Per se, it is an extension of a generalized linear model which allows to incorporate a non-linear function as predictors; therefore, it is an appropriate type of analyses to handle non-linear relationships between response and predictors (Wood, 2017).

The variables in the models were chosen accordingly to the hypotheses and correlation and structure of the variables were explored using “*ggpairs*” from “*ggplot2*” r-package (Wickham, 2016) and, non-linear correlation computed using spatial sampling with the function "*nlcor*". The function "*bam*" from the r-package "*mgcv*" (Wood & Wood, 2019) was used to fit the models as it is preferred when handling large datasets. A Gamma distribution with log as a linking function and the fast-restricted maximum likelihood (fREML) as a smoothing parameter were used. In order to use a Gamma distribution, I converted the zeros present in the response variable to a minimum decimal. Distance in meters was used as response variable and capture ID (individual for each capture and bear) was included as a random effect in all the models. The following explanatory variables were used in the model selection process: hours since the capture, ambient temperature (ºC), day length (h), photoperiod ("Light", "Twilight" and "Dark"), capture type (family or solitary bear), status ("Family", "Solitary female" and "Solitary male"), number of times the individual has been previously captured and two smooth interactions of hours since captures multiplied by an ordered factor for capture type (family vs. solitary) and hours since capture multiplied by an ordered factor of status (solitary male vs. solitary female and solitary male vs. family) (Table 1). The Akaike Information Criterion (AIC) was used for model selection (Akaike, 1974) on a priori formulated relevant candidate models (Table 2 and 3). The residuals were assessed for temporal dependency and the final model refitted with an autoregressive model structure (AR1). These two models were compared with the function "*compareML*" from "*itsadug*" R-package (van Rij et al., 2020) and the model with autocorrelation was chosen over the one without autocorrelation. To select an adequate dimension of *k*, the effective degrees of freedom of each smooth factor were compared to its *k-1* index score (*k'*) using *"gam.check*" function from "*mgcv*" (Wood & Wood, 2019). The model assumptions were verified by plotting and inspecting the residuals with the function "*check.resid*" from "*itsadug*" (van Rij et al., 2020)

Response variable:	distance (rounded meters)
Random effect:	capture_ID
Family:	Gamma
Link:	Log
Smoothing parameter:	fREML

Model	
m0	1
m1	s(h_since_c)
m2	s(h_since_c) + s(temp) + s(day_length) + photoperiod
m3	s(h_since_c) + s(temp) + s(day_length) + photoperiod + fam_sol
m4	s(h_since_c) + s(temp) + s(day_length) + photoperiod + s(n_captures)
m5	s(h_since_c) + s(temp) + s(day_length) + photoperiod + status
m6	s(h_since_c) + s(temp) + s(day_length) + photoperiod + fam_sol + s(n_captures)
m7	s(h_since_c) + s(temp) + s(day_length) + photoperiod + status + s(n_captures)
m8	s(h_since_c) + s(of_fam_sol) + s(h_since_c, by = of_fam_sol) + s(temp) + s(day_length) + photoperiod
m9	s(h_since_c) + s(of_status) + s(h_since_c, by = of_status) + s(temp) + s(day_length) + photoperiod

***Table 2**. Candidate generalized additive mixed models (GAMMs) fitted to determine which factors explains better the post-capture movement patterns of Scandinavian brown bears. All the parameters in the first section are equal for all the models. Below, the explanatory variables included in each model.*

Results

In total, 21 387 GPS locations from 91 captures of 55 bears within 2010 – 2018 were used to calculate the distance travelled by the bears every hour. The top ranked GAMM model to explain the differences in movement patterns following the captures (Table 3), suggested that distance travelled was influenced by the hours since the capture, ambient temperature, light conditions (day length and photoperiod) and status (solitary male, solitary female and family) (Table 4).

Overall, we can observe that bears gradually increased their distances travelled for about 4 days after the capture until they seem to reach a stable level, at approximately 200 m/h (Figure 2).

