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# Study of female brown bear movements and inference of reproductive status

Manon Seu

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# STUDY OF FEMALE BROWN BEAR MOVEMENTS AND INFERENCE OF REPRODUCTIVE STATUS

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THESE D'EXERCICE

pour obtenir le titre de  
DOCTEUR VÉTÉRINAIRE

DIPLOME D'ÉTAT

*présentée et soutenue publiquement  
devant l'Université Paul-Sabatier de Toulouse  
par*

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**Directeur de thèse : M. Guillaume LE LOC'H**

---

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## List of Acronyms

AIC	Akaike's Information Criterion
AR1	Auto-Regressive of order 1
CI	Confidence Interval
COY	Cub(s) of the Year
ID	Identification number
GAMM	Generalized Additive Mixed Model
GPS	Global Positioning System
MCMC	Markov Chain Monte Carlo
MCP	Minimum Convex Polygon
NPV	Negative Predictive Value
PhD	Philosophiæ doctor
PPV	Positive Predictive Value
RF	Random Forest
RI	Reliability Index
SBBRP	Scandinavian Brown Bear Research Project
SSI	Sexually Selected Infanticide
Tb	Body Temperature
VHF	Very high frequency



## Résumé du manuscrit en français

Depuis près de 40 ans, le *Scandinavian Brown Bear Research Project* (SBBRP) étudie les ours bruns en Scandinavie. Leurs recherches, basées sur la capture, le prélèvement d'échantillons, la pose de colliers GPS et la surveillance sur le terrain, ont permis d'acquérir des connaissances approfondies sur la physiologie et l'écologie de l'ours. Aujourd'hui, l'une des problématiques qui intéresse les chercheurs du SBBRP est l'impact du réchauffement climatique et de l'anthropisation sur la survie et le succès reproducteur de l'espèce, ainsi que l'impact des événements de capture sur les individus. Afin d'évaluer le succès reproducteur des ours bruns, un suivi poussé des femelles est réalisé. Ce suivi repose sur une surveillance aérienne, des prospections d'indices de présence d'ours (poils, fèces, empreintes...), et des outils de bio-logging pour déterminer d'éventuelles gestations. Malgré ces efforts, en raison de leur nature évasive, certains individus échappent aux radars de la surveillance, et leur statut reproducteur peut rester inconnu certaines années. De plus, certaines femelles peuvent subir une perte totale de leur portée, due à des événements de mortalité ou à des infanticides perpétrés par d'autres mâles.

Ainsi, connaître le statut reproducteur de l'ensemble des femelles étudiées et la temporalité des événements de perte de portée est essentiel pour répondre aux questions suivantes :

Combien d'ours sont nés cette année ?

Quel est le taux de survie des ours au cours de leur première année de vie ?

La réponse à ces questions permettra de soulever d'autres interrogations et d'évaluer l'impact de l'augmentation des températures en Scandinavie sur le succès reproducteur des ours bruns. En effet, le réchauffement climatique progresse en Arctique à un rythme

deux fois plus rapide que la moyenne mondiale (Bruhwiler et al. 2021), et la Scandinavie, ainsi que les ours bruns qui y vivent, n'échappent pas à cette tendance qui sévit aux latitudes les plus au nord. Évaluer l'impact de ce dérèglement sur les dynamiques de population de l'ours brun présente donc un intérêt considérable afin d'adapter les mesures de gestion de l'espèce et évaluer les capacités de résilience de cette espèce face aux changements de son écosystème.

C'est pour répondre à ces questions et extraire ces informations, difficiles à obtenir via la seule surveillance, que l'écologie du mouvement entre en jeu. Ainsi, un défi majeur en écologie du mouvement est d'identifier les comportements à partir des données de mouvement et de les associer à des contextes intrinsèques et environnementaux spécifiques. Les études précédentes ont montré que les femelles solitaires présentent un mouvement accru par rapport à celles qui sont accompagnées de leurs oursons de l'année (*Cubs of the Year* - COY) (Steyaert, Swenson, Zedrosser 2014; Gardner, Pamperin, Benson 2014).

Cette étude avait deux objectifs principaux : premièrement, démontrer comment le statut reproducteur influence le mouvement des femelles et explorer les facteurs environnementaux susceptibles de l'affecter, en utilisant des Modèles Additifs Mixtes Généralisés (GAMMs). Les femelles avec des petits dépendants se déplaçaient moins que les femelles solitaires, tandis que les femelles avec des oursons d'un an montraient des valeurs intermédiaires. Les facteurs environnementaux étudiés incluaient la pluviométrie, la température et la profondeur du manteau neigeux. Ces trois facteurs ont un impact négatif sur les mouvements des trois statuts reproducteurs (femelles solitaires, femelles avec jeunes de plus d'un an, et femelles avec COY), à l'exception de la profondeur de la neige qui n'a pas d'effet significatif sur les femelles avec COY.

Deuxièmement, l'objectif était d'inférer le statut reproducteur des femelles via l'analyse de leurs données de mouvement et d'identifier des dates de perte de portées. Afin d'associer le statut reproducteur des femelles en sortie d'hibernation, un modèle de

Forêt Aléatoire (*Random Forest* - RF) a été préalablement entraîné. Ce modèle a été capable de distinguer une femelle solitaire d'une femelle avec COY avec une exactitude de 85 % après une phase d'entraînement et de test sur des individus dont le statut reproducteur était connu et identique tout au long de la saison.

Les événements de perte de portée ont été identifiés en utilisant une approche de détection de *changepoints* bayésiens. La difficulté réside dans le fait que nous n'avons pas en notre possession d'information de confirmation nous permettant d'affirmer que la date détectée est bien celle où la portée a été perdue. Ainsi, en guise de confirmation supplémentaire, nous avons utilisé la RF précédemment citée en nous basant sur l'hypothèse suivante : « Une femelle qui expérimente une perte totale de sa portée retrouvera le mouvement d'une femelle solitaire en quelques jours ». C'est ce que la littérature a précédemment mis en évidence (Gardner, Pamperin, Benson 2014). Ainsi, les observations précédant la date de changepoint sont attendues à être classées en tant que « femelle avec ourson », et les observations situées après la date de point de changement devraient être classées en tant que « femelle solitaire ». Les dates de changepoint détectées ont été confirmées grâce à la RF préalablement entraînée avec une exactitude de 74 %. Ces résultats offrent une approche innovante et prometteuse pour combler les lacunes des données reproductives pour les individus sans données de suivi sur le terrain. De plus, il serait possible d'extraire des dates potentielles de perte de portée avec une précision de l'ordre du jour via l'analyse des données GPS. Nous pourrions envisager que cette méthode soit exportée et adaptée pour détecter d'autres événements de la vie d'un individu (conflits, perturbations, etc.).

Malgré les défis liés aux particularités biologiques et à la saisonnalité inhérente aux ours bruns, cette étude a permis l'émergence d'un nouvel outil méthodologique pour évaluer le statut reproducteur des femelles ours bruns après l'hibernation, fournissant des informations précieuses sur les taux de natalité et de mortalité des oursons, et permettant l'élargissement des questions scientifiques inhérentes au succès



reproducteur des ours bruns et aux différents défis et perturbations auxquels ils font face.

Nous pourrions envisager que ces outils : l'analyse bayésienne du changement de point et l'utilisation de forêts d'arbres décisionnels, puissent être appliqués à d'autres espèces pour déterminer le statut reproducteur et la présence de jeunes. Le mouvement permettrait donc de déduire une gamme d'informations sur les populations d'animaux sauvages et le statut reproducteur n'est qu'un des champs d'application possibles. Nous pourrions imaginer, une fois ces méthodes améliorées, être capables de détecter des états de stress, de perturbation ou même des mouvements suggérant une dégradation de la santé de l'animal. Les possibilités offertes par la combinaison de ces méthodes et les récentes contributions du *machine learning* laissent entrevoir un large champ d'applications qui pourrait apporter des éléments de réponses à de nouvelles problématiques concernant les espèces sauvages.



Photographie d'une femelle et ses deux jeunes âgés d'un an durant un évènement de capture.  
Seu Manon

From ...

Theoric & population approach

To

Applied and individual purpose



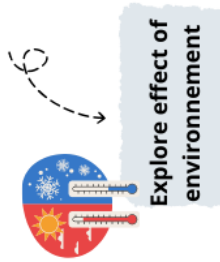
Movement metrics :  
Mean daily step length (m/h)  
Mean daily home range (km2)  
Persistence

1

**Aim n°1**  
Describe movement based on reproductive status

**GAMMs**

- Female accompanied by COYs
- Females accompanied by yearlings
- Solitary female



114 bear\_year  
69 bear\_year

Exclusion of females with yearlings

- Females with COYS
- Solitary female

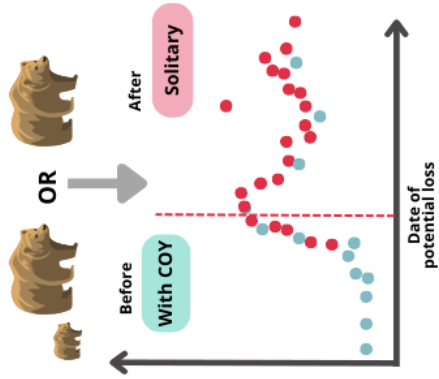
**STEP 1**  
Random forest classification

**STEP 2**  
Changepoint analysis

13 females

That experienced litter loss...

**STEP 3**  
Cross validation with the random forest previously trained



\*This analysis only used step length and home range.

GLOBAL PURPOSE =

Assess female reproductive status

Figure 1: Graphical Abstract proposition

# I. Introduction

## 1. Reproduction & Movement

Reproduction and movement each incur costs, and are interconnected, impacting one another (Trivers 1974; Stephen C. Stearns 1998). Consequently, females must weigh the energy invested in current offspring against the probability of surviving to reproduce again, leading to observable differences in movement patterns between reproducing and non-reproducing animals.

Studies have shown that movement characteristics vary among different reproductive statuses across various species. These differences are already observable between sexes; for instance, male humpback whales tend to have higher local movement frequencies between breeding sites compared to females and females with calves, primarily driven by their search for mating opportunities (Nozomi Kobayashi et al. 2017).

Some studies have attempted to estimate calving events of ungulates by using movement data, such as speed and direction (DeMars et al. 2013; Nicholson et al. 2019). Gaining insights into the reproductive status of individuals within a population is essential for evaluating reproductive rates, fertility, reproductive success, and survival, all of which are pivotal for understanding population demographics and shaping adaptive management and conservation strategies (Oliver Manlik 2019). However, accurately accessing this reproductive data presents significant challenges, particularly due to the elusive nature of many species and/or the extensive areas they inhabit. This is the case of the Brown Bear (*Ursus arctos*) on which this study will focus on.

Thus, a key challenge in movement ecology is to identify behaviors from movement data and to associate these movements with specific environmental contexts. Reproductive status significantly influences individual behaviors (Luana V. P. Ruivo et al. 2017) and as

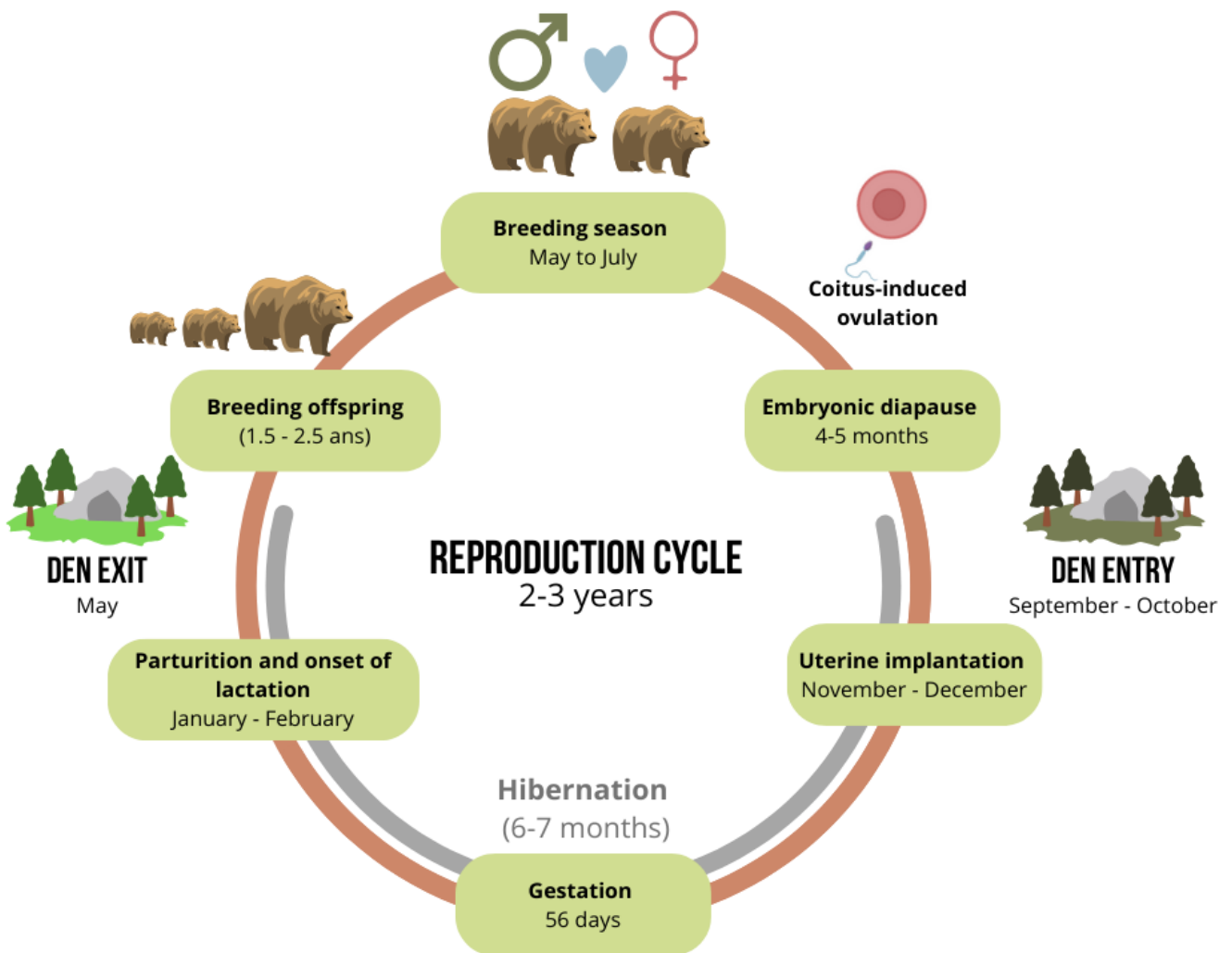
such, movement characteristics serve as a mirror of an internal status, potentially revealing an individual's reproductive status. This opens the possibility for developing a robust tool, which utilizes movement patterns to extract information on the animal's internal, reproductive status, offering a more nuanced understanding of behavior in relation to environmental and physiological conditions. This could potentially help to extract demographic data of interest, enabling better management and conservation of populations. This complex challenge necessitates innovative approaches to reliably monitor and interpret the reproductive dynamics critical to conservation efforts, employing GPS data collection methods that, aside from the initial collaring process, remain minimally invasive. This could potentially facilitate the extraction of valuable demographic data, enabling more effective management and conservation of populations.

In line with these efforts, the Scandinavian Brown Bear Research Project (SBBRP) has employed a comprehensive surveillance approach for the study population, which includes both aerial and ground monitoring since 1987. Throughout the active season from April to August, irregular aerial surveys are conducted to assess natality and the survival of litters. These surveys are crucial for evaluating the presence and number of cubs, and litter losses.

