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Master thesis

Effects of GPS-collars on Svalbard reindeer survival and body condition

Master in Applied Ecology

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Abstract

Modern wildlife and conservation research often relies on GPS collars and on the assumption that collared animals are representative of the study population, but this assumption is rarely tested in the wild. These collars may directly or indirectly affect the animals. Negative effects may include neck wounds, increased locomotion cost and metabolic rate, reduced survival, and others, raising questions about ethics and the representativeness of collared individuals for their populations. Due to the difficulties of incorporating directly-observed control groups into these studies, there is a lack of research regarding these effects. We chose the Svalbard reindeer population from Reindalen–Semmeldalen–Colesdalen valley system to investigate the potential effects of wearing a GPS collar because numerous individuals have been recaptured each year in April since 1994, and censused in August to obtain individual status. Some individuals wear light plastic collars for identification and some are GPS collared,allowing for a control group and evaluation of the effects of the weight of the GPS collar. Additionally, Svalbard reindeer have no natural predators and mortality is mostly caused by starvation or old age, reducing confounding causes of death and complexity of estimating a potential effect of the GPS collar on survival. In this study we test whether wearing a GPS collar has an impact on individual Svalbard reindeer' survival probability and body condition at the end of winter. We studied survival via mark recapture analysis and body condition by comparing GPS collared (N=48) and individuals with light plastic collars (N=771) female individuals' back fat thickness. We found that survival and fat thickness were influenced by episodes of rain on snow, age, and their interaction, but not by the presence of a GPS collar. While there was a slight tendency for lower survival when wearing a GPS collar, this effect was non-significant *(0.52, CrI: -1.35 - 0.47).* We confirm that the maximum 2% body weight to collar weight ratio recommendation was sufficient to avoid detectable negative effects in this population, but the negative trend indicates a possibility that this ratio is close to the tolerable limit for Svalbard reindeer. Although lacking statistical significance, this observed trend highlights the potential effect GPS collars may have on studied populations. To address data quality and animal welfare concerns, possible effects of GPS collars on studied populations should be tested when possible.

Contents

1 - Introduction

GPS tagging has been the gold standard for many aspects of wildlife research since it became available for civilian use in the 1990s. When assessing survival, land use, migration patterns, and many other important traits, GPS studies and analyses rely on the assumption that the GPS tagged animals are representative for their species and for the study population, and that carrying a GPS device does not affect the behaviour or life history traits being studied (Murray, 2006). However, there are numerous studies indicating it is not always the case. Some studies have demonstrated abnormal behaviour on collared individuals (Brooks, Bonyongo, & Harris, 2008; Nussberger & Ingold, 2006), or reduced predator avoidance abilities and selective predation on collared individuals (Marks & Marks, 1987). Other examples of documented effects include increased energy expenditure, either through impaired movement (Rosen, Gerlinsky, & Trites, 2018) or directly increased metabolic rate (Lear, Gleiss, & Whitney, 2018). Research found animal attached devices to be responsible for overall decreased survival and body condition, on a wide range of species, including land mammals (Severson et al., 2019; Swenson, Wallin, Ericsson, Cederlund, & Sandegren, 1999; Tuyttens, Macdonald, & Roddam, 2002). Larger scale effects have also been documented, such as modification of the population's sex ratio (Moorhouse & Macdonald, 2005). Animals partaking sustained, high energy activities such as migration can also have their survival impacted by the presence of a GPS collar, for example in reindeer *(Rangifer tarandus)* (Rasiulis, Festa-Bianchet, Couturier, & Côté, 2014). Young individuals' survival can be impacted by animal-attached location devices on moose *(Alces alces)* (Swenson et al., 1999). Effects of marking on animals could lead to non-representative data and incorrect management decisions. Validity of the data at individual and population level is important, but animal welfare must be considered first in wildlife research (Lov om dyrevelferd - Lovdata, 2010). The animal welfare aspect of animal tagging is receiving increased attention, both among researchers and the public. Negative reported effects causing animal suffering include fur wear and skin wounds on the neck (Krausman et al., 2004), collars becoming physically caught in the environment, in the lower jaw or front legs of the animal (for example in *Lynx lynx*, Arnemo et al., 2006), or gathering ice and forming a heavy clump impairing animal normal behaviour, functions and movements, ultimately leading to death of the individual, as seen in reindeer (Norsk institutt for naturforskning, NINA, 2018). Arriving at general rules of thumb for how much animal tags can weigh is important both for data validity and animal welfare. By design, detecting and quantifying possible effect of marking on animals is a challenge, given the general absence of an observable, unmarked, control group in studies based on GPS or telemetry. Because it is difficult to detect and quantify effects of animal-attached devices, it is also difficult to regulate their use. In Europe, there is an absence of official regulations regarding the weight and fitting of animal-attached devices such as GPS collars. Some researchers recommend a maximum weight of 5% relative to the animal's body mass (Cochran, 1980), but it is based on potentially outdated research. A 5% ratio is unrealistic for flying animals or large mammals. More recently, researchers and wildlife veterinarians have recommended to limit animal-attached devices and implants to maximum 2% of the animal's body mass, for free ranging terrestrial mammals (Arnemo & Evans, 2017; Arnemo, Ahlqvist, & Segerström, 2004; Arnemo et al., 1999) and for flying animals (Kenward, 2000), but the weight threshold has rarely been tested due to lack of control animals.

In my thesis I aim to test the effect of carrying GPS-collars in a high Arctic ungulate, the Svalbard reindeer. Ungulates in general compose a well-studied group where the use of GPS collars is a particularly important research tool. They are commonly used to assess a variety of important variables, such as habitat preferences (Skarin, Danell, Bergström, & Moen, 2008), home range (Kinck, 2014), migration routes (Debeffe, Rivrud, Meisingset, & Mysterud, 2019; B. B. Hansen et al., 2010b), prey-predator interactions (Ditmer et al., 2018), and activity levels (Lyftingsmo, 2016), making this wide range of common analyses susceptible to bias, and evaluation of GPS-collars effect important. Some research previously showed detrimental effects of radio-transmitters on survival of reindeer *(Rangifer tarandus)* females and calves (Haskell & Ballard, 2007) or migratory individuals with poor body condition (Rasiulis et al., 2014). The use of Svalbard reindeer as a study system is particularily appropriate because it is severely energy limited during winter, suggesting that the added burden of a collar could be important. Because predation on Svalbard reindeer is virtually non-existent (Loe et al., 2007; Williamsen et al., 2019), aspects related to survival are only caused by energy balance and age. Svalbard reindeer locate vascular plants and mosses under the snowpack using their olfactory sense, and dig out craters to forage (B. B. Hansen et al., 2010a). In the Arctic, global climate warming generates a phenomenon called rain-on-snow (ROS), which consists of abnormal winter rainfall, refreezing over the snow and the ground, resulting in layers of hard ice. These ice layers make it difficult or sometimes impossible for reindeers to locate and dig out forage under the snow pack (Hansen et al., 2010a). Rain-on-snow episodes result in reduced late winter body mass of individuals reindeer, which leads to lower survival and reproduction rates (Albon et al., 2017). The annual variation in body mass as well as its impact on population dynamics is to a large extent determined by how much fat individuals have left at the end of winter. There can be up to a 50% decrease of body mass by the end of the winter (Reimers, Ringberg, & Sørumgård, 1982). Individuals store fat during summer, and the fat can represent as much as 27-40% of the total body mass in late fall. Fat stores contributes up to one quarter of the total winter energy budget

(Tyler, 1986) and mortality at the end of the winter is due to fat storage being depleted, often because rain-on-snow reduced energy intake. Back-fat thickness has been shown to be an accurate measure of body and nutritional condition in cervids (Cook et al., 2001) including Svalbard reindeer (Milner et al., 2003; Stien, Irvine, Langvatn, & Ropstad, 2003)). If carrying a GPS-collar should have an effect on Svalbard reindeer, it is likely to operate through accelerated fat depletion and in interaction with rain-on-snow, making GPS-collared animals more susceptible to die in the end of the winter. In a study of Svalbard reindeer *(Rangifer tarandus tarandus)* carried out in the Reindalen–Semmeldalen–Colesdalen valley system, 48 individuals have been equipped with GPS collars since 2009, most of them for multiple years. They are captured in late winter to measure their body condition at a time when it is close to its annual minimum. The body condition measures includes, among others, back-fat thickness measure. In summer, the study area is searched for carcasses, marked dead reindeer are retrieved and their year of death recorded, and living individuals are identified. In addition to having body condition and survival of GPS-collared individuals, there are also control animals with light-weight plastic collars of negligible weight in the population (n=960). They receive the same treatment as the GPS-collared individuals. Because of the presence of an observable control group, the yearly recaptures and observations, and an ideal context for survival analysis with few confounding causes of death, this Svalbard reindeer population is an appropriate candidate to detect possible adverse effects of wearing a GPS collar on body condition and survival.