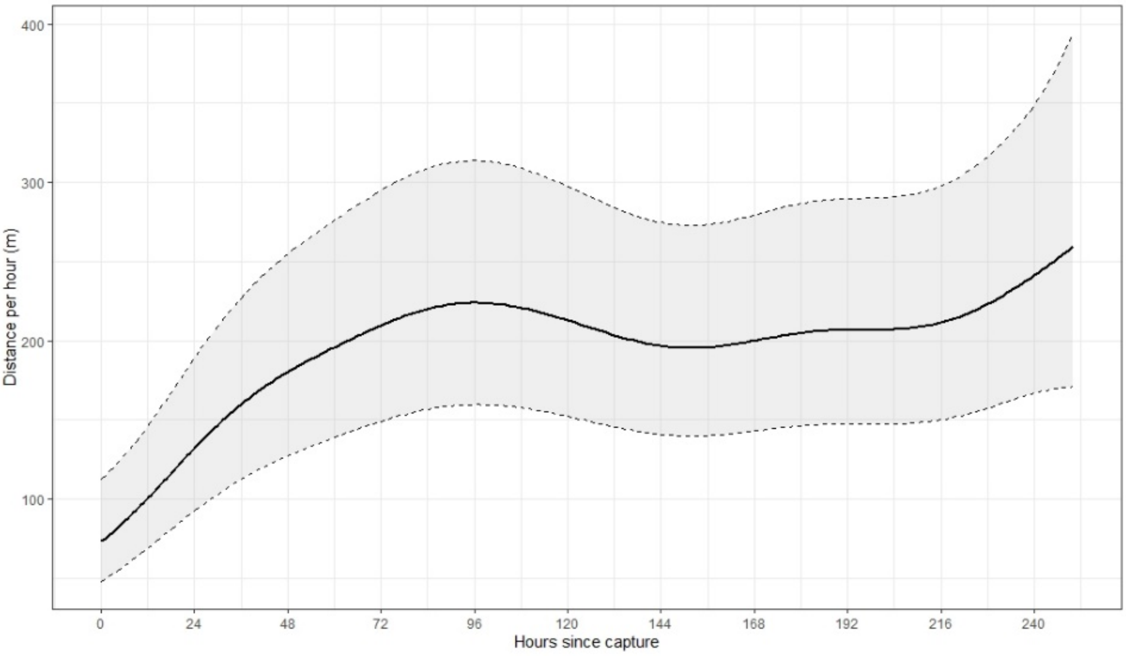

Figure 2. *Predicted values from a GAMM model on the distance moved per hour by brown bears over a period of 10 days after the capture event. The solid lines are predicted means over time, and the shaded grey area are the 95% CI.*

Model	***AIC***	***ΔAIC***	***W***
m9	250599,7	0	1
m8	250634,2	34,6	<0,001
m3	250835,4	235,8	<0,001
m6	250835,6	235,9	<0,001
m5	250836,0	236,3	<0,001
m7	250863,1	236,4	<0,001
m2	250836,7	237,0	<0,001
m4	250836,8	237,1	<0,001
m1	251286,8	687,1	<0,001
m0	251842,2	1242,5	<0,001

Table 3. *Generalized additive mixed model selection using the Akaike information criterion (AIC).*

Parametric coefficients	***Estimate***	***Std. Error***	***t-value***	***p-value***
Intercept	4,58053	0,17510	26,160	<0,00001
status solitary female	0,26678	0,20196	1,321	0,187
status solitary male	0,85775	0,21039	4,077	0,00004
photoperiodLight	0,27244	0,04905	5,554	<0,00001
photoperiodTwilight	0,24607	0,04719	5,215	<0,00001
Approximate smooth terms	***edf***	***Ref.df***	***F***	***p-value***
s(h_since_c)	5,395	6,578	8,45	<0,00001
s(h_since_c):of_statussolitary female	1,833	2,289	0,374	0,672
s(h_since_c):of_statusfamily	5,394	6,509	5,619	<0,00001
s(temp)	6,533	7,713	11,118	<0,00001
s(day_length)	4,659	5,674	5,947	<0,00001
s(capture_ID)	75,484	88,000	7,361	<0,00001