## **2. Chronology of reproduction in brown bears**

Most female brown bears in Eurasia typically reach primiparity at the age of 4–5 years (Zedrosser et al. 2009). The mating season occurs at the end of spring and the beginning of summer (Spady, 2007) as shown in Figure 1. After fertilization, the female brown bear experiences an obligatory embryonic diapause for 5 to 6 months which ends with the implantation of the embryo around November-December (Wimsatt 1963). The active phase of gestation that follows has been reported to be 51 days on average for the study area's population (Lemièrre et al. 2022). Parturition takes place between January and early

February (Lemière et al. 2022) during hibernation. The female will nurse one to four cubs for several months before and after exiting the den, while no paternal care is provided (Friebe et al. 2014). The offspring remains with their mother for 1.5 to 2.5 years before separating (Dahle, Swenson 2003; Joanie Van de Walle et al. 2020) and females generally do not mate while they are caring for their young (Swenson et al. 1994).



*Figure 2: Brown Bear reproduction cycle according to Friebe et al., 2014. Source Canva, by author*

### **3. Movement patterns of brown bears and reproductive status**

The impact of reproductive status on movement can already be seen in the denning phenology. Pregnant females are more selective when choosing a denning area and exhibit increased caution, frequently visiting the future den site several months before hibernation begins to ensure meticulous preparation (Friebe, Swenson, Sandegren 2001). They typically enter hibernation as early as late September, starting earlier than any other reproductive states. They also tend to emerge later in May-June, and therefore experience the longest denning periods (Manchi, Swenson 2005). During hibernation bears remain in their dens without eating, drinking, urinating or defecating for 6-7 months, surviving solely on stored fat reserves while their body temperature, heart rate and metabolic functions slow dramatically to conserve energy until spring (Alina L. Evans et al. 2016).

During the active season, for a solitary individual, average daily movements can vary from 1.5 to 3.5 km, peaking during the mating season when bears, especially males, make longer excursions to find mates and engage in scent marking (Huber, Roth 1993; Seryodkin et al. 2017; Dahle, Swenson 2003; Krofel, Filacorda, Jerina 2010; Steyaert et al. 2012).

The movement of females during the active season is also influenced by the presence and age of offspring. Providing maternal care constitutes a significant parental investment (Robert Trivers, 1974; Celia Moore, 1995) and this costly behavior influences their movement patterns.

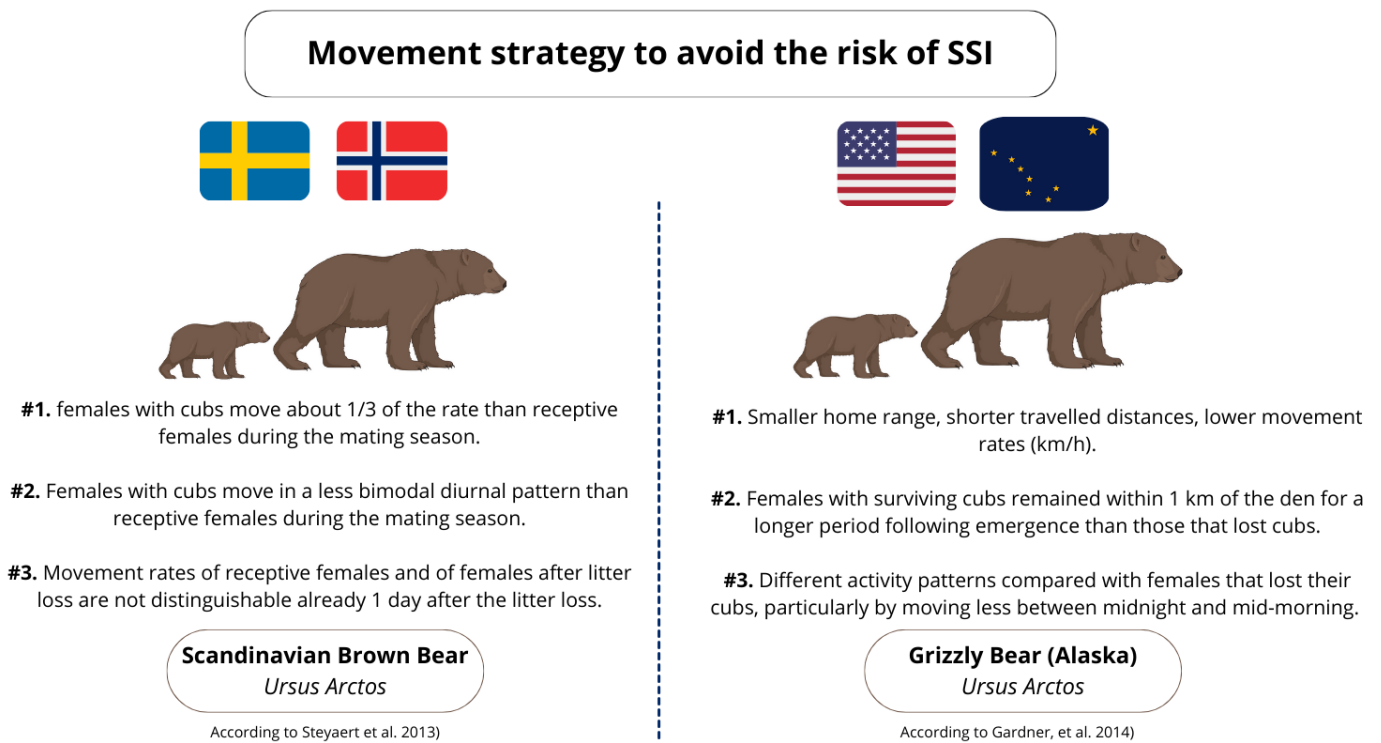
The movement of a female with cubs-of-the-year (COY) is heavily influenced by the mobility of her cubs. COY cannot move as much as yearlings, two-year-old, or solitary females, which the mother must take into consideration in her own movements.

The movement of female brown bears during the active season is highly influenced by the presence and age of their offspring (Steyaert et al. 2012). Cub mortality is high during their first year of life (35% in central Sweden) and is mainly due to the sexually selected infanticide (SSI) perpetuated by males during the mating season that starts right after the female emerges from the den with her litter (Swenson et al. 2001). Infanticide is known to be the most important cause of death for brown bear COY in Scandinavia (Steyaert et al. 2012). SSI is an adaptive male mating strategy that is observed in certain animal species, including bears, where individuals (usually males) kill offspring that are not their own to shorten the time to the mother's next estrus (which is usually suppressed when the female lactates dependent offspring) and enables the perpetrator to sire the next litter (Bellemain, Swenson, Taberlet 2006). It has also been observed that the movement rates of receptive females and those who have lost their entire litter become similar in a few days after the litter loss (Gardner, Pamperin, Benson 2014).

The least costly strategy for females with COY is avoidance to maximize their fitness even if sometimes they can fiercely defend their offspring when they sense danger, especially when males try to attack them (Zedrosser et al. 2009). To minimize the risk of infanticide, females adopt various strategies to increase COY survival. They tend to reproduce with males whose territories overlap with their own (Bellemain, 2006a), and multiple paternity (the fact that cubs of the same litter can have different fathers) could also be a strategy to induce confusion in males when they encounter a female they reproduced with the previous year. Additionally, females with COY restrict their movements and activity, particularly during the mating season, to avoid contact with potentially infanticidal males, often selecting less productive habitats to reduce infanticide risk (Dahle, Swenson 2003; Hertel et al. 2019; Steyaert et al. 2016), which can sometimes lead them to move closer to human infrastructures.

In Alaska it has been proved that females enhance cub safety by staying closer to the den for a couple of weeks following emergence, limiting their movements to selected habitat

patches, and decreasing their activity from midnight to mid-morning and significantly reduce their home range by 63–91% to minimize exposure to potential threats from adult male bears (Gardner, Pamperin, Benson 2014). Similarly, in the Scandinavian population, previous studies have shown that females with COY move at about one-third the rate of receptive females during the mating season and display a less distinct bimodal daily movement pattern compared to receptive females (Steyaert et al. 2013). Females with yearlings show an intermediate movement pattern, probably because they are less at risk of infanticide and can travel faster and over longer distances. These particularities of the movement of females with COY in both Alaska and Scandinavia are summarized in Figure 3.



**Figure 3:** Comparative movement characteristics of female with COY.

Source Canva, by author



#### **4. Framework of the Scandinavian Brown Bear Research Project: Context and Objectives**

The Scandinavian Brown Bear Research Project (SBBRP) is a multidisciplinary research project that has been ongoing for over 40 years. The philosophy of this group is simple: "follow the individual from birth to death" to improve the understanding of the species, which was still poorly developed a few decades ago. Using methods such as GPS/VHF collar tracking, den studies, scat sampling, and habitat surveys, the project explores essential aspects of bear biology.

Today, the project is multidisciplinary, with researchers from various scientific backgrounds: ecologists, veterinarians, biologists, and doctors all work together to study bears comprehensively. The SBBRP focuses its efforts on several key areas. It disseminates up-to-date information on bear biology and ecology, raising public awareness through various means such as webinars and articles. For 40 years, it has translated its research into concrete actions, providing Scandinavian managers with evidence-based data to guide management decisions. The program also collaborates with local communities to address bear management issues, including impacts on livestock and ungulates. Additionally, its research has led to advances in human medicine, using the brown bear as a model to better understand health problems related to sedentary lifestyles. Indeed, the bear's ability to hibernate for several months without losing muscle mass has led to detailed studies aimed at finding treatments to slow down muscle wasting during prolonged bed rest or space missions.

In summary, over 40 years, the SBBRP has made major contributions to brown bear biology and ecology, animal welfare, and human health. It has also developed new scientific methods and collaborated with international researchers, thereby improving bear management in various parts of the world.

## 5. Study aims

Therefore, the objectives are twofold.

**1/** A theoretical and fundamental part describes the movement of females based on their reproductive status and explores the intrinsic and extrinsic factors that may influence it as. Animal movement is affected by an individual's ability to orient within its environment, its physical capacity for movement, internal status, and extrinsic elements such as food availability, predation risk and competition, and climatic conditions (Demšar et al. 2015) such as ambient temperature and precipitation. According to the literature we hypothesize that the distances travelled by individuals and their daily home ranges will differ between the following reproductive statuses: females COY, females with yearlings, and solitary females.

Then, the intrinsic variables examined are reproductive status, and age. The main underlying hypothesis is that females with surviving COY exhibit a different spatiotemporal movement pattern following den emergence compared to those that lost their COY. This work also seeks to explore environmental variables that may influence the movement characteristics of these different statuses. The chosen factors are ambient temperature [°C], daily snow depth [m], and precipitation [mm/day]. We predict that movement will increase as we progress through the year, and that the aforementioned meteorological factors will tend to negatively impact movement.

**2/** Building on this initial reference study, we aim to infer the reproductive status of females through their movement data and detect cub loss events by identifying the breaking points at which the females travel faster and over longer distances following the stressful event of infanticide. After this event of litter loss and according to the previous literature we expect this a transition to occurs at least within few days, we expect that a female who has lost her litter will not return to the movement level of a female accompanied by COY but rather to the movement level of a solitary female seeking to

mate with a male. We will then use a classification model as a cross-validation method to verify if the identified date corresponds to the likely time of cub loss.

To summarize, this work aims to enhance our understanding of the movement of breeding female Scandinavian brown bears and to develop a reference for movement behaviors. This will allow us to consider using GPS data as a genuine monitoring tool capable of inferring the reproductive status of a given female based on her movement patterns and to determine if she experienced litter loss.

## **6. Integration into a Global Research Framework: Contribution and Perspectives**

The work carried out during these five months in Norway is part of the Scandinavian Brown Bear Project's ongoing research and, more specifically, will serve as a methodological tool for the various ongoing doctoral theses. The methodological tool developed aims to assign a reproductive status to a given female bear based on her movements. She will be categorized between two possible statuses: solitary or with COY based solely on the GPS positions recorded by her collar. This methodological tool also allows for the determination, with satisfactory precision and certainty, of the dates of COY loss (during infanticide events or mortality).

Access to this information allows for a broader range of research questions and a better estimation of the demographic parameters of the studied populations.

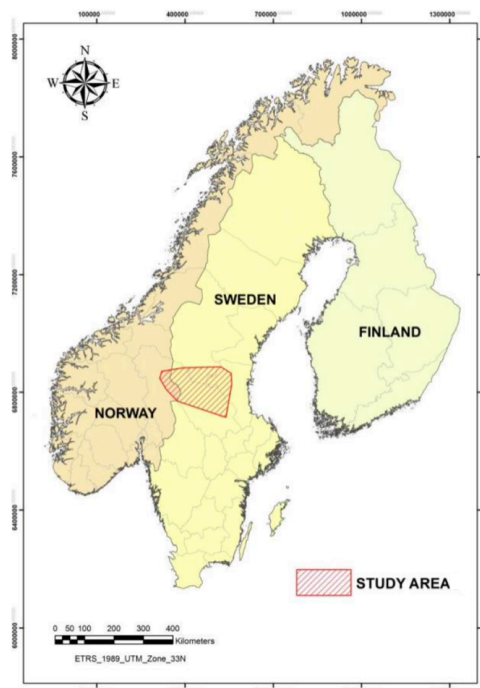
One of the projects that the SBBRP aims to study is the impact of climate change on the reproductive success of brown bears. Indeed, as temperatures rise, den emergence dates tend to occur earlier. However, birthing dates do not seem to follow this trend, which seems to lead to significant phenological mismatches. Female bears tend to emerge from the den earlier, while the COY may not be in a sufficient physical condition to move at that time. This lack of readiness can lead to increased mortality, especially due to infanticide, but also due to inadequate conditions to face winter during that period

of the year. Another PhD project currently underway within the SBBRP is studying the impacts of captures (chemical immobilization, sampling, and implantation of biologging devices, including surgeries) in the short and medium term. One aspect of this PhD would be to examine whether captures tend to increase the probability of a mother separating from her young. A premature separation could also lead to a decrease in the offspring's chances of survival.

## II. Material and Methods

### 1. Study Area

The main study area of the SBBRP is located in the counties of Dalarna and Gävleborg in central Sweden (61°N, 18°E). This area encompasses 13,000 km<sup>2</sup> of intensively managed coniferous forests, with altitudes ranging from 200 meters to 1,000 meters, and 90% of the terrain situated below 750 meters.



*Figure 4 : Map of the study Area*

## 2. Study population

Data were collected from 97 sexually mature female bears (i.e. age > 4 years, (Zedrosser et al. 2009) that have been followed by the SBBRP from 2006 to 2023. However, the statistical unit used is the individual per year, meaning that some individuals appear multiple times in our dataset, each corresponding to a different year. As a result, we have 114 statistical units.

*Table 1 : Study population and reproductive status summary*

Reproductive Status	Status of the Litter	Number of Individuals	Median Age	Min Age	Max Age
Solitary		32	5.0	4.0	17.0
Accompanied by Yearling		26	11.0	6.0	24.0
Accompanied by COYs	All the litter survived	37	11.0	4.0	23.0
	Partial loss of the litter	5	7.0	5.0	9.0
	Total loss of the litter	13	7.5	4.0	16.0
<b>Total</b>		<b>114</b>	<b>7.5</b>	<b>4.0</b>	<b>24.0</b>

## 3. Bear Captures collaring and general monitoring

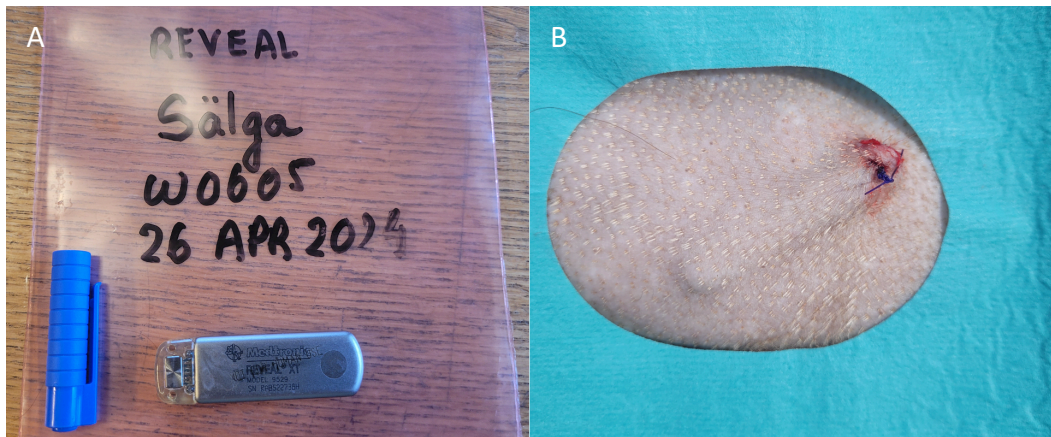
The main purpose of the SBBRP is to follow individuals throughout their life to conduct long-term ecological studies for management purposes. This monitoring involves different type of fieldwork and data collection Figures 5 and 6.