Different age classes of Svalbard reindeer have different survival rates (Lee et al., 2015) and GPS collars and radio-transmitters have been shown to have a negative impact on survival of reindeer (Haskell & Ballard, 2007), especially in individuals with reduced body condition (Rasiulis et al., 2014) and on young individuals in other cervid species (Swenson et al., 1999). Therefore, I hypothesize that GPS collars and rain on snow have a negative influence on Svalbard reindeer survival, and that younger and older individuals will be affected by GPS-collar to a larger extent than prime-aged individuals. Additionally, even if survival rate is not directly impacted, it is possible that general body condition is impacted and back-fat thickness is a good measure of body condition in Svalbard reindeer (Stien et al., 2003). Therefore, I also hypothesize that GPS collars and rain on snow negatively influence the amount of back-fat thickness measured at captures, and that age is an important predictor for fat thickness.

2 - Methods

2.1 - Study area and Data acquisition

The study population is situated in central Spitsbergen, the largest island of Svalbard archipelago. Reindeer have been captured every year in April in the Reindalen–Semmeldalen–Colesdalen valley system (77°92’N- 78°02’N, 15°16’E-15°87’E, Figure 1) since 1995. A more detailed description of the study area can be found in Solberg et al. (2001). Over time, 962 females in the population were marked with light plastic cattle collars (Moen Bjøllefabrikk, Easyfix småfe) during captures. A total of 49 individuals were marked with GPS collars during the study (5% of the marked females). Individuals were always marked with plastic collar at age 10 months. Some individuals had their plastic collar replaced with a GPS, starting at a minimum of 2 years of age (after reaching adult size). In both cases individuals kept the collar for most of their life. GPS collars of three different weights were used, 0.68, 0.85 and 0.95 kg. The mean body-weight/collar-weight ratio for the GPS collars across all observations was 1.4% (1% - 2.2%). For each capture session, an important set of variables were recorded, including measures of back-fat thickness (mm), body weight (kg) and age (years).

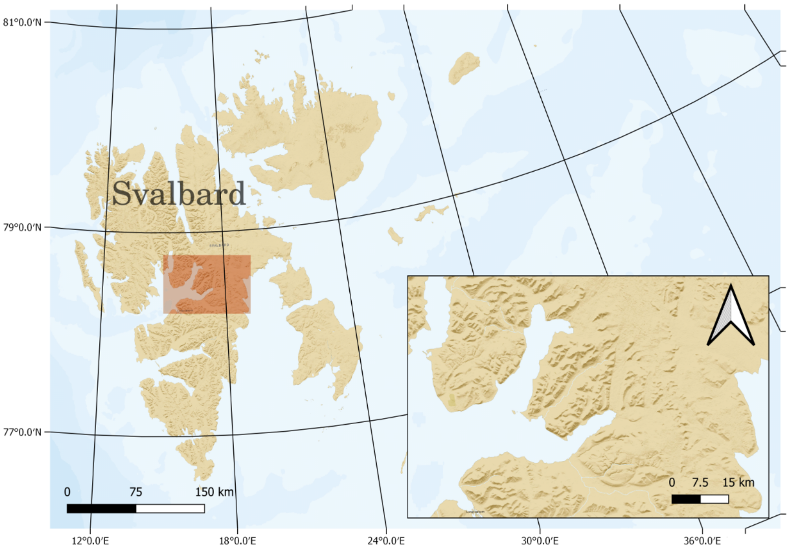

Figure 1: Map of Svalbard and the study area.

Every summer, census counts were conducted by observers on foot using binoculars or telescopes. Due to the geography of the study area and the specificities of the species, individuals could easily be spotted and their collar ID identified from a distance. For individuals that died during winter, carcasses were spotted, markings were recovered and the confirmed death of the individual was recorded (Figure 2). The GPS collars are store-on-board collars, so capture and census efforts are not targeted to known positions. A more comprehensive description of the data acquisition, the April captures and the summer observation process can be found in (Lee et al., 2015; Omsjoe et al., 2009; Pigeon et al., 2019). Rain on snow during a year was calculated as the sum of precipitation in millimetres between November and April when temperature was above 1°C. Weather data was obtained from Longyearbyen weather station (http://eklima.met.no). Bac- fat thickness, as a proxy for body condition, was measured using a portable ultrasound scanner (Scanner 100 linear, 5-MHz transducer, Pie Medical, Maastricht, the Netherlands). Animals were placed in lateral recumbency and measure was taken on the rump (Stien et al., 2003) with the probe placed at one hand distance cranial to the illiac crest. This method does not allow fat layers under 4 mm thick to be detected (Milner et al., 2003).

Figure 2: A reindeer carcass in Svalbard. *Photo credits: Ben McKeown*

2.2 - Statistical analysis

Data handling and statistical analysis have been conducted in R version 3.6.2 (2019-12-12) (R.Core.Team, 2019) and R Studio Version 1.2.5033. All the packages used for analysis are listed in Appendix C.

2.2.1 - Survival model

The survival model used to assess the effect of GPS collars on Svalbard reindeer survival was adapted from the integrated population model developed by Lee et al. (2015) to study survival, fecundity and age-specific population size on the same reindeer population. It is a state-space formulation of a Cormack-Jolly-Seber (CJS) capture-mark-recapture model. This model combines data from April mark-recapture, summer census and harvesting data. The survival of culled and hunted individuals is taken into account in the model up to their death, but their death are not, because they are not caused by natural processes. The hypothesis and predictors for the survival model were chosen according to the existing literature and reindeer biology (Albon et al., 2017; Haskell & Ballard, 2007; Rasiulis et al., 2014; Swenson et al., 1999).

The survival rate (s) is modeled as:

$$logit(s_{i,t}) = \beta^s \chi^s_{i,t} + \zeta^s_t + \gamma_{i,t}$$

Where subscript i denotes individuals and t time (in seasons). ζ^s_t is a random effect drawn from a normal distribution in order to account for the temporal fluctuation in survival shared across all individuals (common responses to seasonal environmental effects). $\gamma_{(i,t),t}$ is a random effect drown from a normal distribution and represents differences among age groups in the temporal fluctuations (different response of different age groups to seasonal environmental effects). $\beta^s {\chi^s}_{i,t}$ is the mean survival on the logit scale, where χ^s is the matrix of predictive variables, β^s the vector of regression coefficients including the effect of age class, rain on snow, presence or absence of a GPS collar and interaction between rain on snow and age. The age classes (calves, 1, 2, 3-8, 9-11 and 12+ years old) used were the same as in Lee et al. (2015). Rain on snow was scaled and centred before being used in the model.

The number of individuals in each age class wearing a GPS collar and dying each season was too small (or often non-existent), so the interaction effects of GPS collar with age class and GPS collar with rain on snow both greatly increased difficulty of convergence of the markov chains and estimates imprecision. Therefore, the interaction effects were not used in the final model. Because the model estimates the survival from april to august and august to april, the preliminary version of the model included season as a predictor for survival to account for possible differences in individual survival between seasons. The effect was found to be non-significant (Appendix A Figure 1) and survival rates were similar between the two seasons, in practice because late winter mortalities occur both before and after the capture period in April. As the effect of season was found to be non-significant, to facilitate model convergence and further calculations of annual survival rates, season was dropped from the final model. Survivals are later presented as annual survival for simplicity. Annual survival was calculated as the product of August-April and April-August survival. Because most individuals wear the GPS collar for their entire life, using individual as a random effect might have hidden the effect of the GPS collar on survival, therefore it was not used in the model. The sighting probability part of the model was estimated as a function of season and the presence of a GPS collar, and was allowed to vary randomly with year.

The model was written in a Bayesian framework, in JAGS language, ran with R2jags package (Su & Yajima, 2015) for 250.000 iterations with a thinning of 10, 5000 of burn in, and 3 Markov chain Monte Carlo (MCMC) chains. All priors in the model were chosen to be non-informative, they consist of uniform distributions $u(0, 10)$ for variance parameters, $u(0, 1)$ for probabilities and normal distributions $N(0, 1000)$ for all other parameters. The influence of the priors on the posterior distributions for all parameters was checked by comparing prior and posterior density overlap by calculation and visually (Appendix A Figure 2). To avoid weak parameter identifiability, Gimenez, Morgan, & Brooks (2009) suggests a 35% threshold guideline for the uniform priors in mark-recapture models.