R-sq(adj) = 0,129, deviance explained = 16,7 %, fREML = 38836

Table 4*. Generalized additive mixed model estimating the effect of hours since capture, status (Solitary male, Solitary female, Family), temperature (ºC), day length (h), photoperiod (Dark, Twilight, Light) and the two-way interaction between hours since capture and ordered status on distance moved per hour (m). Capture ID, unique number per each bear and capture, is fitted as a random intercept*

Additionally, distance moved after capture was influenced by the ambient temperature and light conditions. Bears travelled greater distances when temperatures were between 0 and 10 ºC and gradually decreased their movement to the half when temperatures reached 20 ºC (Figure 3). Furthermore, there is an increasing tendency which showed that the longer the day, the longer distances the bears travelled (Figure 4). Moreover, predicted values show that bears moved significantly more during daylight and in the twilight rather than in the night during the 10 following days of the capture (Figure 5).

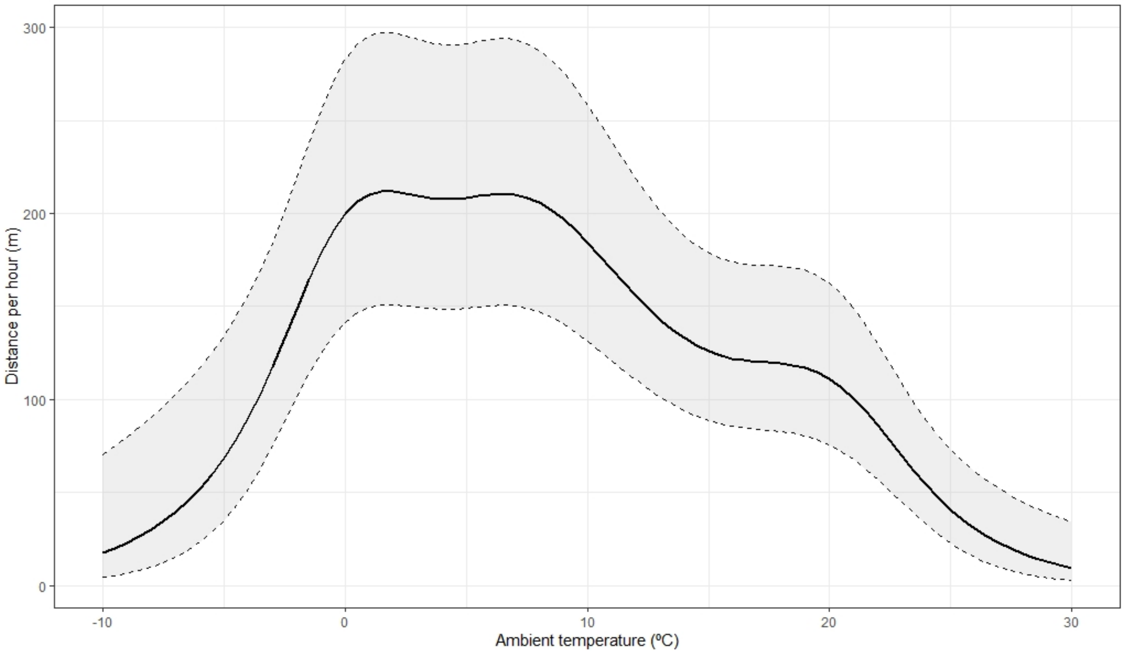

Figure 3. *Predicted values from a GAMM model on the distance moved per hour by brown bears in relationship with the ambient temperature in degrees Celsius (ºC). The solid lines are predicted means over temperature, and the grey shaded area is the 95% CI.*