The SBBRP conducts annual captures of brown bears in Sweden in spring by darting from a helicopter with a combination of medetomidine-tiletamine-zolazepam in accordance with an established protocol (Arnemo, Evans 2017). All procedures were conducted under the approval of the Swedish Ethical Committee on Animal Research, Uppsala, Sweden (Dnr C3/2016 and Dnr C18/15). Individuals are equipped with biologgers including a global positioning system (GPS) collars fitted with a dual-axis accelerometer that records activity since 2003 (Vertex Plus, Vectronic Aerospace GmbH,

Berlin, Germany), and on some occasions with a temperature logger that is surgically implanted in the abdomen since 2010 (DST Centi-T, Star Oddi, Iceland) Figure 5 and 7. Tb (body temperature), used to determine if the female is pregnant, is recorded every 30 min thanks to a biolgger implanted in sternal region (Figure 6).The collars are programmed to record GPS positions at hourly intervals from 1st March - 30th November and at one position per day for the rest of the winter but this frequency can vary depending on the ongoing studies and due to reception issues. Activity is recorded every 5 min at 6–8 Hz and individual indices (ranging from 0 to 510) are calculated by summing the acceleration values of both orthogonal axes for each 5-min interval (Vincenzo Gervasi, Brunberg, Swenson 2006; Friebe et al. 2014).



*Figure 5: GPS collaring. New GPS collar for adults (A) and yearlings (B) Photograph by author.*



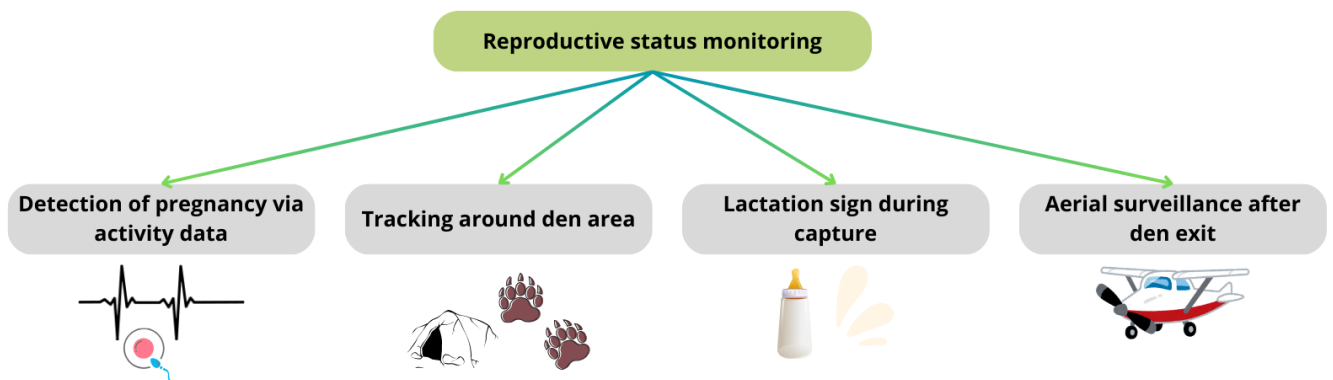
**Figure 6 :** Figure 6: Biologger before (A) and after surgical implantation in sternum area (B). Photograph by author.



**Figure 7:** intra-abdominal VHF radio implant.

To determine den positions, GPS positions transmitted during the winter period are systematically investigated. The observed clusters are visited when possible after the bears have left the denning area and exact positions of the dens are taken with a handheld GPS. For the dens which could not be visited, we use the geographic mean of the cluster comprising at least 6 GPS positions within 100 m for at least 2 consecutive days between January and April.

To assess natality, litter size and cub losses, cubs-of-the-year presence and numbers were monitored on various occasions during the active season (Figure 8 and 9). When denning sites were visited in spring after the family had left the area, signs of presence (i.e., tracks in the snow, scats and climbing marks on the trees) of cubs-of-the-year were reported. Additionally, irregular annual aerial surveys are conducted throughout the active season from April/May to August by plane or helicopter and all females were observed at least twice. In case of GPS collar failure, females were recaptured to replace the collar and the presence and number of cubs was also noted on this occasion. All families were captured the following year in spring for the need of other projects and the presence of cubs was also reported.



*Figure 8: Summary of monitoring methods. Source Canva, by author*



*Figure 9: Signs of lactation observed during spring captures. Photograph by author*



## **4. Data preparation**

All data preparation, visualization and analyses were conducted in R (version 4.3.0). Because the time interval between the recorded positions of an individual could vary, we standardized the GPS data to one position per hour to ensure consistency across the dataset. A comprehensive mind map provided in Appendix 7 relates all the steps of data preparation.

## **5. Movement metrics**

We investigated three different movement metrics to explore the differences in terms of movement among the different reproductive statuses.

### **a) Mean daily Step length**

Step length was calculated with the “bayesmove” package (Cullen et al. 2022) and describes the euclidean distance between two successive locations. Because our dataset was standardized to one position per hour. The step length corresponds to a specific speed given in meters per hour ( $m \cdot h^{-1}$ ). The metric used was the average distance traveled per hour for a given day.

### **b) Mean daily home range**

Daily mean home range was calculated with the “amt” package (Signer, Fieberg, Avgar 2019) and we utilized the 95% Minimum Convex Polygon (MCP) so corresponding to the average home range size of the individual for a given day. The 95% MCP method involves constructing the smallest convex polygon that encloses 95% of the recorded locations, focusing on the core area of animal activity by excluding the outermost data points.

### c) Persistence

Persistence, calculated according to Equation 1, in the context of animal movement refers to the consistency with which an animal maintains its speed and direction over time. Persistence is quantified by evaluating autocorrelation between consecutive steps (relocations) in an animal's movement trajectory. A high persistence value (close to 1) indicates that the trajectory shows a high degree of autocorrelation, meaning the animal moves in a relatively straight line at a constant speed. Conversely, a low persistence value (close to 0) suggests a more erratic movement pattern, resembling a random walk, where the direction and speed change frequently. This metric has been calculated with the “animotum” package (Jonsen et al. 2019).

*Equation 1 :  $d_t$  is the changes in an animal's location  $x$  at times  $t$  and  $t-1$ . The random variable  $\eta_t \sim N(0, \Sigma)$ , with variance-covariance matrix  $\Sigma$ , specifies the magnitude of variability in the two-dimensional movements.  $\gamma_t$  is the time-varying movement*

$$d_t = \gamma_t d_{t-1} + \eta_t$$

## 6. Intrinsic factors

### a) Reproductive status monitoring

From our dataset we differentiated between three reproductive statuses: solitary females not accompanied by cubs, females accompanied by cubs born in the same year (COY) or females accompanied by cubs born the previous year (yearlings). Within the females with COY category, we differentiated between females who retained their COY until at least the end of June and females who lost their cubs at some point before June either completely or partially. We only include females that survived through the study period (until 30th June) in our GAMMs analysis. Bears were monitored irregularly on various

occasions over the course of a year, and the final reproductive status assigned to each female was determined by combining several methods.

### **b) Pregnancy status**

To detect gestation events, different parameters were used sequentially (i.e. if the first parameter could not be assessed, then the second one was evaluated etc.) in the following order:

- (1) observation and counting of COY during aerial surveys the following spring/summer.
- (2) maternal activity or temperature profile compatible with pregnancy during winter (Friebe et al. 2014; Lemière et al., 2022). A pregnancy can be detected when there is a period of high activity and elevated temperature in pregnant females, followed by a significant drop around the time of parturition.
- (3) signs of COY (tracks in the snow, claw marks, remains, scats...) observed at the den site during aerial surveys or when visiting the den site in spring,
- (4) signs of lactation observed during the capture (milk, used nipples...).

Females that filled up at least one of these criteria were classified as pregnant and as non-pregnant otherwise.

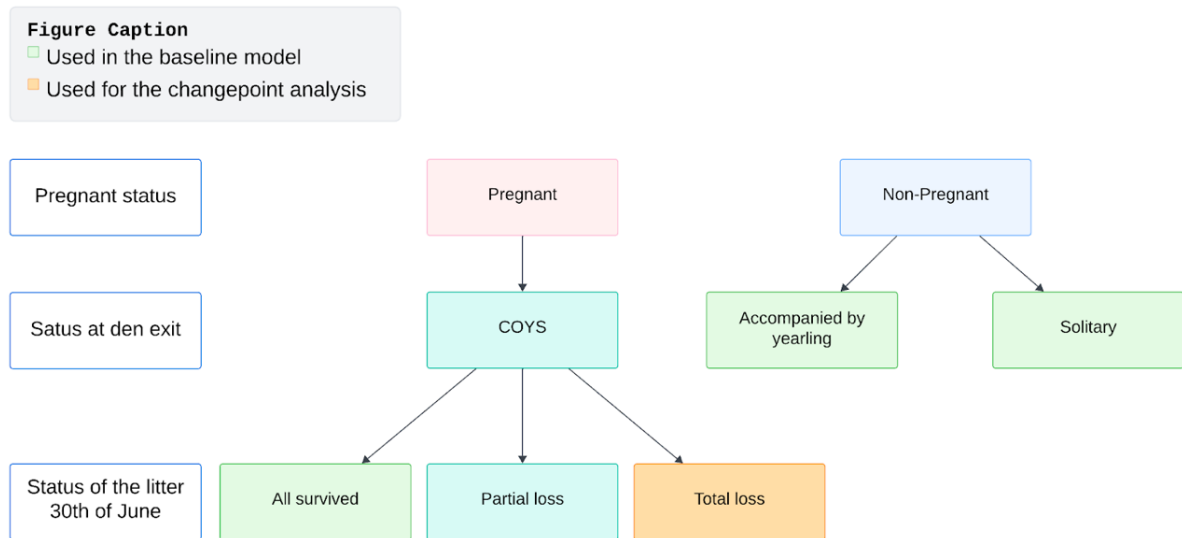
### **c) COY losses**

Cub losses were assessed for the females with COY based on the aerial monitoring conducted throughout the active season (Figure 1).

- If the number of COY counted remained the same throughout the entire active season, we considered that all cubs had survived,
- If the female was never seen again with her litter during the active season, we considered that a total loss had occurred,

- If the female was seen with at least one COY at the end of the active season, but the final number of COY was below the maximum number of COY reported during that year, we considered that a partial loss had occurred.

All reproductive categories and scenarios regarding the survival of bear cubs have been specified in Figure 10.



**Figure 10:** Overview of the different reproductive statuses included in the study.

*Notes: Females accompanied by two-year-olds were excluded from the study because they are very likely to separate and we do not know the exact date of separation. 2. The females accompanied by yearlings included in the study are those for which we are certain there was no separation during the year studied. 3. Some females can be detected as pregnant during hibernation but may emerge from the den without cubs (due to mortality inside the den or late-term abortion). Figure by author.*

The age of the bears was determined by following the offspring of marked females from their first capture as yearlings, or by counting the annuli of cross-section of the root of one of the first premolars after surgical extraction for the females that were captured as adults for the first time (Harshyne et al., 1998). The median age of these females was 8 years (min age : 4 years - max age : 24 years, Fig. 1).

## **7. Extrinsic factors**

The R package “openmeteo” (Zippenfenig 2024) was utilized to extract the following environmental variables: `temperature_2m_max`, representing the maximum daily air temperature at 2 meters above ground, and `precipitation_sum`, indicating the sum of rain, showers, and snow over the preceding day. We obtained daily snow depth data [m] of all Swedish weather stations from the Swedish Meteorological and Hydrological Institute (SE-601 76 Norrköpping, Sweden) and used inverse distance weighted interpolation from the R package *gstat* (Pebesma 2004) based on the five closest weather stations. The GPS positions chosen for each individual per year correspond to the location of the last known den used by the individual during the hibernation for that specific year. Den locations were determined based on GPS clustering observed during winter and subsequent visits in the field the following spring (ref Andrea). (Friebe, Swenson, Sandegren 2001). To avoid biases caused by captures, the locations of individuals captured in the spring or early summer were excluded for three days following the capture date.

## **8. Statistical Analysis**

This research investigated differences in movement patterns of female bears relative to their reproductive status from den emergence to the end of the mating season.

### **a) Baseline movement model**

We used Generalized Additive Mixed Models (GAMMs) to estimate the baseline movement patterns of the three different reproductive states, employing 'mgcv' (Wood 2017) and 'itsadug' (Van Rij et al. 2015). GAMMs allow for a robust handling of non-linear relationships between response and predictor variables and temporally autocorrelated data. We used daily values of mean daily of step length (m/h), home range and persistence parameters from 15th April - 30th June as three separate response variables

and set up a list of candidate models encompassing the following predictor variables: reproductive status as in interaction with the day of the year, age of the female and extrinsic/environmental variables (maximum daily ambient temperature, maximum daily precipitations and daily snow depth) as an interaction with reproductive state. All interactions were modeled as non-linear effects. (Table 2, 3, 4). Correlation and structure of the environmental variables were checked using a correlation matrix (Appendix 2).

A gamma distribution with a log link function was used for models with step length as a response variable, a scat distribution with identity link for home range and a gaussian distribution for persistence. All models included a random intercept for the individual bear to control for inter-individual variability and repeated measurements and an autoregressive model structure (AR1) (José C. Pinheiro 2000) to account for temporal autocorrelation in the error structures. Basis dimensions for the parameter  $k$  were checked with “gam.check” function and diagnostic plots were investigated to validate model assumptions (Appendix 4).

We used the Akaike Information criterion and the R package “bbmle” to compare candidate models with each other and the highest ranked model within  $\Delta AIC \leq 2$  was picked (Burnham, Anderson 2004).

## **b) Development of a new tool to determine reproductive status and detect cub losses**

### **i. Random Forest training**

To verify if movement could be used to determine the reproductive status of a female, we used a random forest (RF) trained on 78% of the dataset and ran it on the remaining 22% (Wright, Ziegler 2017). We aimed to train this model specifically to distinguish between a solitary female and a female with cubs, so the training was conducted on a subset containing only these two reproductive statuses, excluding females with yearlings.

## ii. Identifying the timing of litter loss

For identifying when females with COY may lose their litter, a bayesian changepoint analysis was performed using the 'rbeast' package (Zhao et al. 2019) facilitating a multivariate approach by including both step length and home range into the decomposition of the time series. This approach could detect notable changes in time series data, exemplified by the sudden alterations in movement experienced by females upon losing their COY. It also assigns a probability to each identified changepoint.

Females who have been monitored with COY and confirmed to have lost their entire litter ( $n = 13$ ) were included in this changepoint analysis in order to detect the timing of when this litter loss occurred. The change point algorithm was parameterized to detect up to 3 changepoints and polynomial order could vary from constant to linear.