2.2.2 - Fat thickness model

The data collection method by ultrasound for the fat thickness was not able to detect values under 4 mm, therefore any observation under 4 mm was considered zero. As a result, the distribution of back fat thickness was non-normal, left censored and zero inflated.

Standard Tobit regression models are designed to handle data where the dependent variable is left censored at zero (Tobin, 1958), a requirement which our data met. The hypothesis and predictors were chosen according to existing literature on biology and ecology of Svalbard reindeer (Albon et al., 2017; Haskell & Ballard, 2007; Rasiulis et al., 2014; Stien et al., 2003; Swenson et al., 1999).

The Tobit regression for modelling fat thickness response was expressed as :

$$\hat{y}_{i,t} = \beta^f \chi^f_{i,t} + \zeta^f_t + \alpha_i + \epsilon^f_{i,t}$$

$$y_{i,t} = \begin{cases} 0 & \text{if } \hat{y}_{i,t} \leq 0 \\ \hat{y}_{i,t} & \text{if } \hat{y}_{i,t} \geq 0 \end{cases}$$

Where $y_{i,t}$ is the dependent variable of fat thickness. Subscript $i = 1, ..., N$ indicates individuals and t denotes the year. $\hat{y}_{i,t}$ is the latent part of the model which is observed as $y_{i,t}$ if positive, or observed as equal to zero otherwise.

$\chi^f_{i,t}$ is a matrix of predictive variables, β^f the vector of unknown parameters including age, rain on snow, presence of a GPS collar. ${\zeta^f}_t$ is a normally distributed random effect that represents the temporal fluctuation (common response to annual environmental effects). α_i is a normally distributed random effect that represents the difference in individual response. $\epsilon^f_{i,t}$ represents the residual variation. Rain on snow was calculated in the same manner as for the survival model, and scaled and centred before being used in the model. No age groups were formed and age was used as a factor.

Priors for all parameters were chosen to be non-informative. They consist of uniform distribution $u(0, 10)$ and $u(0, 100)$ for variance parameters, and of normal distributions $N(0, 10000)$ for all other parameters. Prior influence was checked by calculating prior and posterior distributions overlap and by visual assessment (Appendix B Figure 2). The model was written in JAGS language (Bayesian framework) and ran with R2jags (Su & Yajima, 2015) with 3 MCMC chains, 35000 iteration, 3500 burning, 5 thinning.

For both models, convergence was assessed with the Gelman-Rubin statistic (Gelman & Rubin, 1992), R-hat test values with a threshold of 1.05, and visual checks of the chain mixing via trace-plots. Autocorrelation was checked visually with lag plots. I checked that effective sample size for each parameter was sufficient to ensure that possible autocorrelation did not affect estimate precision (Muth, Oravecz, & Gabry, 2018).

For the fat thickness Tobit model, goodness of fit and predictive ability were checked visually with posterior predictive check and posterior predictive scatter plot (Appendix B Figure 1) (Gelman, Meng, & Stern, 1996). The pseudo R^2 was calculated to assess goodness of fit (Veall & Zimmermann, 1996).

For the state-space survival model, predictive ability was checked by calculating the percentage of error in predicted values of observation versus recorded observations and visually with posterior predictive scatter plot (Gelman et al., 1996). Goodness of fit was assessed visually (Appendix A Figure 3).

3 - Results

3.1 - Survival

The survival analysis covered a total of 818 female reindeer (5036 observations), among which 47 had a GPS collar (364 total observations), over 49 seasons (Summer 1994 to Summer 2018). Average recorded rain-on-snow was 46.36 mm (min: 0.2 - max: 92.5). The model estimated winter sighting probability at 50% *(CrI: 43 - 57)* and summer sighting probability at 50% *(CrI: 45 - 55)*. Wearing a GPS collar did not significantly influence the probability of observation or recapture with 54.26% *(CrI: 46.25 - 62.21)* on the probability scale. The random effect of year on survival had a mean standard deviation of 0.46 *(CrI: 0.12 - 0.77)* and the random interaction between year and age on survival had a standard deviation of 0.92 *(CrI: 0.63 - 1.30)* (both estimates are on the logit scale). Although some amount of auto-correlation was detected for the parameters of age, for the interaction between age and rain-on-snow, and for the random effect of the interaction of year and age, all parameters in the model (including interactions and random effects) had Gelman-Rubin and R-hat test values of 1 (Appendix A Figure 4), sufficient effective sample size (Appendix A Figure 6), and good chain mixing, showing convergence of the model. All priors that were normally distributed overlapped the posterior distribution by less than 2% and all priors that followed a uniform distribution overlapped the posterior distribution by less than 35% (Appendix A Figure 2). The model displayed a correct goodness of fit (Appendix A Figure 3) and good predictive ability although there was a a 27% mismatch between observation and posterior prediction (Appendix A Figure 5).

3.1.1 Rain-on-snow and age

Rain-on-snow was estimated to have a significant negative effect on survival with a mean logit scale estimate of -0.62 *(CrI: -1.05; -0.22)* (Appendix A Figure 6 & Figure 4B). Age was a significant predictor for survival. As previously reported by Lee et al. (2015), survival was high for age classes 2 (1 year old), 3 (2 years old), peaked at age class 4 (3-8 years old) and started decreasing at age class 5 (9-11 years old). Calves (age class 1) and older individuals (12+) had lower survivals (Figure 3). Figure 4B shows different survival responses with the interaction of rain-on-snow and age classes. There is a faster decrease in survival for calves (age class 1) and individuals over 12 years old (age class 6) as rain-on-snow increases (Figure 4B).

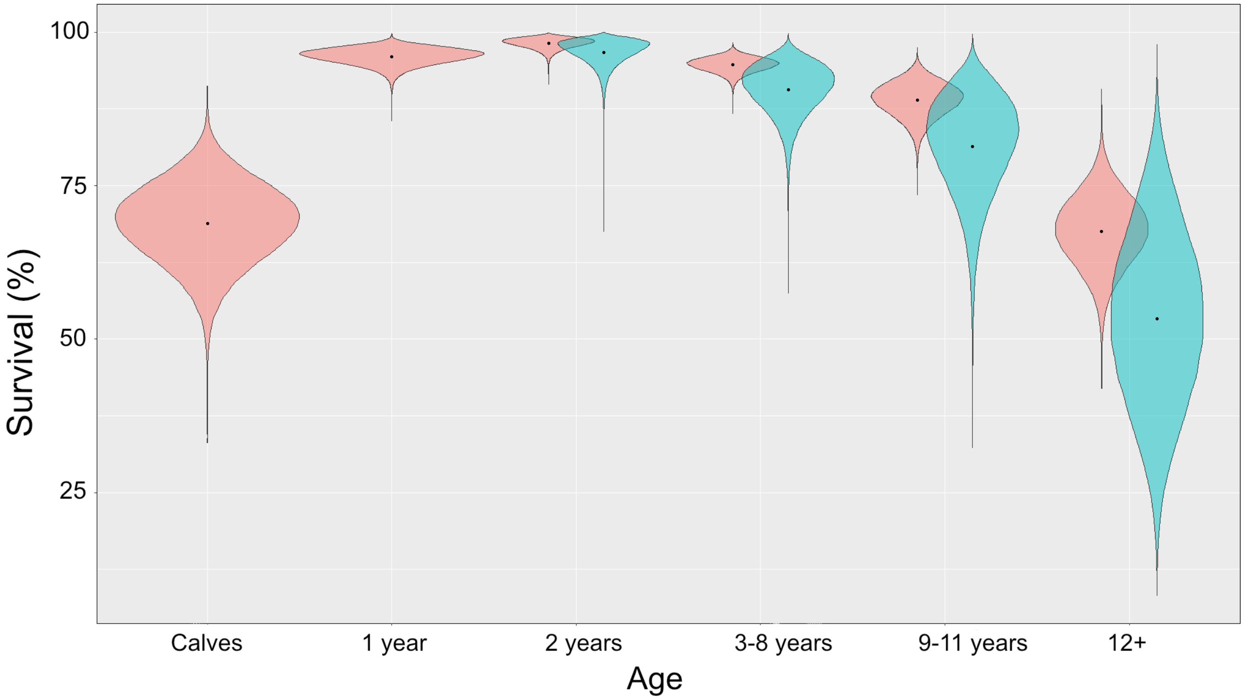

Figure 3: Survival estimate for each age class for GPS collared and light plastic collared individuals. *Red:* Light plastic collared individuals. *Blue:* Collared individuals. Survival is lower for calves and individuals over 12 years old. It increases after the first year of life, peaks at 2 years old (age class 3), and decreases as individuals get older. Survival estimates for GPS collared and light plastic collared individuals overlap each other and uncertainty is higher for collared individuals. Survival estimates for GPS collared calves and 1 year old individuals are not displayed because reindeer are only collared with GPS when they are 2 years old.