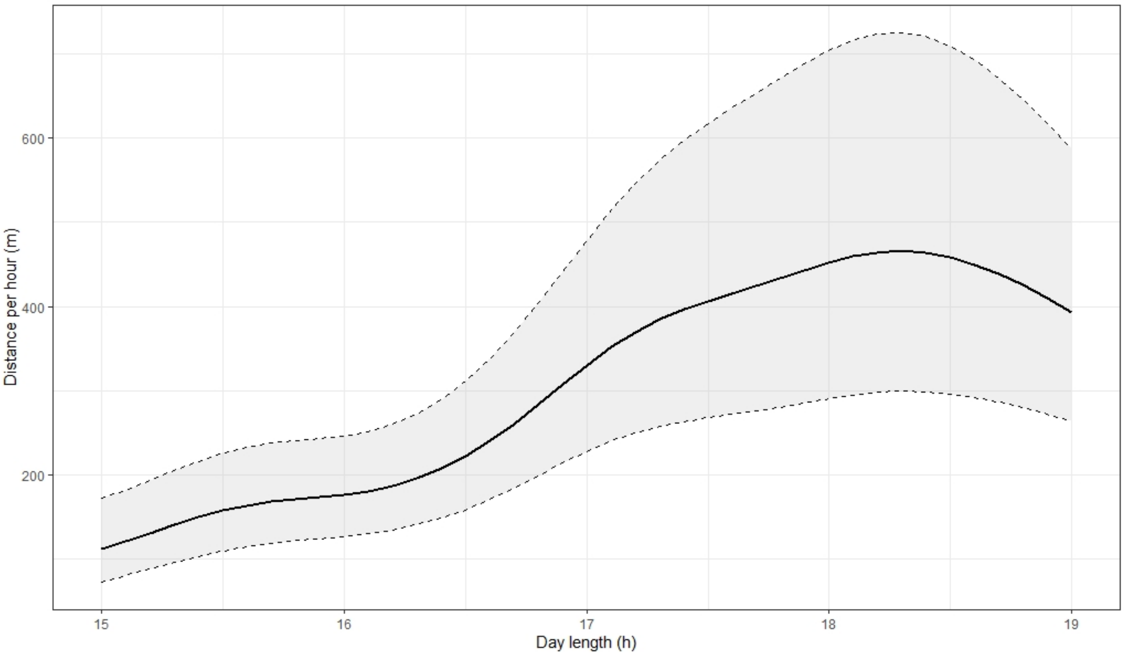

Figure 4. *Predicted values from a GAMM model on the distance moved per hour by brown bears in relationship with the hours of light per day (day length). The solid lines are predicted means over hours of daylight per day, and the grey shaded area is the 95% CI.*