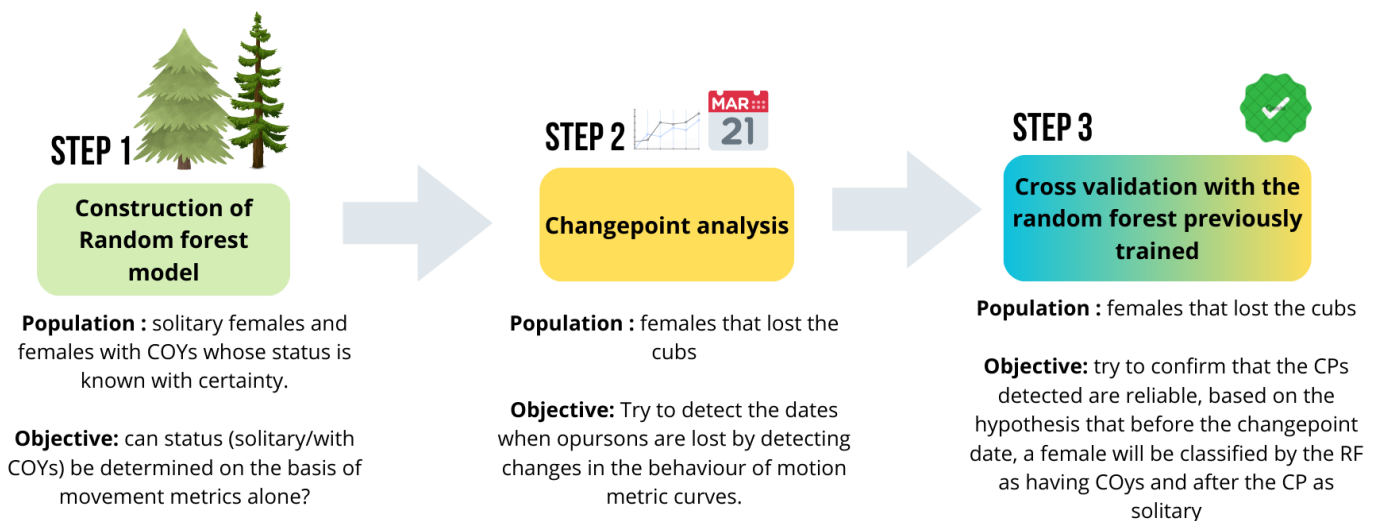
The MCMC process included a burn-in of 5000 iterations and 15000 samples post-burn-in and the analysis accounts for deseasonalization and detrending. For each changepoint identified as a potential date of cub loss, we assigned a reliability index (RI). An RI of 1 indicates that no changepoint matched the monitoring table, and the changepoint with the highest probability was selected. A RI of 2 denotes a changepoint that was not the most probable but aligned with the observations from the monitoring table. An RI of 3 represents the most probable changepoint occurring during a period consistent with the aerial monitoring table. Priority was given to choosing the changepoint with the highest RI.

To exclude the possibility that a detected changepoint corresponds to den exit when bears resume their activity in spring, we identified that event based on using GPS positions data before running the changepoint analysis. Following (Lemière et al. 2022) we considered that a bear had left its den when it moved further than 100 m from the den position in the following spring.

### iii. Cross Validation of the changepoint analysis through the Random Forest method

After assigning a litter loss date (changepoint) for each individual, a subset was created for each individual, and all observations were classified using the Random Forest model. This step aimed to assess the accuracy of the changepoint method. To determine COY losses, time periods before and after a changepoint for females who had lost all their COY were analyzed individually to categorize their movement patterns as either corresponding to females accompanied by COY or to solitary females. The RF model categorizes observations based on these changepoints, identifying periods when a female should still be accompanied by COY (before the changepoint) and periods when she should be classified as solitary (after the changepoint). An example of a misclassified observation occurs when the RF model incorrectly categorizes a movement pattern, such as classifying a female still accompanied by COY as solitary, or vice versa after the changepoint. This misclassification leads to a decrease in accuracy.

The entire methodological process is visually represented in Figure 11.



*Figure 11: Summary of the methodological process. Source Canva, by author*



### III. Results

#### 1. Baseline movement model

##### a) Mean daily step length

The highest-ranked model for step length included both of the variable's day of the year and snow depth in an interaction with reproductive status as non-linear predictor variables, and included precipitation as an additional variable (Table 1). For solitary females and females with yearlings, step length increased from day 105 (April 15), but those with yearlings moved 50% less than solitary females. For females with cubs of the year, step length increased gradually from day 130 (May 10), however moving 90% less than solitary females this day. By day 150, solitary females and those with yearlings move 504 m/h and 354 m/h averaged over a day, respectively, while those with cubs move 78% less [112 m/h (95% CI:)]. From day 157 (June 6), the mean distance travelled by solitary females decreased, and by day 182 (July 1), there were no significant differences among reproductive statuses (Figure 2 - A).

**Table 2:** AIC model selection table for mean daily step length [m/h]. All models included a random intercept for the Bear ID. The highest ranked model (highlighted in blue) included an autocorrelation structure AR1.

Model	Model Candidates	AIC	ΔAIC	df	Weight
m9	s(day, by = repro_status) + repro_status + s(snow_depth, by = repro_status) + precipitation	64,484.3	0.0	64.0	0.67
m11	s(day, by = repro_status) + repro_status + s(precipitation, by = repro_status) + s(snow_depth, by = repro_status)	64,485.8	1.5	65.9	0.33
m8	s(day, by = repro_status) + repro_status + snow_depth + precipitation + temperature	64,567.6	83.3	61.7	<0.001
m7	s(day, by = repro_status) + repro_status + snow_depth + precipitation	64,572.0	87.7	60.8	<0.001
m10	s(day, by = repro_status) + repro_status + s(precipitation, by = repro_status) + snow_depth	64,574.9	90.6	62.6	<0.001
m6	s(day, by = repro_status) + repro_status + snow_depth	64,580.3	96.0	59.6	<0.001
m4	s(day, by = repro_status) + repro_status	64,763.5	279.2	58.0	<0.001
m5	s(day, by = repro_status) + repro_status + age	64,768.2	283.9	58.3	<0.001
m3	s(day) + repro_status	65,196.4	712.1	48.1	<0.001
m2	s(day) + s(bear_id, bs = 're')	66,588.5	2,104.2	50.2	<0.001
m1	1	67,920.4	3,436.1	44.8	<0.001

## b) Mean daily Home range

The highest-ranked model for mean daily home range included the day and reproductive status in a non-linear interaction term (Table 3). (Figure 2 - B) shows that all reproductive states follow an increasing trend in home range with solitary females having the highest predicted daily home range values, followed by females accompanied by yearlings and females accompanied by COY. On day 156 (5th of June 5), solitary females reach their maximum predicted daily home range (3.3 km<sup>2</sup>), while females with yearlings have a 38% smaller home range (2.0 km<sup>2</sup>), and females with cubs have a home range of 0.9 km<sup>2</sup>, which is 78% smaller than that of solitary females on the same day (Figure 2 - B).

**Table 3 :** AIC model selection table for mean daily Home range (km<sup>2</sup>). All models included a random intercept for the Bear ID. The highest ranked model (highlighted in blue) included an autocorrelation structure.

Model	Model Candidates	AIC	ΔAIC	df	Weight
m4_hr	s(day, by = repro_status) + repro_status	4,461.3	0.0	58.1	1
m11_hr	s(day, by = repro_status) + repro_status + s(precipitation, by = repro_status) + s(snow_depth, by = repro_status)	25,642.4	21,181.1	79.2	<0.001
m10_hr	s(day, by = repro_status) + repro_status + s(precipitation, by = repro_status) + snow_depth	25,650.0	21,188.7	71.7	<0.001
m9_hr	s(day, by = repro_status) + repro_status + s(snow_depth, by = repro_status) + precipitation	25,651.7	21,190.5	71.3	<0.001
m8_hr	s(day, by = repro_status) + repro_status + snow_depth + precipitation + temperature	25,661.6	21,200.3	67.1	<0.001
m5_hr	s(day, by = repro_status) + repro_status + age	25,665.4	21,204.1	64.9	<0.001
m3_hr	s(day) + repro_status	25,885.0	21,423.8	50.2	<0.001
m2_hr	s(day)	26,191.5	21,730.2	50.8	<0.001
m1_hr	1	26,798.1	22,336.8	47.6	<0.001

### c) Persistence

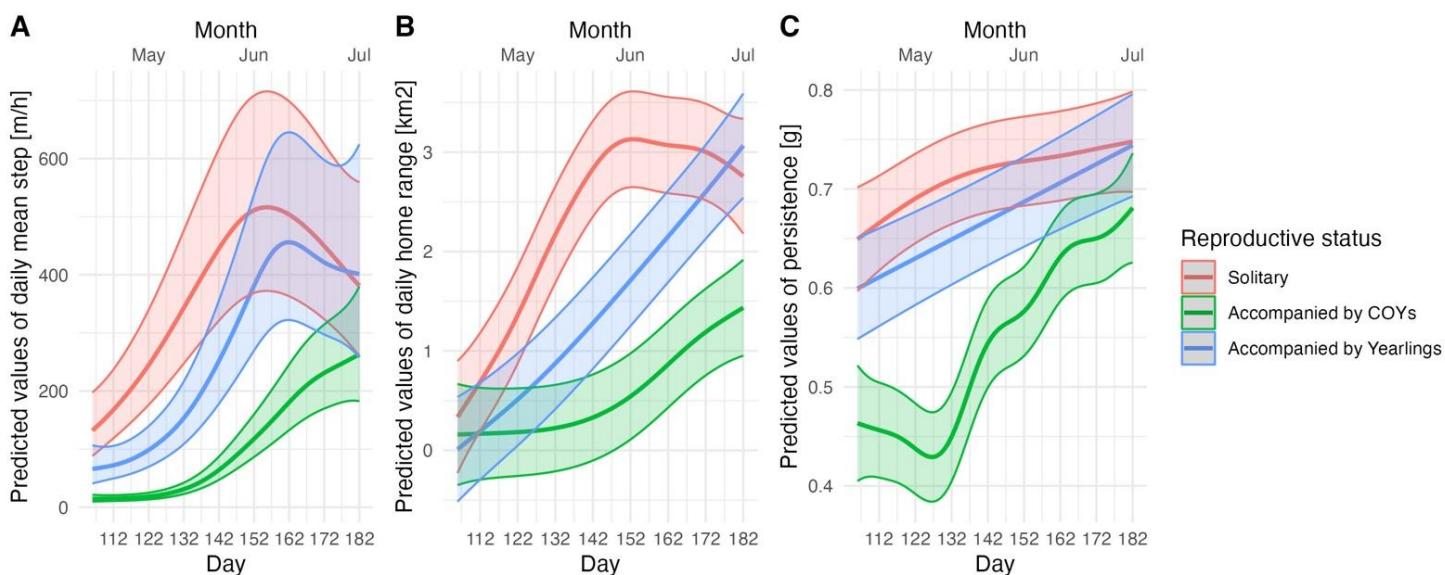
The highest ranked model for persistence included the factor-smooth interactions of day, snow depth, and temperature with reproductive state each, as well as age and precipitation as predictor variables (Table 4) and (Figure 2 - C) shows that solitary females had the highest predicted persistence values over time, followed by females accompanied by yearlings, while females accompanied by COY have the lowest predicted persistence values, with all groups demonstrating an overall increasing trend.

**Table 4 :** AIC model selection table for mean daily persistence (g). All models included a random intercept for the Bear ID. The highest ranked model (highlighted in blue) included an autocorrelation structure.

Model	Model Candidates	AIC	ΔAIC	df	Weight
m10_g	s(day, by = repro_status) + repro_status + age + s(snow_depth, by = repro_status) + precipitation + s(temperature, by = repro_status)	-5,175.5	0.0	75.9	0.6843
m14_g	s(day, by = repro_status) + repro_status + age + s(snow_depth, by = repro_status) + s(precipitation, by = repro_status) + s(temperature, by = repro_status)	-5,173.9	1.6	77.9	0.3032
m8_g	s(day, by = repro_status) + repro_status + age + s(snow_depth, by = repro_status) + precipitation + temperature	-5,166.9	8.6	70.0	0.0093
m9_g	s(day, by = repro_status) + repro_status + age + s(snow_depth, by = repro_status) + s(precipitation, by = repro_status) + temperature	-5,164.8	10.7	72.0	0.0033
m11_g	s(day, by = repro_status) + repro_status + age + snow_depth + precipitation + s(temperature, by = repro_status)	-5,100.6	74.9	67.9	<0.001
m12_g	s(day, by = repro_status) + repro_status + age + snow_depth + s(precipitation, by = repro_status) + s(temperature, by = repro_status)	-5,098.6	76.9	69.9	<0.001
m13_g	s(day, by = repro_status) + repro_status + age + snow_depth + s(precipitation, by = repro_status) + temperature	-5,088.9	86.6	64.0	<0.001
m7_g	s(day, by = repro_status) + repro_status + age + snow_depth + precipitation + temperature	-5,085.5	90.1	60.0	<0.001
m6_g	s(day, by = repro_status) + repro_status + age + snow_depth	-5,085.5	90.1	60.0	<0.001
m5_g	s(day, by = repro_status) + repro_status + age	-5,048.7	126.8	60.7	<0.001
m4_g	s(day, by = repro_status) + repro_status	-5,034.9	140.6	59.6	<0.001
m3_g	s(day) + repro_status	-4,778.3	397.3	48.1	<0.001
m2_g	s(day)	-4,340.6	834.9	49.3	<0.001
m1_g	1	-3,470.5	1,705.1	44.6	<0.001

#### d) Global representation of the GAMMs

Figure 12 illustrates the predictions of the generalized additive mixed model for three movement metrics: mean daily step length (A), mean daily home range (B), and mean daily persistence (C), from April 15th to July 1st. The curves are segmented by the reproductive status of females: green represents those with cubs of the year (COY), blue represents those with yearlings, and red corresponds to solitary females. The lighter areas represent the 95% confidence interval. This figure provides an overview and serves as a reference model, demonstrating that the three selected metrics were relevant and showed significant differences between the three reproductive statuses at specific times of the year.