3.1.2 GPS collar

The mean effect of the GPS collar on survival was estimated to be (on the logit scale) -0.52 *(CrI: -1.35 - 0.47)*. Its 95% credible interval crosses zero (Appendix A Figure 6). This corresponds to a 4% *(CrI: -12.9 - 2)* decrease in survival for collared individuals of age class 4 (3-8 years old) during a year with average rain-on-snow (Appendix A Figure 7). The predicted annual survival rates for GPS collared and light plastic collared individuals during a year with average rain-on-snow (46.36 mm) overlap each other (Figure 4A). The mean difference in survival between GPS collared and light plastic collared individual of all age classes was calculated for a year with average rain-on-snow (Appendix A Figure 7). In all age classes, the credible interval for estimated difference in survival crossed zero (Appendix A Figure 7). Age class 3 (2 years old) had the smallest estimated decrease in survival between GPS collared and light plastic collared individuals with -1.5% *(CrI: -5.7 - 0.7)*. Calves and individuals over 12 year old had a stronger estimated decrease in survival when wearing GPS collar in a year with average rain-on-snow (46.36 mm) with respectively -14% *(CrI: -36.9 - 9.5)* and -14.3% *(CrI: -37.3 - 9.9)*, but it is important to note that reindeer are only collared after turning 2 years old, so estimated survival when wearing a GPS collar for calves and 1 year old individuals is hypothetical.

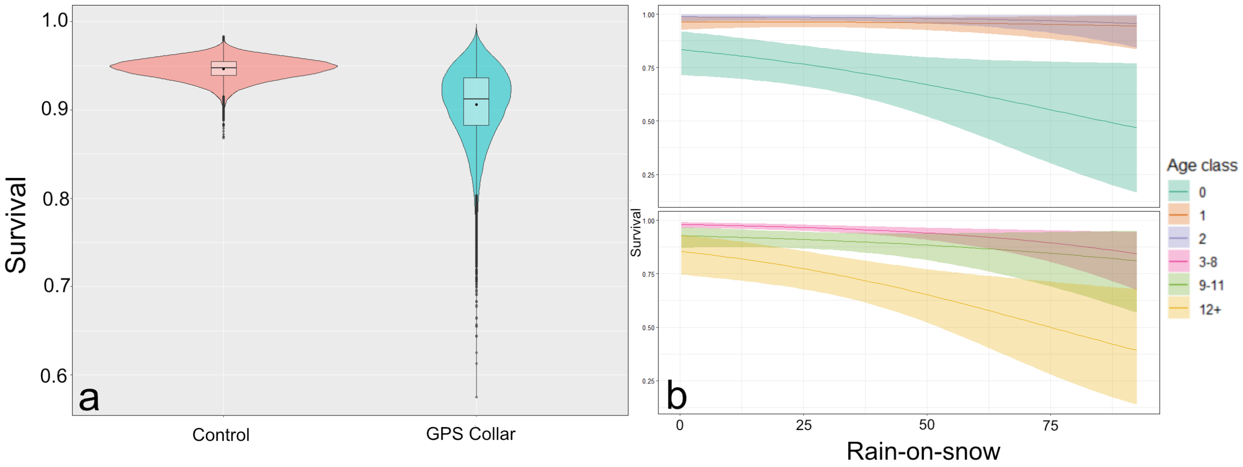

Figure 4: Estimated survivals. **A:** Estimated survival for individuals of age class 4 *(3-8 year old)* for average *(46.36 mm)* rain-on-snow. The dot represents the mean value. *Red:* Control group. *Blue:* Collared individuals. The control group displays a slightly higher survival, the violins overlap each other. Collared group displays more uncertainty toward low survival values. **B:** Estimated annual survival for Svalbard reindeer in function of rain-on-snow. The upper panel shows age classes 1 (yearlings), 2 (1 years old) and 3 (2 year old); the lower panel shows age classes 4 (3-8 years old), 5 (9-11 years old) and 6 (12 and older). Yearlings and individuals over 12 years old display more sensitivity to rain-on-snow and a steeper decrease in survival.

3.2 - Fat thickness

The back-fat thickness analysis covered 960 female (3252 observations) reindeer between 1995 and 2017, of which 48 wore a GPS collar (160 observations). Median age was 4 years old (1-17). Average observed rain-on-snow was 45.65 mm (min: 0 - max: 88.7) per year. The random effect of year on fat thickness had a standard deviation of 4.75 mm *(CrI: 3.34 - 6.89)* and the random effect of individual on fat thickness had a standard deviation of 1.84 mm *(CrI: 1.43 - 2.24)*. The residual variance of the model was 4.86 mm *(CrI: 4.66 - 5.07)*

All parameters in the model had Gelman-Rubin's test values of 1 (Appendix B Figure 3), a sufficient effective sample size, and good chain mixing, showing convergence of the model. The priors for each parameter did not influence the posterior distributions, with less than 1% overlap for normally distributed parameters (Appendix B Figure 2) and less then 26% for priors with a uniform distribution. Along with the pseudo R^2 of 0.60, posterior predictive check and scatter plot showed a correct fit of the model and predictive ability (Appendix A Figure 2). No parameter displayed auto-correlation except the individual variation random effect, but it did not affect its convergence or accuracy (Gelman-Rubin and R-hat test values of 1).

3.2.1 - Rain-on-snow and age

The effect of rain-on-snow on fat thickness was not significant with a mean estimate of -1.36 mm fat decrease per standard deviation of rain on snow, with its 95% credible interval crossing zero *(CrI: -4.30 - 1.58)* (Appendix B Figure 4). Age had a non-linear effect on fat thickness (Figure 5). On a year with average recorded rain on snow (45.65 mm), mean predicted fat thickness started at 3.29 mm *(CrI: 0.06 - 6.57)* for yearlings, increased to reach a peak at age 4, with 10.35 mm *(CrI: 7.75 - 13)*, and decreased as individuals got older to reach its minimum for 16 years old individuals with mean 1.15 mm *(CrI: -3.74 - 5.94)*.

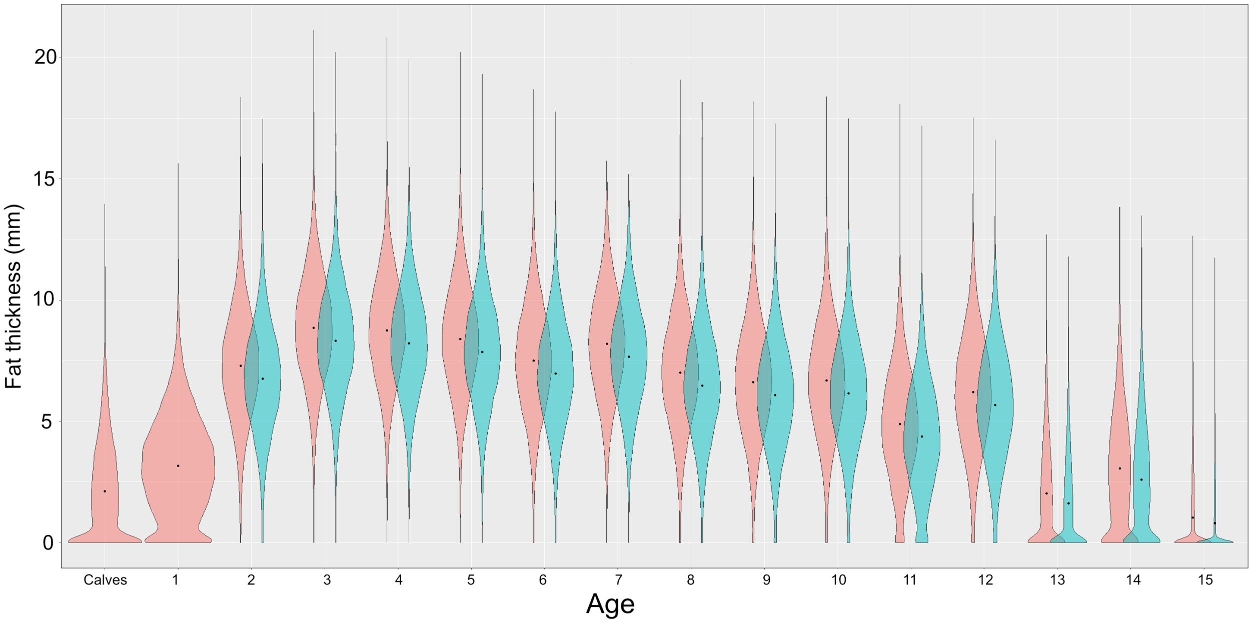

Figure 5: Estimates of fat thickness in function of age and for average rain-on-snow *(45.6 mm)*. Black dots represent estimated fat thickness for both GPS collared and light plastic collared individual. *Red:* Estimated fat thickness for light plastic collared individuals. *Blue:* Estimated fat thickness for GPS collared individuals. Estimated fat thickness is low for calves and yearlings and increases until it peaks at age 4. It then decreases as individuals get older and is low after age 13. Fat thickness estimates for GPS collared calves and 1 year old individuals are not displayed because reindeer are only collared with GPS when they are 2 years old.