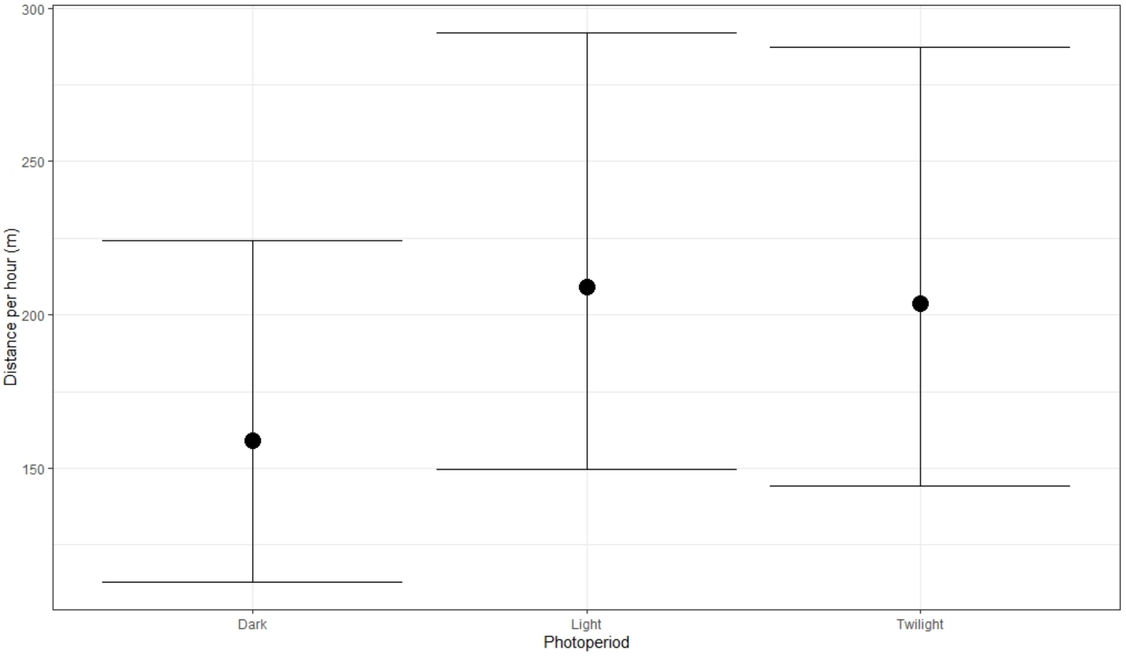

Figure 5. *Predicted mean values from GAMM model on the distance moved per hour by brown bears during the different the light conditions (photoperiod: dark, twilight and light) over a period of 10 days after the capture event.*

The average distance traveled per hour was 175 meters (95% confidence interval (CI): 166 – 185 m) for families, 216 (95% CI: 208 – 225 m) solitary females and 330 (95% CI: 316 – 344 m) for solitary males. In Figure 6, we can observe that solitary bears, both males and females, have a similar pattern and move similar distances after being captured. The solitary bears slowly increased the distance travelled, peaking around 96 hours after the capture and decreasing to a level where it stabilizes at around 120 hours after capture. In contrast, bears captured in family groups moved greater distances during the first hours after being captured. However, they showed two depressions on their movement around 48 and 150 hours since the capture occurred.

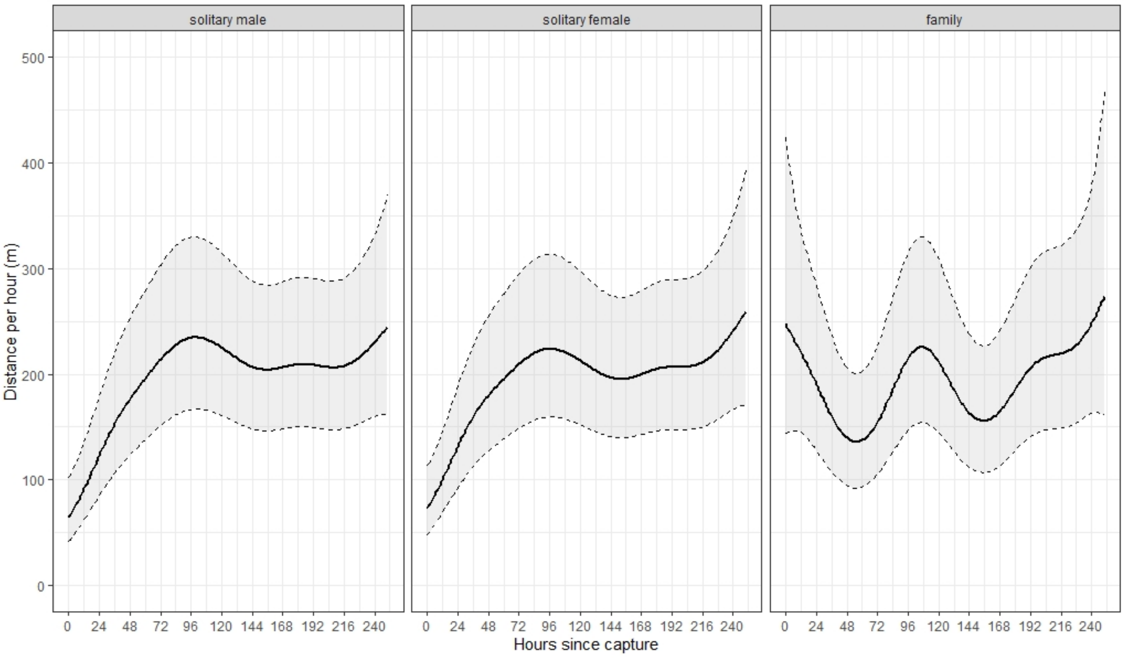

Figure 6. *Predicted values from GAMM models on the distance moved per hour by brown bears and their status (Solitary male, Solitary female and Family) over a period of 10 days after capture event. The solid lines are predicted means over time, and the grey shaded area are the 95% CI.*