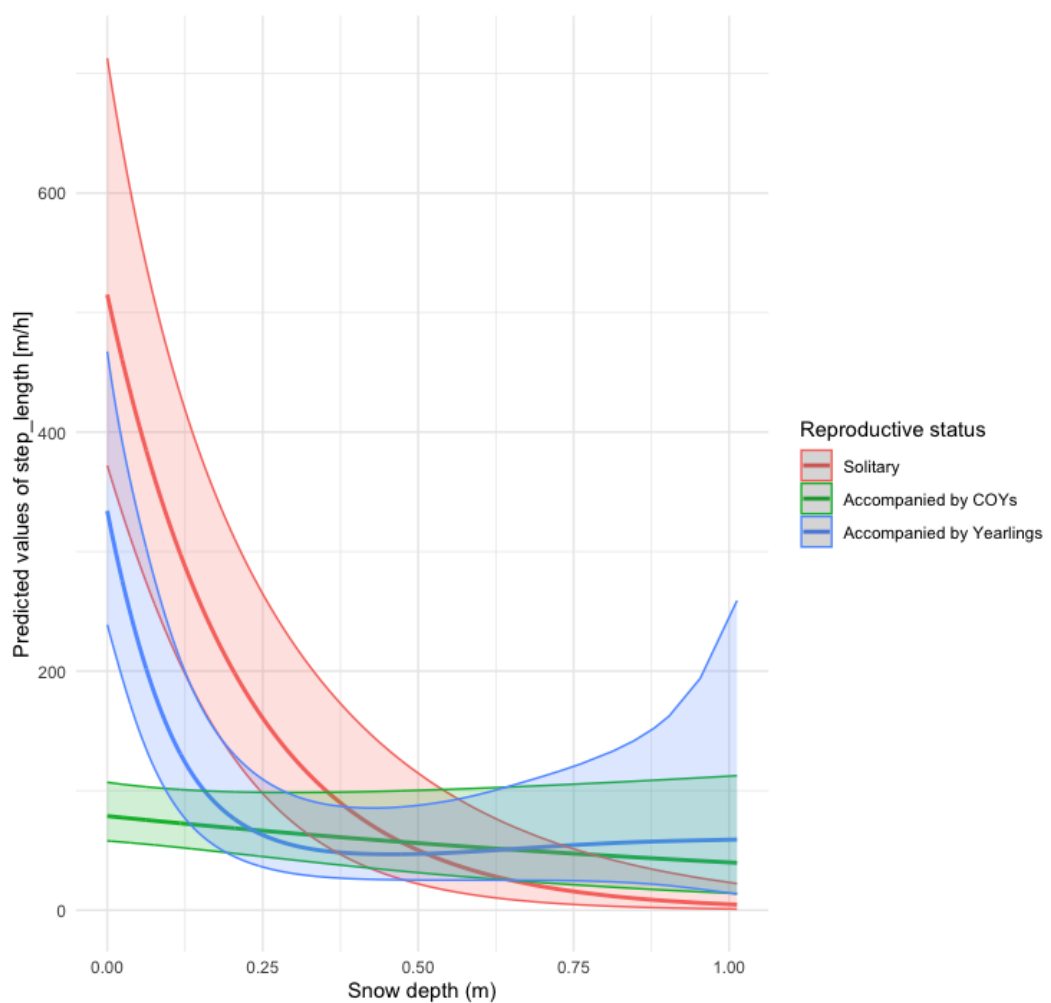
**Figure 12:** Predictions of the Generalised additive mixed model for the three selected movement metrics.

Mean daily step length [m/h] (A), Mean daily home range [km<sup>2</sup>] (B) and Mean daily persistence [g] (C) from 15<sup>th</sup> of April (105<sup>th</sup> day of the year) to the 1<sup>st</sup> of July (182<sup>th</sup> day of the year) for each reproductive status. The lighter areas represent the 95% confidence interval (CI). Green correspond to females with COY, blue to those accompanied by yearlings when red is corresponding to solitary females.

## 2. Effect of environmental factors

Precipitation had a negative effect on step length for all reproductive states, while snow depth negatively impacted step lengths only in solitary females and females accompanied by yearlings (Appendix 4 - A)

Snow depth and temperature negatively impact persistence for females accompanied by yearlings and females accompanied by COY, respectively (Appendix 4 - C). Effect of snow on mean daily step length for each reproductive status is given in Figure 13.



**Figure 13:** Effect of snow depth (m) on Mean daily step length (m/h)

### 3. Classification model performance

Following a training phase on a subset representing 78% (14 752 observations for 54 individuals) of the total dataset, 22% of the data were used for testing (4089 observations 7 females solitary and 8 with COYs). As shown in the following confusion matrix (Table 5). The model correctly predicted the reproductive status in 73.9% of cases, with a positive predictive value of 0.76 and a negative predictive value of 0.72. sensitivity was 0.61 and specificity was 0.85. The classification details for each observation provided by the random forest are presented in the confusion matrix in Table 5. Each observation/unit corresponds to a daily average value of step length, home range, and persistence.

*Table 5: Confusion matrix*

Predicted status	Reference status	
	Solitary	Survived
Solitary	1204	372
Survived	775	2046

*'Positive' class: Solitary*

### 4. Change point analysis

Out of three possible change points for each of the 13 individuals, one was selected as described in the methods and the associated date extracted. The Bayesian analysis typically detected a change point when a sudden increase in mean daily step length and home range.

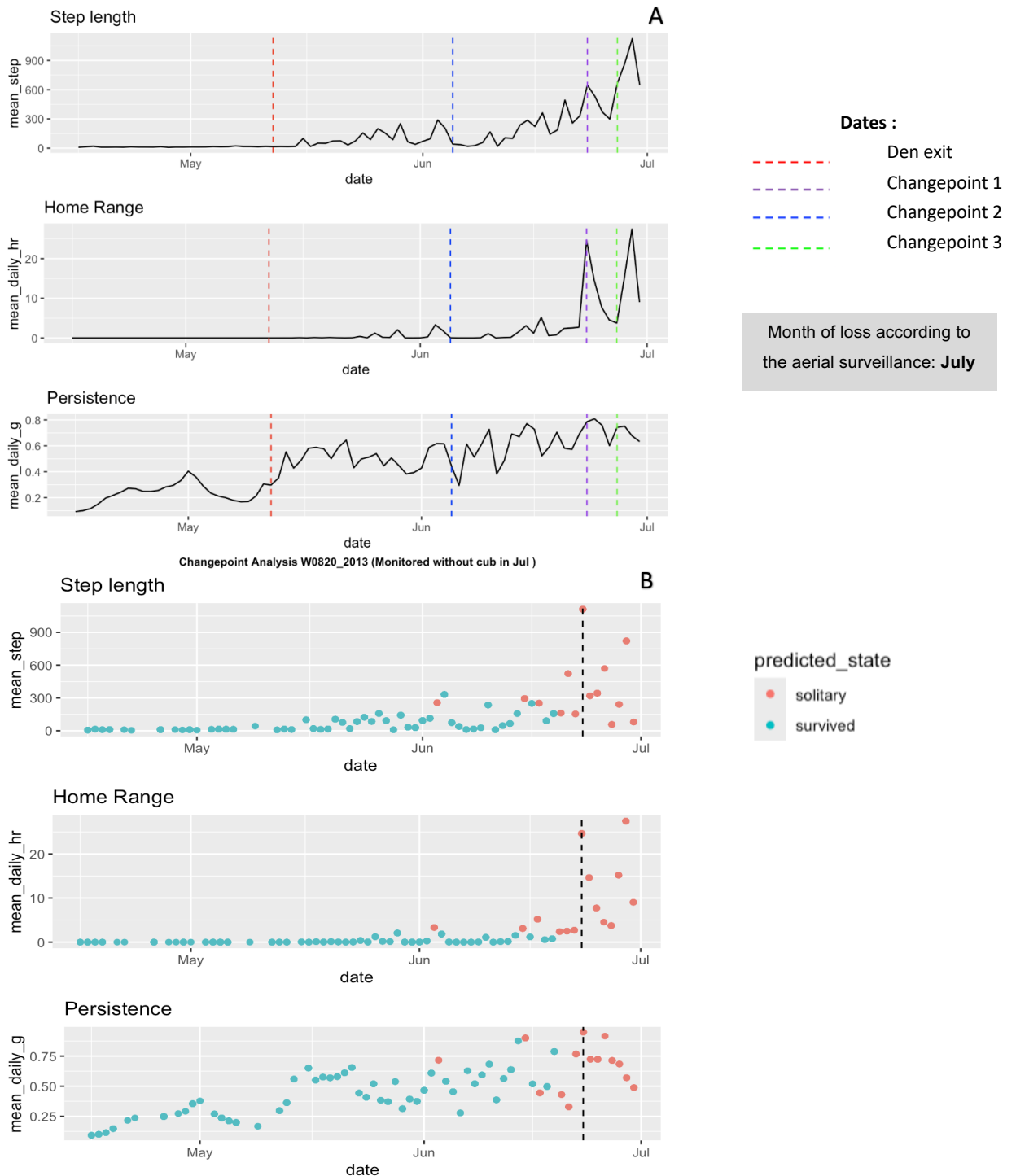
Six change points were associated with a reliability index of 1, five with an index of 2, and two with an index of 3. The highest probability based on the change point algorithm was 1, while the lowest was 0.2 and associated with a reliability index of 2.

## 5. Assess litter loss dates – Cross-Validation of Changepoint Detection through Random Forest Approach

The RF model categorizes observations based on selected changepoints, delineating periods when a female is accompanied by COY and when she transitions to solitary movement. The overall accuracy of the model is 74%, which increases to 85% when less reliable changepoints are excluded ( $RI < 2$ ). Performance metrics for the other RI values are presented in Table 6. An example of changepoint detection for one individual, along with the associated reproductive state classifications based on the random forest algorithm, is illustrated in Figure 14.

**Table 6 : Performance Metrics of Random Forest Model by Reliability Index of Changepoints**

Reliability.Index	Number.of.Changepoints	Accuracy	Sensitivity	Specificity	PPV	NPV
Global	13	0.74	0.78	0.69	0.69	0.76
3	3	0.85	0.83	0.91	0.68	0.84
2	5	0.85	0.73	0.91	0.82	0.86
1	5	0.57	0.80	0.33	0.56	0.61



**Figure 14:** Cross validation of Litter loss detection for individual W0820 (Åsanissa) in 2013

**(A)** - Results of Bayesian Changepoint: Variation in Mean Daily Step Length and Home Range. Persistence haven't been used for the changepoint analysis but is presented for visualization purposes. The litter loss occurred in July according to aerial monitoring. Changepoint 2 (purple dotted line) was the changepoint with the highest probability and used as the date of cub loss. **(B)** Classification by the Random Forest model previously trained to assess the reproductive status (Solitary female: red or female accompanied by COYs: blue) to each observation. (RI = 1. Accuracy of the Random forest analysis: 0.89 %.



## **IV. Discussion**

### **1. Baseline movement rates of the different reproductive states**

In this study, we showed that reproductive status influences the movement of female brown bears both temporally and spatially. The resumption of movement (i.e., increase in step length and home range) after den emergence occurs on average 25 days earlier for solitary females and those accompanied by yearlings compared to females accompanied by COY. This shift is consistent with what had been reported in our population between 1986 and 1998: solitary individuals emerged from the den on average on April 13, individuals accompanied by yearlings on April 12, and females with COY on May 7 (Friebe et al. 2001).

The baseline models for step length and home range are supported by findings from previous studies (Steyaert, Swenson, Zedrosser 2014; Gardner, Pamperin, Benson 2014) in which females with COY had comparatively smaller home ranges, and travelled shorter distances from den exit until the end of the mating season. Females accompanied by yearlings exhibited intermediate movement capacities between solitary females and those with COY. This can be explained by the fact that dependent offspring may restrict their mother's movements and cub's movement capabilities gradually improve as they grow, both due to an increase in size and a decrease in their vulnerability to climatic conditions due to their high surface/ratio volume and low hair insulation which lead to higher thermoregulation expenses. Additionally, the mother needs to stop regularly to lactate her cubs until weaning, which occurs between 6 and 8 months-old (Farley, Robbins 1995; Steyaert et al. 2012), and may need to increase her movement to find other food sources afterwards. Reproductive strategies could further explain the observed difference in movement between reproductive states, as it has been shown that females with COY decrease their home range during the mating season to avoid males and minimize the risk of predation and infanticide, whereas solitary females increase their

movement to find a partner to mate with, a behavior refers to as roam-to-mate behavior (Dahle and Swenson, 2003a). The fact that movement rate for solitary receptive females reached its maximum in early June, which coincides with the peak of the mating season (Steyaert, 2012), supports this hypothesis.

By the end of June, the differences in movement patterns among reproductive states could no longer be seen, which coincides with the end of the mating season (solitary females, then, decrease their movement) and the time when cubs are older and lactation slowly starts to decrease (Farley SD, Robbins CT, 1995). Females with yearlings exhibit an intermediate pattern probably because they are older, can travel faster, are less at risk of infanticide, and depend less on the mother's milk (Steyaert, 2012). Future studies examining the effect of cub number on movement metrics could provide better insights into this phenomenon.

As far as we know, the persistence indicator has never been used in studying bear movement characteristics or in characterizing their reproductive status. This study shows that females with COYs exhibited lower persistence values compared to the other two reproductive statuses studied. Movement persistence captures autocorrelation in both speed and direction indicating that females with COY had slower and less directional movement patterns compared to solitary females (Jonsen et al. 2019). Females with COY initially stay close to the den for a few weeks, resulting in very low movement persistence (alternating between short movements and rest periods) (Gardner, Pamperin, Benson 2014; Rogers, 2020). After leaving the den area, movement remains less directional as COY explore their surroundings, causing the mother to frequently travel back and forth to keep them together.

Female age had little influence on their movement, except for persistence, where older individuals exhibited higher levels of persistence. We could assume that experience, as previously suggested by other authors on other ecological parameters (Zedrosser, 2009; Steyaert, 2014; Lemièrre, 2022), could be an explanation for such difference. Older females, familiar with their home range, could tend to move less randomly which could

explain why their persistence values are on average higher. However, it would be helpful to support this idea with studies on speed and turning angles in young versus older individuals.

The extrinsic factors explored were temperature, snow depth, and precipitation. Each tended to reduce movement regardless of reproductive status. For females with COY, snow depth had no effect on their movement. This can be explained by the fact that females are generally still in the den when snow depths are significant enough to impact movement, as indicated by the delayed onset of movement for this status group in our study. Females with COY in our study leave the denning area (distance > 100m from the den) on average on May 4 ± 3 days. On this date, the average snow depth over the years was 3 cm. In contrast, solitary females leave the den on April 10, when the snow depth is on average 23 cm. Despite important annual variations in snow depth, it illustrates why snow depth does not significantly impact the movement of females with COY.

This initial part of the study confirms our preliminary hypothesis that females accompanied by their offspring (both COYs and Yearlings) move less during the post-denning period and until the end of the reproductive season. However, Yearlings quickly increase their movement and reach a level comparable to solitary females by mid-season. The first part of this suggests that these three metrics could be used in our analysis to assess the reproductive status of a given female and potentially detect litter losses after den exit and confirm that significant differences exist between the different reproductive status studied.

## **2. Solitary or with COY? Insights from Classification Performance**

The random forest classification training model presented a good accuracy (73%) to determine the reproductive status of each daily value for 15 females, distinguishing between solitary and accompanied by COYs. Solitary females are not restricted in their movement after leaving the den. However, bears, after emerging from hibernation, are at the end of a period of hypometabolism. Consequently, the days following den emergence

often involve alternating phases of rest and movement, which can lead to some misclassifications of solitary female positions as females with COY.

Even if those first results are promising, accounting the number of individuals in our dataset (n = 143) the performance of this model could likely be improved by exploring additional metrics, using a bigger sample size and incorporating them with the ones used in this study. This approach of using random forest models to assess reproductive status is quite recent and innovative. In the field of mammal movement ecology, these models have primarily been applied to accelerometry data to determine and classify different behaviors such as grazing, resting, and ruminating in moose and cows at finer-scale time series (Kirchner Theresa et al. 2023; Erik Versluijs & Laura J. Niccolai et al. 2023)(Kirchner et al., 2023; Versluijs, Niccolai et al., 2023). Hooven et al. (2022), also determined the reproductive state and parturition events successfully with this method on a large mammal (the elk, *Cervus canadensis*) (Hooven et al. 2022).

### **3. Evaluation of Changepoint method to detect Litter Loss Dates - Cross-Validation Using the Random Forest Approach**

The Bayesian changepoint analysis in our study detected abrupt changes in step length and home range that could be linked to the loss of cubs (Steyaert, Swenson, Zedrosser 2014; Gardner, Pamperin, Benson 2014) or events necessitating a temporary increase in female mobility (e.g. human disturbance). However, for 5 out of the 13 tested females, the detected changepoint had the lowest reliability index (RI), indicating that the detected cub loss date was not consistent with the most probable period of litter loss determined by aerial monitoring. The dates of changepoints with low RI correspond to females who supposedly lost their litters very early, around the denning area (late April – mid May, N= 5). There are several possible explanations for the difficulty in detecting changepoints during this period. One reason could be the highly seasonal nature of the bear and its physiology. Even for solitary females, movement resumes gradually after leaving the denning area (Evans, 2016). For a female with cubs, this resumption is even more gradual.