3.2.2 - GPS collar

Back-fat was estimated to decrease by 0.53 mm *(CrI: -1.58 - 0.52)* on individuals wearing a GPS collar (Figure 6), with its 95% credible interval crossing zero (Appendix B Figure 4). The probability densities for predicted fat thickness in GPS collared and light plastic collared individuals largely overlapped each other (Figure 6).

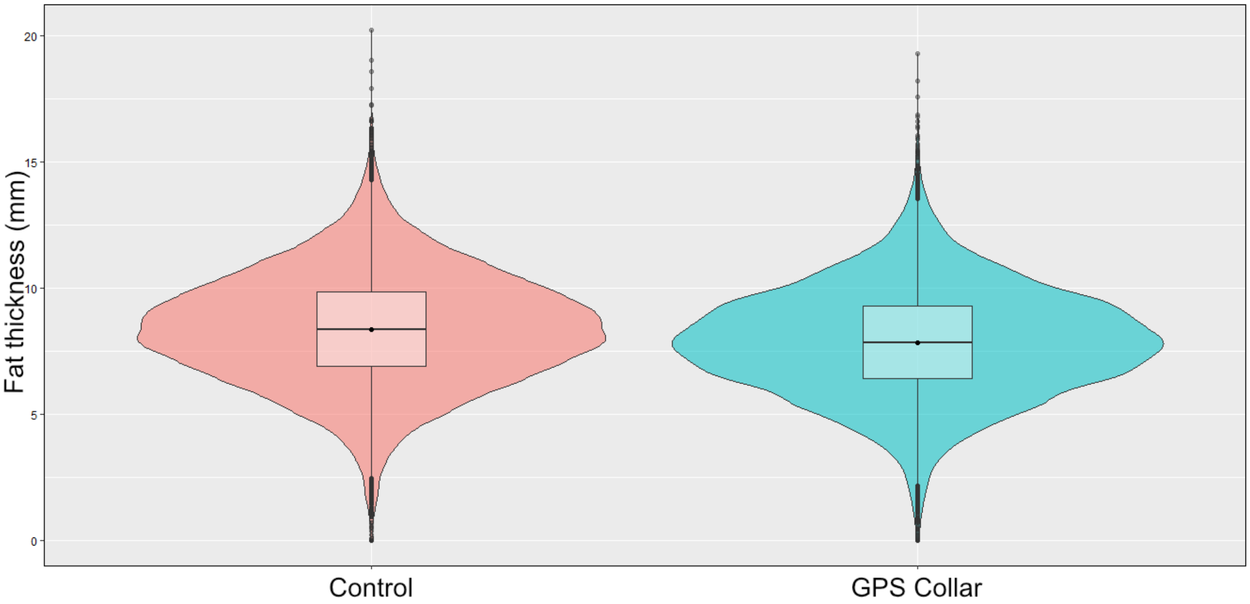

Figure 6: Estimated fat thickness *(mm)* for light plastic collared *(Red)* and GPS collared *(Blue)* 6 years old individuals, in a year with average of rain-on-snow *(45.6 mm)*. The mean predicted fat thickness of collared individuals is slightly lower than for the control group, the violins almost completely are overlapping each other.

4 - Discussion

In this study I aimed at investigating the impact of GPS collars on Svalbard reindeer. We studied potential effect on both survival, and fat thickness, as an indicator of body condition and energy reserves at the end of the winter. In addition to the effects of GPS collars, we tesed for a possible effects of rain on snow, and individual's age, and tested if specific age classes were more sensitive to rain on snow when it comes to survival. The existence of two distinct groups of marked individuals (light plastic cattle collars and GPS collars) made it possible to constitute a control group, which is not a common opportunity in studies that aim at testing for a radio-collar effect. Contrary to our hypotheses, the GPS collar did not significantly affect survival nor fat thickness, but there was an observable negative trend in both. Rain on snow and age were the best predictors for survival, and age was the best predictor for fat thickness.

4.1 - Survival

The survival estimates we observed are consistent with results from Lee et al. (2015) and Albon et al. (2017) where age classes 3 and 4 (2-8 years old) had the highest survival rates, and individuals younger than one and over twelve years had the lowest. The effect of rain on snow on survival in our study is in accordance with Putkonen & Roe (2003), Solberg et al. (2001), Kohler & Aanes (2004) and Albon et al. (2017), who describe an influence of icing events on survival, growth rate and body condition of Svalbard reindeer populations. The youngest and oldest individuals displayed a steeper decrease in survival with increasing rain on snow (Figure 4B). This could be due to younger and older individuals having generally poorer fat reserves and body condition, thus being more sensitive to loss of forage and increased energy expenditure due to environmental conditions. This matches with Tyler (1986) who describes a relationship between Svalbard reindeer fat content and death from starvation. Contrary to Haskell & Ballard (2007) and Rasiulis et al. (2014), who observed lower survival rates in female reindeer fitted with telemetry collars, we did not observe a statistically significant effect of the GPS collars on reindeer survival. We only observed a non-significant tendency (Appendix A Figure 6 and Appendix A Figure 8). In Rasiulis et al. (2014) the satellite collars used were significantly heavier than the GPS collars used in our study (1630 grams against 680-950 grams for ours), and were compared to light-weight VHF collar (514g). As our collars were under 2% body-weight ratio, the result seem to validate Arnemo & Evans (2017) and Arnemo et al. (2004) who advise keeping animal attached devices and implants under 2% body weight ratio to avoid possible adverse effects. Note that the heavy satellites collars in the Rasiulis et al. (2014) study population are not in use any more and have been replaced by light-weight 500g GPS collars since 2000. Although Rasiulis et al. (2014) observed an effect of heavy satellite collars (1630g) compared to light-weight VHF collars (514g) on migrating caribou survival, and some authors have described GPS collar effect such as increased energy expenditure and metabolic rate (Lear et al., 2018; Rosen et al., 2018) in other species, this does not seem to apply to Svalbard reindeer. Indeed, Svalbard reindeer do not migrate, have a strongly seasonal metabolism, and comparatively to other reindeer sub-species, they can slow down their metabolic rate while lying down and standing, to respectively 60-78% and 44% of the values normally observed in mainland individuals (Cuyler & Øritsland, 1993). Additionally, they spend a large proportion of time in winter laying down to save energy (Cuyler & Øritsland, 1993). It is possible that the GPS collar does not cause any adverse effect in these conditions and may only affect more active species. Other documented effects of GPS collars do not apply to Svalbard reindeer, such as lessened predator avoidance abilities and selective predation on collared individuals (Marks & Marks, 1987), as Svalbard reindeer do not have predators (Loe et al., 2007; Williamsen et al., 2019).

The imbalance between the small number of GPS collared individuals compared to the important control group, along with the generally very high survival in Svalbard reindeer, might play in the uncertainty in the estimates. A possible influence of the GPS collar on survival might be over-shadowed by more important sources of mortality, such as blocked access to forage and starvation. In this study we could not test for interactions between GPS collar and age, GPS collar and rain on snow, or between the three of them. To do so, the model parametrization requires a larger sample size. The next step could be to enter longer time series in the model and to use current posterior results as informed priors to bring more precision to the estimates. Finally, it might be useful to control for population density effects. Density-dependent feedback processes are modulating the outcomes of environmental stochasticity for population dynamics, and individuals of different ages are not impacted in the same way. Hansen et al. (2019) demonstrated that single extreme events are not always good predictors for population persistence and dynamics in Svalbard reindeer, due to density-dependent feedbacks. That study found that extreme events such as rain on snow decreases survival rates of vulnerable age classes at high population densities, resulting in a population with more individuals of resilient ages and a reduced population sensitivity to subsequent bad conditions. .