By comparing the family captures and the solitary females to the reference level (solitary males), we can observe that distances travelled by families become significantly different from solitary males during three periods (Figure 7). Although not significant differences are shown, the predicted mean distance travelled over the two weeks of solitary females were consistently lower compared to the solitary bears.

In addition, the models including the number of times the bears have been captured before were visually explored; and it seemed that models were overfitted when including the continuous variable. Therefore, this variable was excluded from the more complex models which included two-way interactions. (Table 2 and 3).

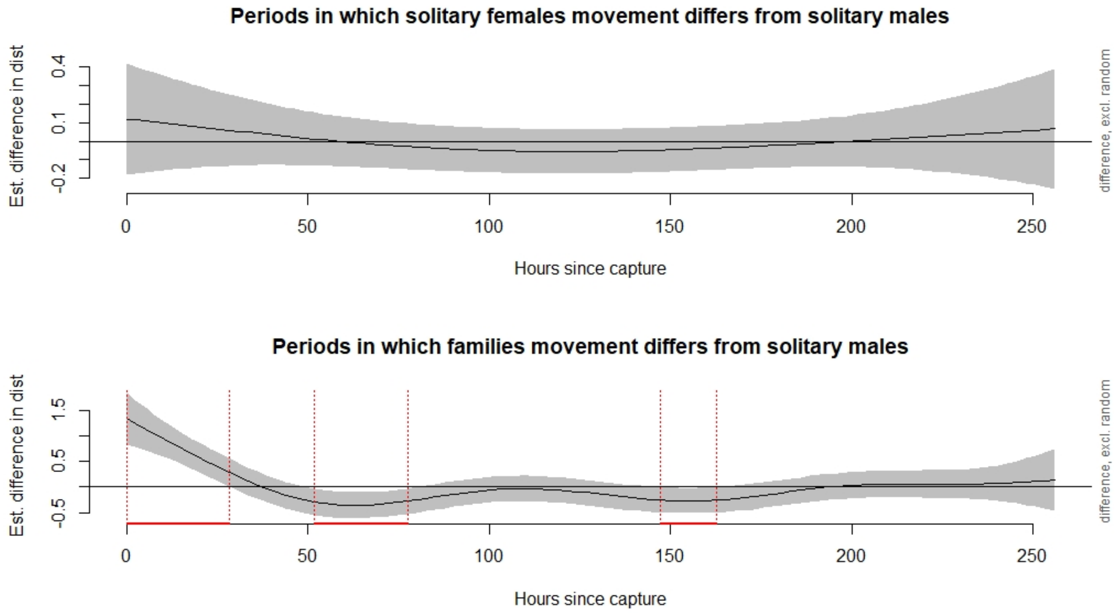

Figure 7. *The predicted difference from a GAMM model on the solitary female (up) and family (down) distance moved per hour while the distance of the solitary male is set to zero. Grey shaded areas show the 95% CI. Red dashed lines show the period when the distances travelled are significantly different from its reference at zero.*

Discussion

Capture and handling of free-ranging wildlife for research purposes has increased during the last decades. In addition, the development of GPS technology permits the study of animal movement, including movement after captures at a fine scale. As a result, the study of these movements has recently gained the attention of many researchers with the concern that captures may result in short- or long-term effects on the animal's behavior. For this reason, the investigation of post-capture movement and the assessment and identification of the factors influencing its variation will facilitate the refinement of current protocols and help minimize the negative effects. Also, refinements may improve the accuracy of data-censoring after captures that will permit better inferences in research.