Therefore, it can be assumed that even after a sudden loss of her entire litter, possibly due to infanticide, the female might have temporarily increased her movement as described later during the active season (Steyaert, Swenson, Zedrosser 2014). However, the hypometabolic state characteristic of the post-denning phase may cause the signal to be not strong enough to be detected.

A solution to this issue would be to increase the number of detectable changepoints using Bayesian analysis, making them visible even if their intensity is lower than the mid-season movement peaks observed in females that lost their cubs early later during the active season, or by observing these changes at finer temporal scales rather than relying on daily averages.

Another explanation could be the nature of the loss itself. In central Sweden, documented COY losses after den emergence can be attributed to poor nutritional conditions before the start of the mating season (~1rst of May) and are mainly due to sexually selected infanticide during the mating season (Zedrosser et al., 2009). It is possible that the impact of cub mortality due to malnutrition on movement metrics differs from the impact of infanticide. At a minimum, the latter case, resulting from a stressful event, would be expected to show an increase in step length and average home range to escape the male perpetrating the infanticide or to distract the male and lure him away from the cubs in potential danger from infanticide (Steyaert, 2014).

The pressing question after detecting these changepoints is: how can we be certain that the observed change truly corresponds to the event we aim to detect (i.e., a litter loss)?

#### **4. Cross-validation based on Random Forest classification model**

The difficulty in assessing events like offspring mortality stems from the elusive nature of these animals and the lack of validation data. Overall, few studies on wildlife had validation data on the exact timing of the event of interest or predefined criteria for a

successful event identification. Without such validation data, the success of models for determining when loss of the litter occurred cannot be confirmed or quantified.

For this reason, we cross-referenced this information with field monitoring data, which documented whether females categorized as “with COY” were observed without their cubs during aerial surveys, using our Random Forest classification model trained on movement data from 147 pair of bear/year. This monitoring table may contain errors, as COY might not always have been detected, so the certainty of their absence cannot be guaranteed. However, if a loss is documented, it provides an approximate timeframe (within a few weeks) of when the litter loss happened. To confirm the loss of cubs, we relied on one main hypothesis from a study conducted in our study population, which demonstrated that females who lost their cubs regained the movement characteristics of solitary females within a maximum of four days (Steayear, 2014). We therefore expected that before this changepoint, observations would be classified as “female accompanied by COY,” and after the changepoint date, we expected a majority of observations would be classified as “solitary female”.

Based on this hypothesis we then could make a confusion matrix and the method demonstrated an overall accuracy of 74% (Table 6).

Our results show that selecting a changepoint matching the monitoring table (Accuracy of 0.85 for RI = 2) improves the classification performance of the Random Forest model, while choosing the most probable changepoint does not seem to have an impact. It suggests that these methods could allow for detecting the date with an accuracy of a few days, but they do not yet support reducing the efforts in monitoring and aerial surveillance.

These results are promising and appear to support the hypothesis we proposed at the beginning of our study: that after a litter loss, a female will move similarly to a solitary individual, increasing her movement in a more persistent manner. Even though these

initial results are satisfactory, it is necessary to discuss the sources of misclassification that can occur with the random forest. Possible sources are detailed in Table 7.

**Table 7:** Sources of misclassifications by the RF model

Temporality	Misclassification Type	Possible sources
Before the Changepoint	False Positive: Position classified as solitary when cubs are present.	Disturbance and stressful events requiring transient movement increase (e.g., human disturbance, monitoring event, avoiding a male).
After the Changepoint	False Negative: Classified as having cubs when solitary.	<ul style="list-style-type: none"> <li>- It may take up to 4 days to return to the movement level of a solitary female. (Gardner et al. 2014) so the transition phase could lead to some misclassification.</li> <li>- Bears are highly seasonal (Thiel et al. 2022), and at the end of the breeding season, females exhibit a general decrease in movement.</li> <li>- Important meteorological event (precipitation, or late spring snow episode)</li> </ul>

It is important to note that specificity, which refers to the correct classification of a positive reference status (e.g., solitary), will vary throughout the study period. Indeed, as shown in (Figure 2), the difference between solitary status and being accompanied by COY is not consistent for the three metrics used to train the random forest model (mean daily step length, mean daily home range, and mean daily persistence).

These variations are likely to produce false positives at the beginning of the study period (day 105, April 15) before the changepoint and false negatives towards the end of the period. For instance, there is no longer a significant difference in step length by day 182 (i.e. June 30), and the confidence intervals for the other two metrics also converge between the different statuses.

Even if those first results are promising, accounting the number of individuals in our dataset ( $n = 143$ ) the performance of this model could likely be improved by using a bigger sample size. Additionally, we could use a broader range of metrics that capture specific aspects of female movement based on their reproductive status and experiment with finer temporal scales. Future studies could, for instance, focus on activity data obtained through collars equipped with accelerometers. This approach has already been

successfully used for Scandinavian brown bears to detect parturition timing (Lemière et al. 2022; Friebe et al., 2014). Therefore, it could be a viable method for detecting when females lose their cubs and add a new metric that could potentially strengthen the classification model established in this study.

## **V. CONCLUSION**

This study confirms our preliminary hypothesis that reproductive status significantly influences the movement patterns of female brown bears. We demonstrated that females with COY move less during the post-denning period until the end of the reproductive season, while females with yearlings quickly increase their movement, reaching levels comparable to solitary females by mid-season. This first descriptive step with the GAMMs showed that this difference in movement is significant and captured by the three metrics used in this study: mean daily step length, mean daily home range, and persistence. In addition, it showed that movement pattern was modulated by climatic conditions (snow depth, precipitations and ambient temperature).

We then built and trained a Random Forest on the three previous metrics to verify if movement alone would suffice to correctly classify a female as “solitary” or “with COY”, which proved to be the case (accuracy = 73%).

Subsequently, using Bayesian changepoint detection on these movement metrics in cross-validation with the previously trained Random Forest model, we were able to obtain a date for the litter loss of relevance on the order of days. This brings precision to the aerial surveillance, which remains indispensable but only allowed for determining this loss on the order of weeks. The model achieved an overall accuracy of 85% when excluding changepoints with a reliability index (RI) of 1.

The biological particularities of brown bear biology involve some challenges in using such methods, but we have hope for some improvement. This study was unable to pinpoint a precise date of litter loss of relevance for dates very close to the den exit due to the progressive resurgence of movement after hibernation and the strong influence of



seasonality. Future research should focus on incorporating additional metrics and larger sample sizes, as well as exploring accelerometry data and finer-scale analysis and a timeframe centered around the month of loss.

This study serves as a foundational method for assessing the reproductive status of female brown bears after hibernation, providing a robust framework for future advancements in wildlife monitoring and research. By employing a theoretical and population-level approach (using Generalized Additive Mixed Models (GAMMs) and analyzing the influence of intrinsic and extrinsic factors, we can extract individual-level information. This approach allows us to identify life history traits, such as litter loss, with a precision of within a day. Consequently, we can accurately assess the reproductive status of female brown bears, providing valuable insights into natality and mortality rates, parameters that are paramount to understanding population dynamics and adapt management and conservation measures accordingly. This information will pave the way for new research opportunities and advancements in understanding bear reproduction and broader ecological studies.

We could envisage that these tools - Bayesian analysis of changepoint and the use of RF, which is a form of machine learning - could be exported to other species to determine reproductive statuses and the presence of young. But also, as has already been done, to detect events that imply a change in movement behavior, as has already been done on certain ungulates for parturition.

Movement would therefore make it possible to deduce a range of information about wild animal populations. Reproductive status is just one of the possible fields of application and we could imagine, once these methods have been improved, being able to detect states of stress, disturbance or even a movement that suggests a decline in the animal's health. The possibilities offered by the combination of multiple methods and the new contributions of machine learning mean that we can envisage a very vast field of applications that will perhaps provide new knowledge inherent in wildlife.

## References

Bruhwieler, Lori, Parmentier, Frans-Jan W., Crill, Patrick, Leonard, Mark, & Palmer, Paul I. (2021). The Arctic Carbon Cycle and Its Response to Changing Climate. *Current Climate Change Reports*, 7(1), 14-34. DOI: 10.1007/s40641-020-00169-5.

\* Evans, A. L., Friebe, A., Arnemo, J. M., Laske, T. G., Fröbert, O., Swenson, J. E., Blanc, S., & Blanc, S. (2016). Drivers of hibernation in the brown bear. *Frontiers in Zoology*, 13(1), 7-7. DOI: 10.1186/s12983-016-0140-6.

*This article explores the seasonality of bears and examines how environmental drivers can impact the physiology of brown bears, particularly concerning the detection of changepoints around the hibernation emergence period.*

Arnemo, J. M., & Evans, A. L. (2017). Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx. Disponible en ligne à l'adresse : <http://rgdoi.net/10.13140/RG.2.2.30359.37286>. DOI: 10.13140/RG.2.2.30359.37286.

\*Bellemain, E., Swenson, J. E., & Taberlet, P. (2006). Mating Strategies in Relation to Sexually Selected Infanticide in a Non-Social Carnivore: the Brown Bear. *Ethology*, 112(3), 238-246. DOI: 10.1111/j.1439-0310.2006.01152.x.

*This article helps us understand how bears are mating and the evolutionary reasons behind the selection of SSI behavior. It provides a dual understanding: firstly, the reasons for the movements of solitary females (which is important for reproduction), and secondly, it explains the avoidance strategy of females with COYs to prevent conflicts, clearly showing the completely divergent interests of these two reproductive statuses.*

Burnham, K. P., & Anderson, D. R. (2004). *Model Selection and Multimodel Inference*. New York, NY: Springer. ISBN: 978-0-387-95364-9. Disponible en ligne à l'adresse : <http://link.springer.com/10.1007/b97636>.

Moore, C. L. (1995). Maternal Contributions to Mammalian Reproductive Development and the Divergence of Males and Females. *Advances in The Study of Behavior*, 24, 47-118. DOI: 10.1016/s0065-3454(08)60392-7.

Cullen, J. A., Poli, C. L., Fletcher, R. J., & Valle, D. (2022). Identifying latent behavioural states in animal movement with M4, a nonparametric Bayesian method. *Methods in Ecology and Evolution*, 13(2), 432-446. DOI: 10.1111/2041-210X.13745.

Dahle, B., & Swenson, J. E. (2003). Seasonal range size in relation to reproductive strategies in brown bears *Ursus arctos*. *Journal of Animal Ecology*, 72(4), 660-667. DOI: 10.1046/j.1365-2656.2003.00737.x.

Demars, C. A., Auger-Méthé, M., Schlägel, U. E., & Boutin, S. (2013). Inferring parturition and neonate survival from movement patterns of female ungulates: a case study using woodland caribou. *Ecology and Evolution*, 3(12), 4149-4160. DOI: 10.1002/ece3.785.

**\* Demšar, U., Buchin, K., Cagnacci, F., Safi, K., Speckmann, B., Van de Weghe, N., Weiskopf, D., & Weibel, R. (2015).** Analysis and visualisation of movement: an interdisciplinary review. *Movement Ecology*, 3(1), 5. DOI: 10.1186/s40462-015-0032-y.

*This article helped me understand the general background of movement. It allowed me to comprehend what individual movement is and the pillars that constitute it. Additionally, it highlighted the issues underlying the ecology of movement.*

Verluis, E., Niccolai, L. J., Spedener, M., Zimmermann, B., Hessle, A., Tofastrud, M., Devineau, O., & Evans, A. L. (2023). Classification of behaviors of free-ranging cattle using accelerometry signatures collected by virtual fence collars. *Frontiers in Animal Science*, 4. DOI: 10.3389/fanim.2023.1083272.

Farley, S. D., & Robbins, C. T. (1995). Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. *Canadian Journal of Zoology*, 73(12), 2216-2222. DOI: 10.1139/z95-262.

**\*Friebe, A., Evans, A. L., Arnemo, J. M., Blanc, S., Brunberg, S., Fleissner, G., Swenson, J. E., & Zedrosser, A. (2014).** Factors Affecting Date of Implantation, Parturition, and Den Entry Estimated from Activity and Body Temperature in Free-Ranging Brown Bears. *PLoS ONE*, 9(7), e101410. DOI: 10.1371/journal.pone.0101410.

*This article is the first to provide a detailed account of the physiology and reproductive phenology of Scandinavian brown bears in such detail. It offers comprehensive information on bear biology, which evidently has a significant impact on post-hibernation movement.*

Friebe, A., Swenson, J. E., & Sandegren, F. (2001). Denning Chronology of Female Brown Bears in Central Sweden. *Ursus*, 12, 37-45. JSTOR.

Gardner, C. L., Pamperin, N. J., & Benson, J. F. (2014). Movement patterns and space use of maternal grizzly bears influence cub survival in Interior Alaska. *Ursus*, 25(2), 121-138. DOI: 10.2192/URSUS-D-14-00015.1.

Hertel, A. G., Zedrosser, A., Kindberg, J., Langvall, O., & Swenson, J. E. (2019). Fluctuating mast production does not drive Scandinavian brown bear behavior. *The Journal of Wildlife Management*, 83(3), 657-668. DOI: 10.1002/jwmg.21619.

Hooven, N. D., Williams, K. E., Hast, J. T., McDermott, J. R., Crank, R. D., Jenkins, G., Springer, M. T., & Cox, J. J. (2022). Using low-fix rate GPS telemetry to expand estimates of ungulate reproductive success. *Animal Biotelemetry*, 10(1), 5. DOI: 10.1186/s40317-022-00276-0.

Huber, D., & Roth, H. U. (1993). Movements of European brown bears in Croatia. *Acta Theriologica*, 38, 151-159. DOI: 10.4098/AT.arch.93-13.

Van de Walle, J., Zedrosser, A., Swenson, J. E., & Pelletier, F. (2020). Disentangling direct and indirect determinants of the duration of maternal care in brown bears: Environmental context matters. *Journal of Animal Ecology*, 90(2), 376-386. DOI: 10.1111/1365-2656.13371.

Jonsen, I. D., McMahon, C. R., Patterson, T. A., Auger-Méthé, M., Harcourt, R., Hindell, M. A., & Bestley, S. (2019). Movement responses to environment: fast inference of variation among southern elephant seals with a mixed effects model. *Ecology*, 100(1), e02566. DOI: 10.1002/ecy.2566.

Pinheiro, J. C. (2000). *Mixed-Effects Models in S and S-PLUS*. Disponible en ligne à l'adresse : <https://link.springer.com/book/10.1007/b98882>.

Kirchner, T., Devineau, O., Chimienti, M., Thompson, D. P., Crouse, J. A., Evans, A. L., Zimmermann, B., & Eriksen, A. (2023). Predicting moose behaviors from tri-axial accelerometer data using a supervised classification algorithm. *Animal Biotelemetry*, 11(1). DOI: 10.1186/s40317-023-00343-0.

Krofel, M., Filacorda, S., & Jerina, K. (2010). Mating-related movements of male brown bears on the periphery of an expanding population. *Ursus*, 21(1), 23-29. DOI: 10.2192/09SC015.1.

Lemière, L., Thiel, A., Fuchs, B., Gilot-Fromont, E., Hertel, A. G., Friebe, A., Kindberg, J., Støen, O.-G., Arnemo, J. M., & Evans, A. L. (2022). Extrinsic and intrinsic factors drive the timing of gestation and reproductive success of Scandinavian brown bears. *Frontiers in Ecology and Evolution*, 10, 1045331. DOI: 10.3389/fevo.2022.1045331.

Ruivo, L. V. P., Stone, A. I., & Fienup, M. (2017). Reproductive status affects the feeding ecology and social association patterns of female squirrel monkeys (*Saimiri collinsi*) in an Amazonian rainforest. *American Journal of Primatology*, 79(6). DOI: 10.1002/ajp.22657.