4.2 - Body condition

The pattern of back fat thickness we observed as a function of age was similar to that observed by Milner et al. (2003). It is also similar to the survival pattern as a function of age we and Lee et al. (2015) observed, which confirms the observation by Stien et al. (2003) that back-fat thickness can be used as a body condition indicator in Svalbard reindeer. We found no significant effect of the GPS collars on fat thickness. We only observed a non-significant negative tendency (Appendix B Figure 6), but the effect size was relatively small (Appendix B Figure 4), pointing to no effect of the GPS collar on fat thickness. There are currently no studies on the effects of GPS collar on ungulate's fat thickness to directly compare our results to. Svalbard reindeer have a highly plastic fat metabolism and cycle (Reimers et al., 1982), so it may be possible that GPS collar do not influence back fat thickness. Because every individual responds differently to its environment and has a slightly different metabolism, we accounted for individual variation in the model. There is a possibility that a relatively small effect of the GPS collar on fat thickness in the model would be hidden by individual variation, because collared individuals wear the collar for a large part of their life. Additionally, the capture and fat thickness measuring processes go on for several weeks, in a period when female reindeer are entering the last phase of gestation, when snow is still present and plant growth has not started yet (Albon et al., 2017). Svalbard reindeer experience a decrease in their body mass during this period, and it is possible that the measures taken throughout the capture process are not comparable to each other, giving potentially biased estimates. A subsequent model analysis showed a significant effect of capture date on back fat thickness measure (Appendix B Figure 9). Therefore, adjustment of fat thickness measures for capture date should be implemented in a future analysis. As Milner et al. (2003) suggests that blood parameters are more sensitive than back-fat thickness to variation in body condition in individuals with poor body condition, possibly because of the 4 mm threshold of detectable fat thickness by the ultra-sound method, blood parameters could be included in further analysis. Rain on snow did not show a statistically significant effect in the model, but there was a strong tendency for a negative effect on fat thickness, as shown by the large effect size (Appendix B Figure 4 and Appendix B Figure 5). Not finding a significant effect of rain-on-snow on fat tickness is an unexpected result, as other studies have found a significant effect of rain on snow on body mass (Albon et al., 2017) and survival (Kohler & Aanes, 2004; Lee et al., 2015; Putkonen & Roe, 2003; Solberg et al., 2001). We account for annual environmental variation in the model, which could over-shadow the effect of rain on snow, which is an annual measurement. The prior we used was uninformative, it is possible that using of more informed prior would yield more precise estimates. Additionally, muscle mass is also part of the animal body reserves, there is potentially more variation in the body mass metric than fat thickness metric. Finally, Svalbard reindeer have the ability to mitigate the negative effects of rain-on-snow events by changing their foraging niche and migrating. Hansen & Aanes (2012) described Svalbard reindeer migrating to the seashore, to feed on kelp and seaweed.

This model did not take into account possible interactions between GPS collar, age and rain on snow. Because of the important differences in fat thickness between different ages and the documented impact of rain on snow on survival and body mass, one could expect an interaction effect between GPS collar, age and rain on snow. It would be a natural next step in the analysis to test for it, but it would require a larger data set than the one available in this study.

4.3 - Further research and regulations

Solberg et al. (2001) showed that "bad winters" for Svalbard reindeer were characterized by total winter precipitation, whether it manifested as ground icing or not. Including total winter precipitation as a predictor, rather than winter precipitation when the temperature is above 1 °C, could give further insight in both the survival and the fat thickness model. Studying a possible effect on behaviour and foraging via acceleration data could show smaller scale effects. Small accelerometers can be attached to the lightweight plastic marking of the reindeer and recovered at a later capture, so a study design with a control group is possible. Although in our study reindeer wore the GPS collar for many years, we did not consider the length of time wearing the collar. There could be differences between newly collared individuals and individuals that had the collar for a long time. There could be either a cumulative long-term effect, either a short-term negative effect followed by habituation and adaptation. Tuyttens et al. (2002) observed on badgers *(Meles meles)* that individuals which had a radio collar for less than 100 days had a lowered body condition compared to individuals that had a radio collar for longer than 100 days. Additionally, in his extensive literature review, Balmori (2016) warns about several possible documented effects of the radio-frequency radiation emitted by collars. Because Svalbard reindeer keep their GPS collar for a long period of time and the availability of a control group, they would be good candidates to test for long term effect of GPS collar radio-frequency. Finally, testing for a difference in survival between individuals wearing collars of different weights could give more detailed information about the maximum acceptable collar/body weight ratio, which is important because of the lack of official guidelines and regulations. Even though our study population is equipped with three different weights of collars, our data does not include a sufficient sample size to differentiate between collar weights as Svalbard reindeer have generally high survival, and there are not enough individuals dying each year within each class of collar weight to yield precise estimates. The range of different collar weights in our population is also possibly too small to detect differences.

It is not possible to foresee and take into account every possible effect of the multiple treatments we apply to wild animals during research. Our goal should be to collect as much valuable data as possible while minimizing the negative effects on animals. In the absence research and regulations, we can rely on the "Three R's" (Replace, Reduce, Refine) to take decisions related to tagging. Zemanova (2020) provides an extensive review of possible problems with wild life capture and marking and how the "Three R's" can be used to mitigate adverse effects. In the context of GPS collars, "Refine" is the most relevant, urging that capture and collaring methods are improved as much as possible for minimizing detrimental effects on the animals and the research results. It is good practice to choose battery packs as light and small as possible, and to ensure a good fitting of the collar to the animal to avoid wear and wounds. For example, Collins, Petersen, Carr, & Pielstick (2014) observed in free roaming horses *(Equus caballus)* that after modifying and custom fitting collars with padding specifically to each individual's morphology, they caused no wear on the neck and detached with 89% success rate. This type of special care should be standard. For example, although they concluded there was no significant effect of the GPS collar on foraging behaviour in *Rupicapra rupicapra rupicapra*, Nussberger & Ingold (2006) described one individual who grazed head up, and after further observation, this individual had its neck emaciated, the fur torn down and it was observed that when it was grazing head down, the collar hit its lower jaw at each head movement. Krausman et al. (2004) observed neck lesions on ungulates due to the collars and Brooks et al. (2008) attributes differences in travel speed to collar fit and model. Although these are isolated occurrences, custom fitting the collars to the individuals might have prevented adverse effects in these cases.

5 - Conclusion

In conclusion, our findings point to a relative safety of GPS collars on Svalbard reindeer, although we observed a non-significant negative tendency in the effect of GPS collar on survival and fat thickness. Rain on snow, age, annual and individual variation explained more of the survival variation than the GPS collars. Our collars were below 2% collar/body weight ratio and this recommended limit was sufficient to prevent detectable adverse effects. GPS location devices are of invaluable importance to research and conservation, and preventive measures such as using low collar weight and ensuring good collar fitting should be applied in all studies. There should be a general effort in wildlife research to continuously encourage manufacturers to improve their technology, to decrease batteries size, and reduce telemetry devices' "clutter" and weight.

Figure 7: Picture of two adult Svalbard reindeer and a calf. *Photo credits: Witek Kaszkin.*

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Effects of GPS-collars on Svalbard reindeer survival and body condition - Appendix A

Guillaume Borquet

State-space survival model

Model validation

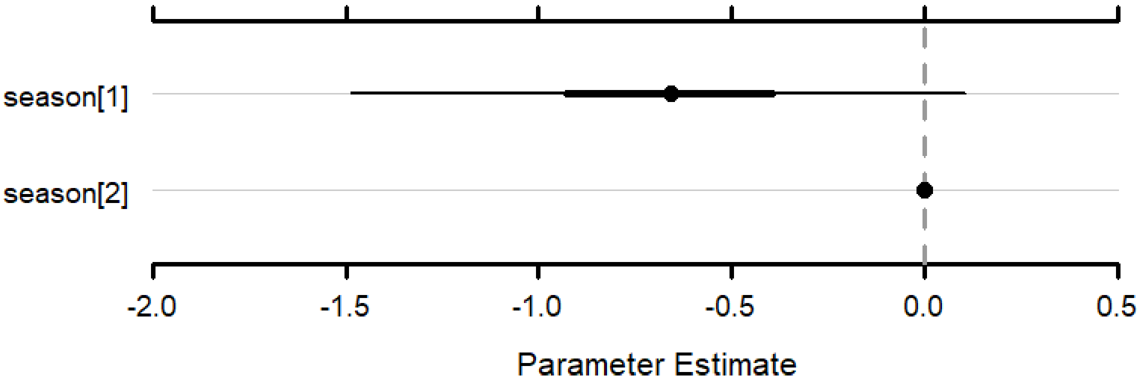


Figure 1: Forest plot of the season parameter. The credible interval crosses zero, season is not a significant parameter for predicting survival.