In this study, I investigated the post-capture movement patterns of 55 Scandinavian free-ranging brown bears over 91 captures carried out in spring and early summer from 2010 to 2018. My analysis suggests that helicopter-based captures and handling had a short-term effect on the movement of the study animals for up to four days after capture. Movement after capture was additionally influenced by both environmental factors and the bear's social status.

My results show, in accordance with my first prediction, that brown bears exhibited low movement rates immediately after capture followed by a gradual increase that lasted about 4 days until it stabilized. This is a short period compared to a previous study where Cattet et al. (2008) observed that grizzly bears needed an average of 28 days to return to mean levels, or the 36 days in black bears. In addition to the length of the recovery period, the mean movement rate of grizzly bears observed by Cattet et al. (2008) during the 28 days after capture was lower in comparison to the predicted values at the stabilized level of my study individuals, approximately 120 m/h and 200 m/h respectively, which make me consider general behavioral differences and movement rates between bear populations. Moreover, only 36% of the captures were helicopter-based while the rest was captured with leg hold snares or barrel traps. Further, Cattet et al. (2008) also found that captures by leg hold snare were more stressful and more prone to cause muscle injuries to the animals than the helicopter-based captures, which may explain why the individuals in their study needed more time to recover or travelled smaller distances. Consequently, the level of stress caused by the capture method may result in different movement responses and lengths of the recovery period. Previous studies on movement of free-ranging polar bears after a helicopter-based capture showed a short recovery periods (Thiemann et al., 2013) where the majority of the individuals had returned to baseline movement rates within 3 days and almost all of them (93%) within 12 days. Similarly, ungulates captured from helicopter showed short recovery periods too despite the fact that the nature of the post capture movement was the opposite of what my results show; ungulates display an immediate increase of movement and activity rates followed by a decrease until a stable level. Moose movement was altered for 4.5 days following the capture (Neumann et al., 2011). Jung et al. (2019) observed in bison that more than 80% of the individuals, despite individual variation, returned to pre-capture movement rates within the 5 days after capture. Mule deer needed up to 7 days to stabilize its movement rates, although significant differences were shown only during the first 24 h after capture (Northrup et al., 2014).

In addition to this general trend of the brown bear's movement stabilizing 4 days after capture, I found evidence that family groups follow a different pattern after capture than solitary bears, consistent with my second prediction. Reproductive class (male, female and female with cubs) and sex was also included in the highest-ranked models even though Cattet et al. (2008) found that the period the bears' movement rate was altered after captures was irrespective of sex and reproductive class. In my study, individuals in family groups had approximately 1.5 times higher movement rates immediately after capture than the solitary males. Moreover, the confidence interval of the family groups' movement was larger from the beginning on. Females with cubs as well as the cubs themselves were defined as family. Cubs often wake up before the mother and probably walk around in the vicinity of the mother, which might explain this variation. Additionally, a possible explanation to the variance observed may be the age of the cubs (up to 2 years old) and the number of them although, Thiemann et al. (2013) did not find differences in the recovery movement rates among female polar bears with dependent young (cubs-of-the-year and older cubs). Another explanation to the different movement pattern of family groups after capture might be due to the seasonal and reproductive factor. The captures for my study were carried out during the mating season. Dahle and Swenson (2003) studied the home-range sizes in relation to reproductive strategies and found that female brown bears with dependent offspring restricted their home range size to avoid contact with infanticidal males which is an important cause of cub mortality. Furthermore, the cyclic pattern of the movement rate after the capture may indicate disturbances in circadian rhythms and investigating this further would be an interesting follow-up study. In contrast to the movement over time of the family groups, the confidence intervals around the mean movement rate were smaller during the first hours after capture for solitary bears than for families. That suggests that solitary bears travelled similar distances shortly after captures, and, over time the individual variation increased.