Manchi, S., & Swenson, J. E. (2005). Denning behaviour of Scandinavian brown bears *Ursus arctos*. *Wildlife Biology*, 11(2), 123-132. DOI: 10.2981/0909-6396(2005)11[123]2.0.CO;2.

Nicholson, K. L., Warren, M. J., Rostan, C., Månsson, J., Paragi, T. F., & Sand, H. (2019). Using fine-scale movement patterns to infer ungulate parturition. *Ecological Indicators*, 101, 22-30. DOI: 10.1016/j.ecolind.2019.01.004.

Kobayashi, N., Okabe, H., Kawazu, I., Higashi, N., Kato, K., Miyahara, H., Nakamura, G., Kato, H., & Uchida, S. (2017). Distribution and Local Movement of Humpback Whales in Okinawan Waters Depend on Sex and Reproductive Status. *Zoological Science*, 34(1), 58-63. DOI: 10.2108/zs160012.

Manlik, O. (2019). The Importance of Reproduction for the Conservation of Slow-Growing Animal Populations. *Advances in Experimental Medicine and Biology*, 1200, 13-39. DOI: 10.1007/978-3-030-23633-5\_2.

Pebesma, E. J. (2004). Multivariable geostatistics in S: the gstat package. *Computers & Geosciences*, 30(7), 683-691. DOI: 10.1016/j.cageo.2004.03.012.

Trivers, R. (1974). Parent-Offspring Conflict. *Integrative and Comparative Biology*, 14(1), 249-264. DOI: 10.1093/icb/14.1.249.

Seryodkin, I. V., Paczkowski, J., Borisov, M. Y., & Petrunenko, Y. K. (2017). Home ranges of brown bears on the Kamchatka peninsula and Sakhalin Island. *Contemporary Problems of Ecology*, 10(6), 599-611. DOI: 10.1134/S1995425517060129.

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution*, 9(2), 880-890. DOI: 10.1002/ece3.4823.

Spady, T. J., Lindburg, D. G., & Durrant, B. S. (2007). Evolution of reproductive seasonality in bears. *Mammal Review*, 37(1), 21-53. DOI: 10.1111/j.1365-2907.2007.00096.x.

Stearns, S. C. (1998). *The Evolution Of Life Histories*. DOI: 10.1093/oso/9780198577416.001.0001.

Steyaert, S. M. J. G., Endrestøl, A., Hackländer, K., Swenson, J. E., & Zedrosser, A. (2012). The mating system of the brown bear *Ursus arctos*. *Mammal Review*, 42(1), 12-34. DOI: 10.1111/j.1365-2907.2011.00184.x.

\* **Steyaert, S. M. J. G., Swenson, J. E., & Zedrosser, A. (2014)**. Litter loss triggers estrus in a nonsocial seasonal breeder. *Ecology and Evolution*, 4(3), 300-310. DOI: 10.1002/ece3.935.

*This article is one of the cornerstones of our thinking. On one hand, it comparatively describes the movement characteristics of solitary females or those with COYs in our population (clearly demonstrating that females with COYs have reduced movement). But it is also this article that showed that a female experiencing a litter loss reverts to the behavior of a solitary female within 4 days. This is one of the fundamental elements on which the entire second part of our analysis is based.*

Steyaert, S. M. J. G., Kindberg, J., Swenson, J. E., & Zedrosser, A. (2013). Male reproductive strategy explains spatiotemporal segregation in brown bears. *Journal of Animal Ecology*, 82(4), 836-845. DOI: 10.1111/1365-2656.12055.

Swenson, J. E., Sandegren, F., Bjärvall, A., Söderberg, A., Wabakken, P., & Franzén, R. (1994). Size, trend, distribution and conservation of the brown bear *Ursus arctos*

population in Sweden. *Biological Conservation*, 70(1), 9-17. DOI: 10.1016/0006-3207(94)90293-3.

Van Rij, J., Wieling, M., Baayen, R. H., & Van Rijn, D. (2015). *itsadug: Interpreting time series and autocorrelated data using GAMMs*. Disponible en ligne à l'adresse : <https://research.rug.nl/en/publications/itsadug-interpreting-time-series-and-autocorrelated-data-using-ga>.

Gervasi, V., Brunberg, S., & Swenson, J. E. (2006). An Individual-Based Method to Measure Animal Activity Levels: A Test on Brown Bears. *Wildlife Society Bulletin (1973-2006)*, 34(5), 1314-1319. JSTOR.

Wimsatt, W. A. (1963). Delayed implantation in the Ursidae, with particular reference to the black bear (*Ursus americanus* Pallus). In: A. C. Enders (Ed.), *Delayed implantation* (pp. 49-76). Chicago Press.

Wood, S. N. (2017). *Generalized additive models: an introduction with R* (2nd ed.). Boca Raton, London, New York: CRC Press/Taylor & Francis Group. Texts in statistical science. ISBN: 978-1-4987-2833-1.

Wright, M. N., & Ziegler, A. (2017). ranger: A Fast Implementation of Random Forests for High Dimensional Data in C++ and R. *Journal of Statistical Software*, 77(1). DOI: 10.18637/jss.v077.i01. Disponible en ligne à l'adresse : <http://www.jstatsoft.org/v77/i01>.

Zedrosser, A., Dahle, B., Støen, O.-G., & Swenson, J. E. (2009). The effects of primiparity on reproductive performance in the brown bear. *Oecologia*, 160(4), 847-854. DOI: 10.1007/s00442-009-1343-8.

Zhao, K., Wulder, M. A., Hu, T., Bright, R., Wu, Q., Qin, H., Li, Y., Toman, E., Mallick, B., Zhang, X., & Brown, M. (2019). Detecting change-point, trend, and seasonality in satellite time series data to track abrupt changes and nonlinear dynamics: A Bayesian ensemble

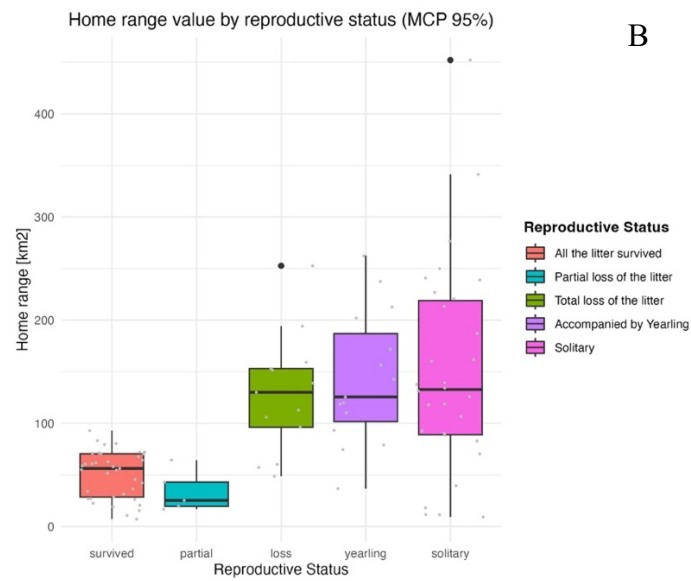
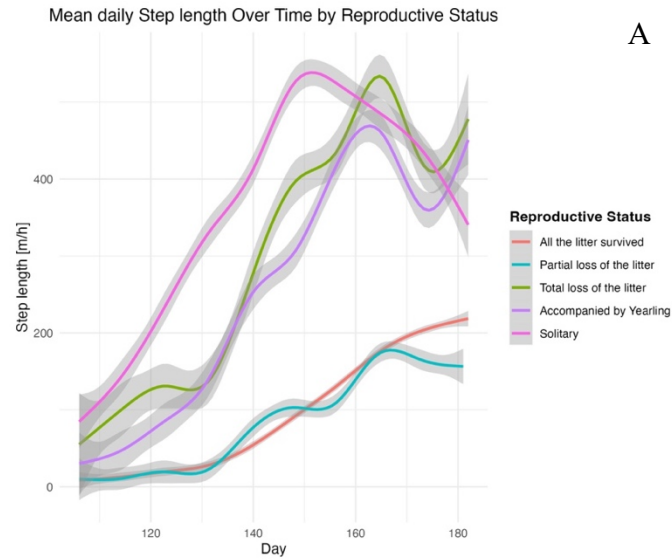


algorithm. *Remote Sensing of Environment*, 232, 111181. DOI: 10.1016/j.rse.2019.04.034.

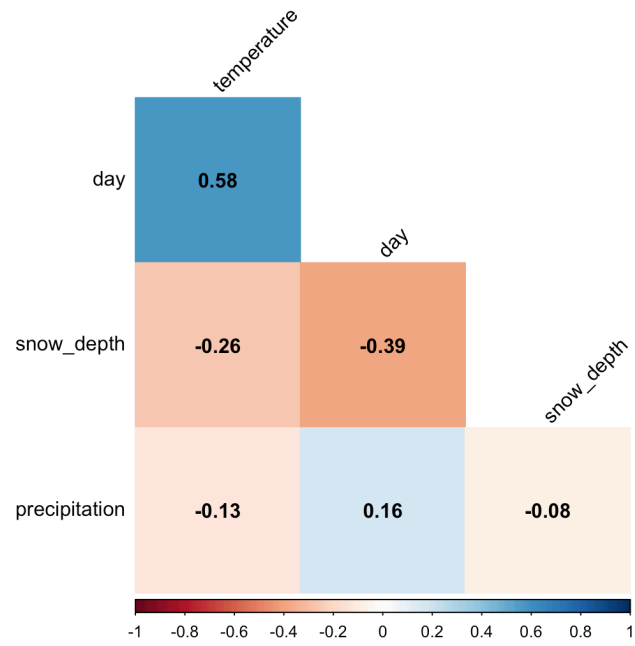
Zippenfenig, P. (2024). Open-Meteo.com Weather API. Zenodo. DOI: 10.5281/zenodo.7970649. Disponible en ligne à l'adresse : <https://zenodo.org/doi/10.5281/zenodo.7970649>.

# Appendix

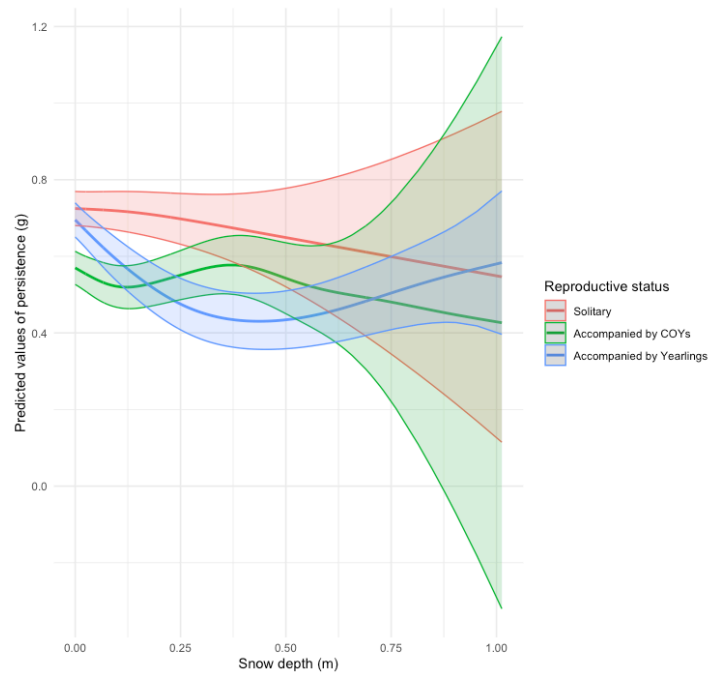
**Data exploration** We explored different metrics for the different reproductive statuses using ggplot2. Here are the graphs, which allowed us to select the 3 metrics used to describe the movement of the females.



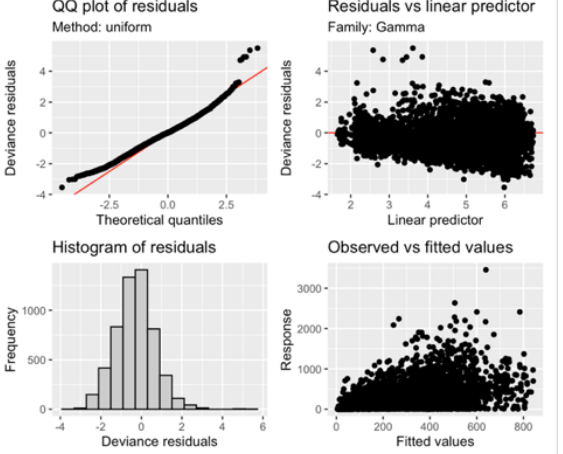
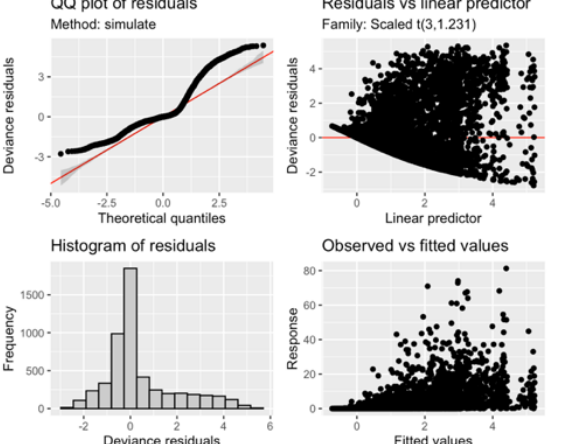
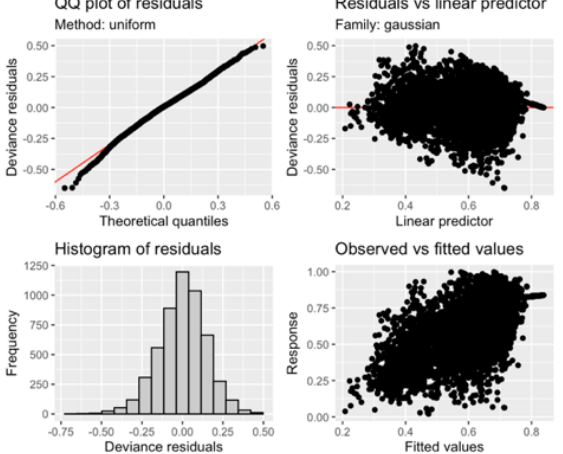
**Appendix 1 : Exploratory Graphs for Mean Daily Step Length (A) and Mean Daily Home Range (B)**



**Appendix 2 :** Correlation matrix for environmental factors



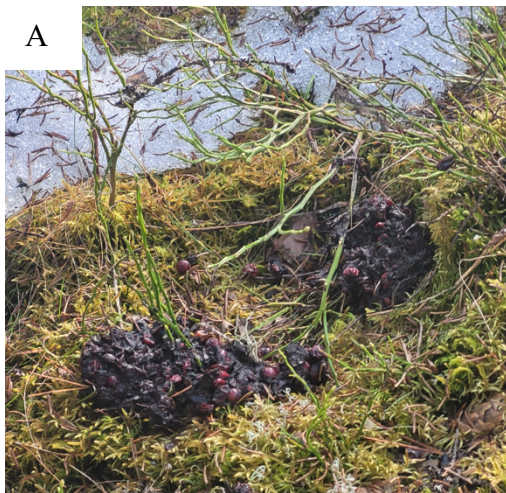
**Appendix 3:** Effect of snow depth (m) on persistence