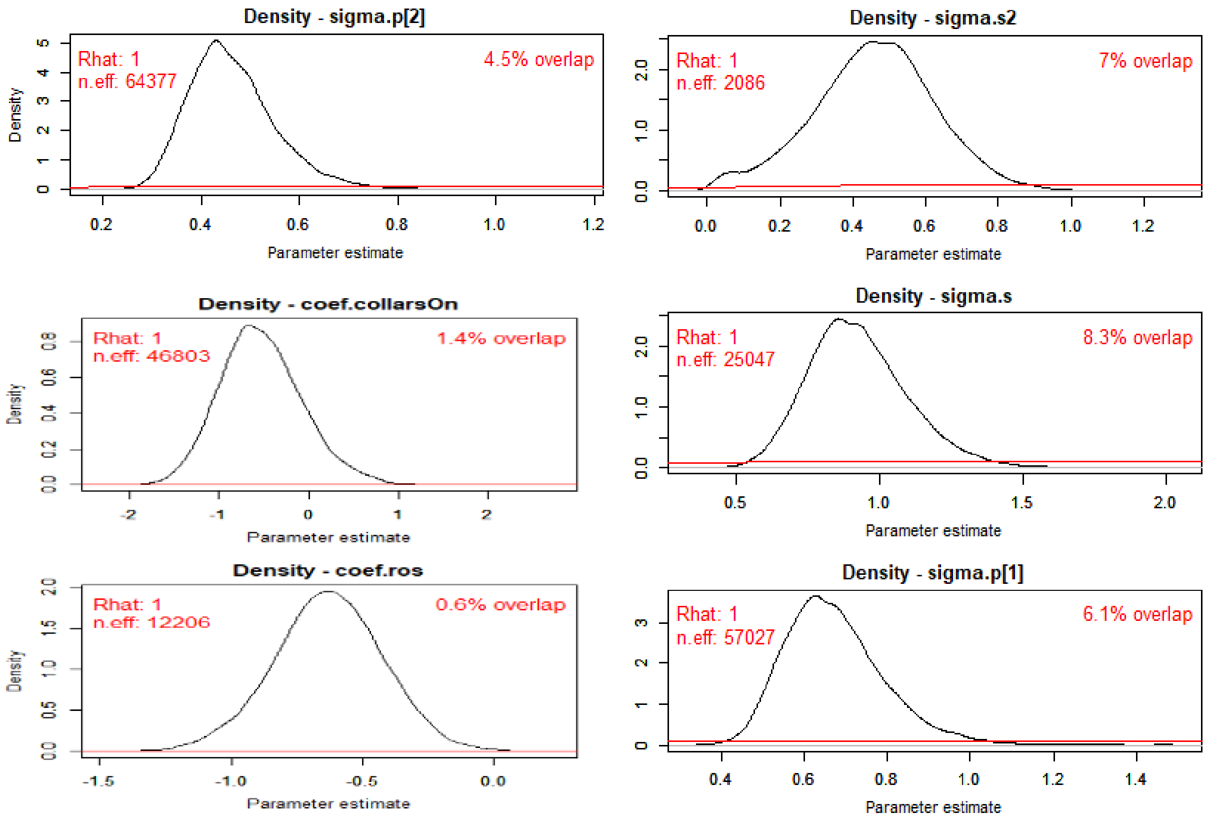


Figure 2: Prior / Posterior density overlap for certain parameters of the state space survival model. “sigma.p(1)” is the standard deviation of the sighting probability in winter, “sigma.p(2)” is the standard deviation of the sighting probability in summer, “sigma.s” is the standard deviation of the random effect of year, “sigma.s2” is the standard deviation of the random effect of the interaction between year and age, “coef.collarsOn” is the effect of the GPS collar and “coef.ros” is the effect of rain on snow. “n.eff” is the effective sample size for each parameters. The red line and and the value on the upper right corner of each pannel is represent the overlap between the prior and the posterior density. No parameter had important overlap.

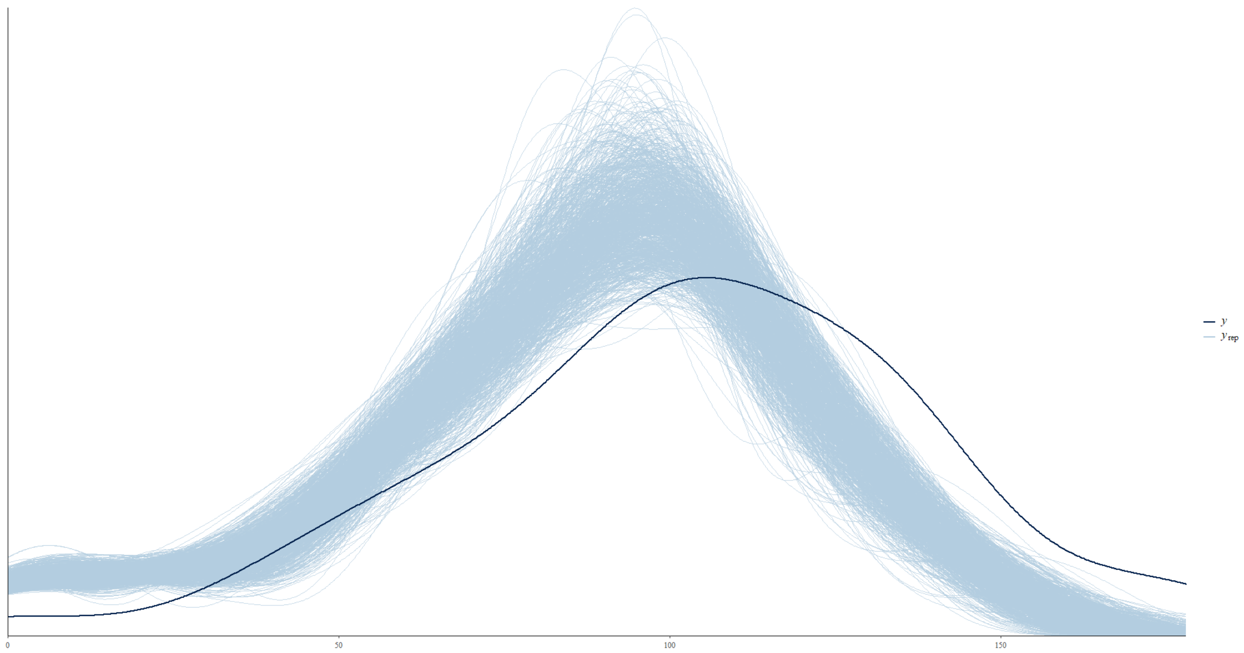
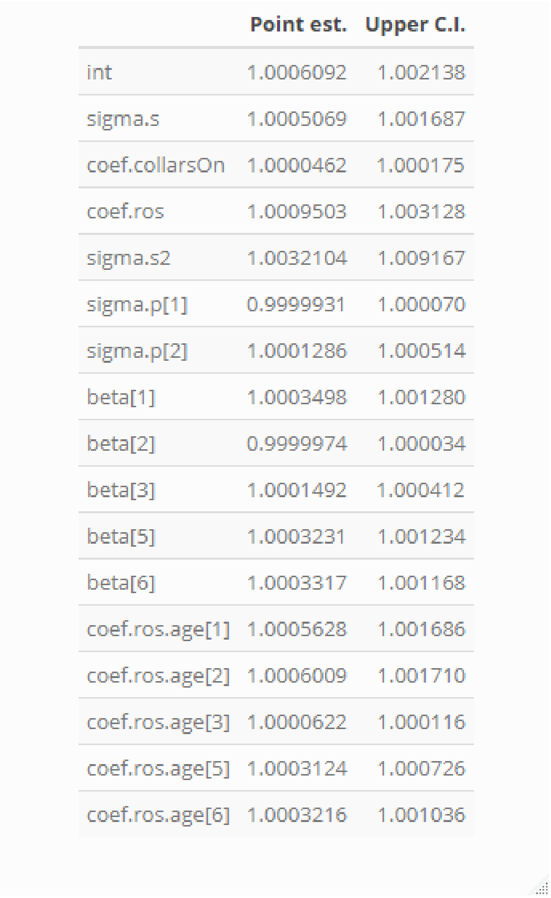


Figure 3: Posterior predictive check plot for the state space survival model. The black line (Y) is the observed values distribution and the blue lines (Yrep) represent the predicted values distribution. The state space model for survival showed a correct fit and predictive ability.