Consistent with prediction 3, my results show that movement rates differed with ambient temperature, length of the day and light conditions. Bears had highest movement rates when ambient temperature ranged between 0 - 10 ºC. The predicted movement rate pattern in relation with the ambient temperature may be due to bears trying to avoid overheating on a daily basis by moving less when it is warm. Chasing and capturing from a helicopter may also result in high body temperatures of the individuals (Thompson et al., 2020). Thompson et al. (2020) observed that body temperature of wild moose was elevated up to 48 hours after capture. I did not analyze body temperature, but because bears are also captured by chasing with helicopter, I expect that the bears' body temperature would be elevated, too. For this reason, thermoregulatory constraints in the individuals and their movement post-capture should be considered when capturing in warm temperatures. Furthermore, high movement rate values were predicted at days with more hours of daylight. Bears are hibernating from 4 to 6 months a year (Evans, Singh, Friebe, et al., 2016). In order to accumulate fat for winter they have to optimize their foraging in spring and summer which it may be facilitated by longer days or a seasonality factor. Moreover, bears usually show a crepuscular and nocturnal behavior (Kaczensky et al., 2006; Moe et al., 2007), probably to avoid contact with humans (Ordiz et al., 2012; Ordiz et al., 2013). Yet, my highest ranked model predicted higher movement rates during day light and twilight hours of the day than in the night, suggesting alteration in their normal behavior and shifting of their daily resting patterns. Kaczensky et al. (2006) found that yearlings and subadults (up to 3 years) were more diurnal than adult bears. In my study, an age variable was not included as initial model estimations showed non-significant effects. Other reason to exclude age was the sexual dimorphism and the growth rate, where males are up to 2.2 times bigger than the females and this difference in body mass is influenced by age at sexual maturity among others (Schwartz et al., 2003). For this reason, I decided to simplify the models by creating a social status which included sex and most of the differences by age since solitary bears are mostly adults already.

Lewis and Rachlow (2011) found that black bears were most active during crepuscular times, moderately active during the day and the least active at night similarly to my predictions. Moreover, they also observed that adult males moved significantly more during crepuscular times during spring an early summer than late summer. Even though this behavior is not specifically observed after captures, the differences observed in my results might be influenced by intrinsic factors like sex or age and therefore interactions with these variables might be interesting to explore in further analyses.

Lastly, I predicted that the movement patterns of individuals will be impacted differently, depending on how many times they have been captured before. My top ranked model did not include the number of previous captures as a variable. I explored the possibility of including this variable in my models but it led to an overfit of the models. Furthermore, I also explored the possibility to convert it to a categorical variable but the data set was unbalanced, since just 4 out of 91 were first time captures. Perhaps another approach is needed to possibly identify an effect on the movement pattern after capture depending on how many times the individual has been captured before.

Studies assessing the effects of capture on mammals are few which makes the comparison of results difficult. Hence, it is important that more studies evaluate the movement behavior of free-ranging wildlife after captures.

The models of movement rates among all bears had poor fit. Several distributions were explored to fit our response variable and seemed that a Gamma distribution was the best fit even though it did not fit perfectly. Moreover, the nature of the brown bear captures sometimes lead to incomplete data sets. Therefore, I did not assess the impact of certain factors which probably would have been important when explaining the post-capture movement behavior of brown bears. Chasing times, length of the handling, surgeries performed are variables that might contribute to explain better the variance of the movement rates. Although, individuals with missing data could have been excluded I chose not to because that would have meant a significantly reduction of the sample size. Also, a longer period should be evaluated to check for effects beyond the two-week period studied here as found previously.

In conclusion, any capture event that includes chemical immobilization is likely followed by behavioral alterations. I observed a period of low movement rate during the following four days after captures over all bears. Moreover, solitary bears showed similar movement patterns after capture regardless of the sex. Family groups, however, showed significant differences in the post-capture movement when compared to solitary bears. Additionally, temperature and light conditions influenced the movement patterns observed the days following capture. Therefore, data from a period of 4 days should be excluded for further analyses of brown bear movement and distribution. In order to understand better the factors that explain this variation and how it affects the movement of the individuals, further studies focusing on the behavioral and physiological effects of captures are needed.

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