Best Model	Diagnostic plot																																																																	
<p><b>A</b></p> <p>Family: Gamma Link function: log</p> <p>Formula: mean_step ~ s(day, by = repro_status) + repro_status + s(bear_id, bs = "re") + s(snow_depth, by = repro_status) + precipitation</p> <p>Parametric coefficients:</p> <table border="1"> <thead> <tr> <th></th> <th>Estimate</th> <th>Std. Error</th> <th>t value</th> <th>Pr(&gt; t )</th> </tr> </thead> <tbody> <tr> <td>(Intercept)</td> <td>5.143826</td> <td>0.118653</td> <td>43.352</td> <td>&lt; 2e-16 ***</td> </tr> <tr> <td>repro_statussurvived</td> <td>-1.202722</td> <td>0.133364</td> <td>-9.018</td> <td>&lt; 2e-16 ***</td> </tr> <tr> <td>repro_statusyearling</td> <td>-0.603598</td> <td>0.155862</td> <td>-3.873</td> <td>0.000109 ***</td> </tr> <tr> <td>precipitation</td> <td>-0.007976</td> <td>0.003617</td> <td>-2.205</td> <td>0.027510 *</td> </tr> </tbody> </table> <p>--- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>Approximate significance of smooth terms:</p> <table border="1"> <thead> <tr> <th></th> <th>edf</th> <th>Ref.df</th> <th>F</th> <th>p-value</th> </tr> </thead> <tbody> <tr> <td>s(day):repro_status solitary</td> <td>3.571</td> <td>4.440</td> <td>26.188</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(day):repro_status survived</td> <td>5.091</td> <td>6.211</td> <td>226.886</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(day):repro_status yearling</td> <td>4.147</td> <td>5.126</td> <td>39.706</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(bear_id)</td> <td>36.140</td> <td>46.000</td> <td>5.937</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(snow_depth):repro_status solitary</td> <td>1.000</td> <td>1.000</td> <td>36.220</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(snow_depth):repro_status survived</td> <td>1.000</td> <td>1.000</td> <td>1.860</td> <td>0.173</td> </tr> <tr> <td>s(snow_depth):repro_status yearling</td> <td>3.318</td> <td>4.105</td> <td>19.359</td> <td>&lt;2e-16 ***</td> </tr> </tbody> </table> <p>--- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>R-sq.(adj) = 0.324 Deviance explained = 51.6% FREML = 7889.4 Scale est. = 1.2233 n = 5474</p>		Estimate	Std. Error	t value	Pr(> t )	(Intercept)	5.143826	0.118653	43.352	< 2e-16 ***	repro_statussurvived	-1.202722	0.133364	-9.018	< 2e-16 ***	repro_statusyearling	-0.603598	0.155862	-3.873	0.000109 ***	precipitation	-0.007976	0.003617	-2.205	0.027510 *		edf	Ref.df	F	p-value	s(day):repro_status solitary	3.571	4.440	26.188	<2e-16 ***	s(day):repro_status survived	5.091	6.211	226.886	<2e-16 ***	s(day):repro_status yearling	4.147	5.126	39.706	<2e-16 ***	s(bear_id)	36.140	46.000	5.937	<2e-16 ***	s(snow_depth):repro_status solitary	1.000	1.000	36.220	<2e-16 ***	s(snow_depth):repro_status survived	1.000	1.000	1.860	0.173	s(snow_depth):repro_status yearling	3.318	4.105	19.359	<2e-16 ***	
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<p><b>B</b></p> <p>Family: Scaled t(3,1.231) Link function: identity</p> <p>Formula: mean_daily_hr ~ s(day, by = repro_status) + repro_status + s(bear_id, bs = "re")</p> <p>Parametric coefficients:</p> <table border="1"> <thead> <tr> <th></th> <th>Estimate</th> <th>Std. Error</th> <th>t value</th> <th>Pr(&gt; t )</th> </tr> </thead> <tbody> <tr> <td>(Intercept)</td> <td>2.2375</td> <td>0.1082</td> <td>20.680</td> <td>&lt; 2e-16 ***</td> </tr> <tr> <td>repro_statussurvived</td> <td>-1.7237</td> <td>0.1034</td> <td>-16.666</td> <td>&lt; 2e-16 ***</td> </tr> <tr> <td>repro_statusyearling</td> <td>-0.9047</td> <td>0.1172</td> <td>-7.717</td> <td>1.42e-14 ***</td> </tr> </tbody> </table> <p>--- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>Approximate significance of smooth terms:</p> <table border="1"> <thead> <tr> <th></th> <th>edf</th> <th>Ref.df</th> <th>F</th> <th>p-value</th> </tr> </thead> <tbody> <tr> <td>s(day):repro_status solitary</td> <td>4.284</td> <td>5.283</td> <td>65.004</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(day):repro_status survived</td> <td>2.889</td> <td>3.604</td> <td>28.966</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(day):repro_status yearling</td> <td>1.878</td> <td>2.345</td> <td>84.489</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(bear_id)</td> <td>37.902</td> <td>47.000</td> <td>5.942</td> <td>&lt;2e-16 ***</td> </tr> </tbody> </table> <p>--- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>R-sq.(adj) = 0.14 Deviance explained = 14% FREML = 11057 Scale est. = 1 n = 5283</p>		Estimate	Std. Error	t value	Pr(> t )	(Intercept)	2.2375	0.1082	20.680	< 2e-16 ***	repro_statussurvived	-1.7237	0.1034	-16.666	< 2e-16 ***	repro_statusyearling	-0.9047	0.1172	-7.717	1.42e-14 ***		edf	Ref.df	F	p-value	s(day):repro_status solitary	4.284	5.283	65.004	<2e-16 ***	s(day):repro_status survived	2.889	3.604	28.966	<2e-16 ***	s(day):repro_status yearling	1.878	2.345	84.489	<2e-16 ***	s(bear_id)	37.902	47.000	5.942	<2e-16 ***																					
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s(day):repro_status yearling	1.878	2.345	84.489	<2e-16 ***																																																														
s(bear_id)	37.902	47.000	5.942	<2e-16 ***																																																														
<p><b>C</b></p> <p>Family: gaussian Link function: identity</p> <p>Formula: mean_daily_g ~ s(day, by = repro_status) + repro_status + age + s(bear_id, bs = "re")</p> <p>Parametric coefficients:</p> <table border="1"> <thead> <tr> <th></th> <th>Estimate</th> <th>Std. Error</th> <th>t value</th> <th>Pr(&gt; t )</th> </tr> </thead> <tbody> <tr> <td>(Intercept)</td> <td>0.706853</td> <td>0.011598</td> <td>60.946</td> <td>&lt; 2e-16 ***</td> </tr> <tr> <td>repro_statussurvived</td> <td>-0.152517</td> <td>0.009824</td> <td>-15.525</td> <td>&lt; 2e-16 ***</td> </tr> <tr> <td>repro_statusyearling</td> <td>-0.049788</td> <td>0.011477</td> <td>-4.338</td> <td>1.46e-05 ***</td> </tr> <tr> <td>age</td> <td>-0.004254</td> <td>0.001180</td> <td>-3.606</td> <td>0.000314 ***</td> </tr> </tbody> </table> <p>--- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>Approximate significance of smooth terms:</p> <table border="1"> <thead> <tr> <th></th> <th>edf</th> <th>Ref.df</th> <th>F</th> <th>p-value</th> </tr> </thead> <tbody> <tr> <td>s(day):repro_status solitary</td> <td>3.031</td> <td>3.770</td> <td>19.28</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(day):repro_status survived</td> <td>7.185</td> <td>8.217</td> <td>120.30</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(day):repro_status yearling</td> <td>3.787</td> <td>4.684</td> <td>63.84</td> <td>&lt;2e-16 ***</td> </tr> <tr> <td>s(bear_id)</td> <td>39.886</td> <td>46.000</td> <td>10.78</td> <td>&lt;2e-16 ***</td> </tr> </tbody> </table> <p>--- Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1</p> <p>R-sq.(adj) = 0.371 Deviance explained = 37.8% FREML = -2454.7 Scale est. = 0.022265 n = 5287</p>		Estimate	Std. Error	t value	Pr(> t )	(Intercept)	0.706853	0.011598	60.946	< 2e-16 ***	repro_statussurvived	-0.152517	0.009824	-15.525	< 2e-16 ***	repro_statusyearling	-0.049788	0.011477	-4.338	1.46e-05 ***	age	-0.004254	0.001180	-3.606	0.000314 ***		edf	Ref.df	F	p-value	s(day):repro_status solitary	3.031	3.770	19.28	<2e-16 ***	s(day):repro_status survived	7.185	8.217	120.30	<2e-16 ***	s(day):repro_status yearling	3.787	4.684	63.84	<2e-16 ***	s(bear_id)	39.886	46.000	10.78	<2e-16 ***																
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**Appendix 4: Summary & Diagnostic Plots for GAMMs (Generalized Additive Mixed Models)**

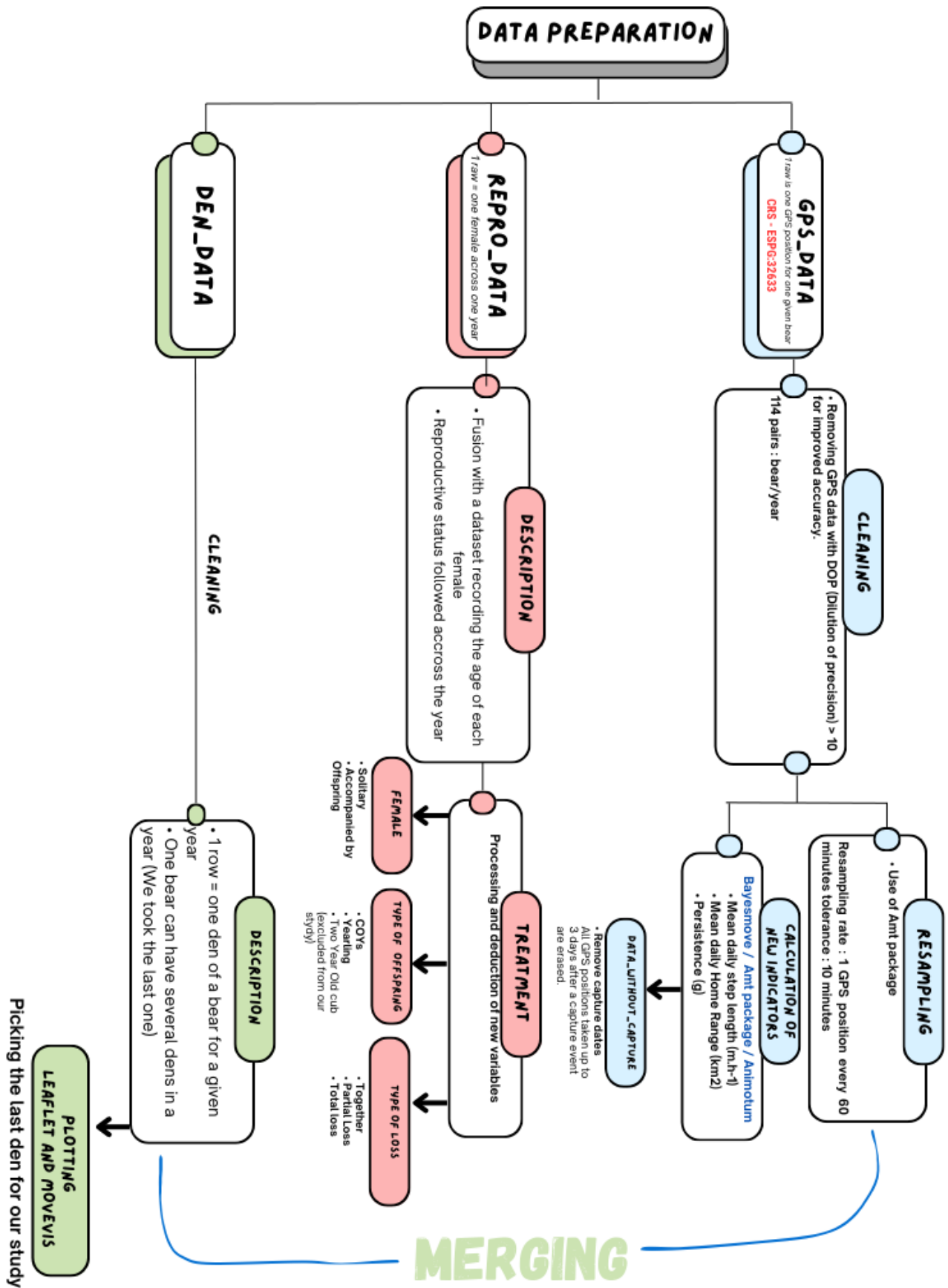


**Appendix 5:** Surgery to remove a VHF intra-abdominal implant from a young female



**Appendix 6:** Presence indicators around an infanticide scene

(A) Bear feces. (B) Consumed ant nest. Typical food for a female with cubs.



Appendix 7: Data preparation, cleaning, standardisation and calculation of the different metrics



**NOM :** SEU

**PRÉNOM :** Manon

**TITRE :** Étude des mouvements des femelles ours bruns et inférence du statut reproducteur

### Résumé

Cette étude avait deux objectifs principaux : premièrement, démontrer comment le statut reproducteur influence les déplacements des femelles et explorer les facteurs environnementaux pouvant les affecter à l'aide de Modèles Additifs Mixtes Généralisés (GAMMs). Les femelles avec des oursons de l'année (COY) se déplaçaient moins que les solitaires, tandis que celles avec des oursons d'un an présentaient un schéma intermédiaire. Le second objectif visait à inférer le statut reproducteur des femelles et à détecter des événements de perte de portée via l'analyse de leurs données de mouvement. Une méthode de machine learning, la *Random Forest* (RF) ou forêt d'arbres décisionnels, a permis de déterminer le statut reproducteur des femelles à la sortie de la tanière avec 85 % de précision. Les dates de pertes de portée ont été identifiées par détection de *Bayesian Changepoint* ou points de rupture bayésiens, et validées avec une précision de 75 % grâce à la RF préentraînée. Ces résultats offrent une approche innovante et prometteuse pour combler les lacunes des données de certains individus ayant échappé à la surveillance sur le terrain. Cette approche pourrait potentiellement servir à détecter d'autres événements de leur cycle de vie (conflits, perturbations, dégradation de l'état de santé etc.) mais également s'appliquer à d'autres espèces équipées de colliers GPS. Malgré les défis liés aux spécificités biologiques et à la saisonnalité des ours bruns, cette étude pose les bases pour évaluer le statut reproducteur des femelles après l'hibernation, fournissant des informations précieuses sur les taux de natalité et de mortalité des oursons, tout en ouvrant de nouvelles perspectives pour la recherche sur la dynamique des populations des ours bruns.

**Mots clés :** Ours brun, Statut reproducteur, Mouvement, Point de rupture bayésien, Forêt d'arbres décisionnels.

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**TITLE:** Study of female brown bear movements and inference of reproductive status

### Abstract

This study had two main objectives: first, to demonstrate how reproductive status influences the movements of females and to explore the environmental factors that may affect them using Generalized Additive Mixed Models (GAMMs). Females with cubs of the year (COY) moved less than solitary females, while those with yearling cubs exhibited an intermediate pattern. The second objective aimed to infer the reproductive status of females and detect litter loss events through the analysis of their movement data. A machine learning method, the Random Forest (RF) or decision tree forest, was used to determine the reproductive status of females upon den emergence with 85% accuracy. Litter loss dates were identified through Bayesian Changepoint detection and validated with 75% accuracy using the pre-trained RF. These results offer an innovative and promising approach to filling data gaps for certain individuals that escaped field monitoring. This approach could potentially be used to detect other events in their life cycle (conflicts, disturbances, health deterioration, etc.) and could also be applied to other species equipped with GPS collars. Despite challenges related to the biological specifics and seasonality of brown bears, this study lays the foundation for evaluating the reproductive status of females after hibernation, providing valuable insights into cub birth and mortality rates, while also opening new perspectives for research on the population dynamics of brown bears.

**Key words:** Brown bear, Reproductive status, Movement, Bayesian Changepoint, Random Forest.