	Point est.	Upper C.I.
int	1.0006092	1.002138
sigma.s	1.0005069	1.001687
coef.collarsOn	1.0000462	1.000175
coef.ros	1.0009503	1.003128
sigma.s2	1.0032104	1.009167
sigma.p[1]	0.9999931	1.000070
sigma.p[2]	1.0001286	1.000514
beta[1]	1.0003498	1.001280
beta[2]	0.9999974	1.000034
beta[3]	1.0001492	1.000412
beta[5]	1.0003231	1.001234
beta[6]	1.0003317	1.001168
coef.ros.age[1]	1.0005628	1.001686
coef.ros.age[2]	1.0006009	1.001710
coef.ros.age[3]	1.0000622	1.000116
coef.ros.age[5]	1.0003124	1.000726
coef.ros.age[6]	1.0003216	1.001036

Figure 4: Gelman test values for the state space survival model. All parameters had Gelman test values of 1, showing a good convergence of the model.

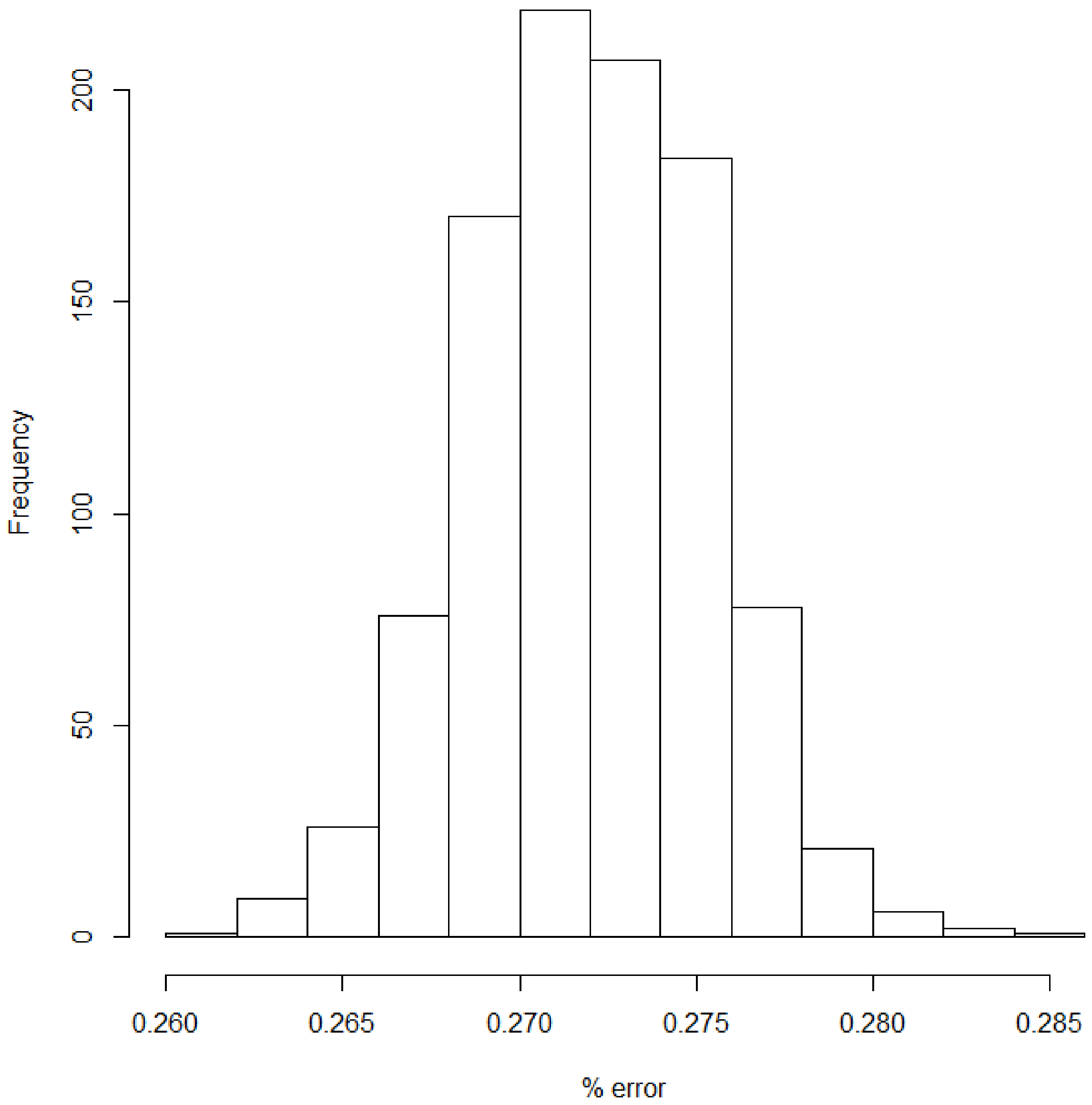
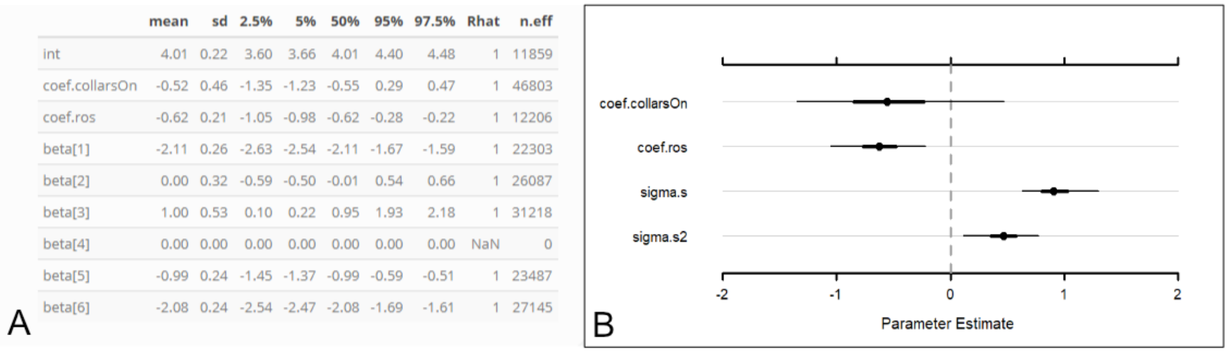


Figure 5: Percentage of mismatch between posterior prediction and observations in the survival model. There is a 27% mismatch between predicted and observed values.

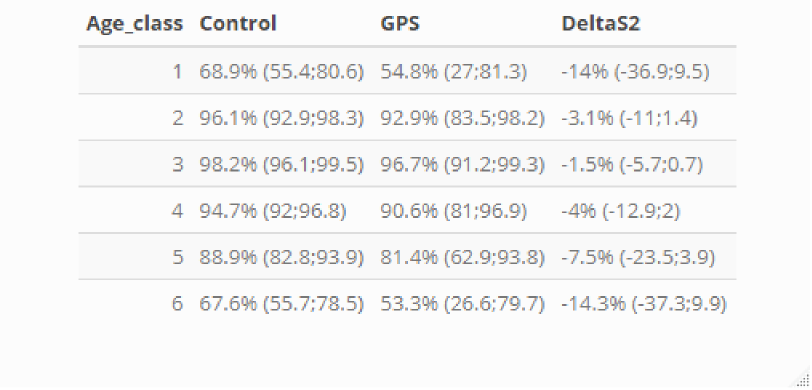
Results



A

	mean	sd	2.5%	5%	50%	95%	97.5%	Rhat	n.eff
int	4.01	0.22	3.60	3.66	4.01	4.40	4.48	1	11859
coef.collarsOn	-0.52	0.46	-1.35	-1.23	-0.55	0.29	0.47	1	46803
coef.ros	-0.62	0.21	-1.05	-0.98	-0.62	-0.28	-0.22	1	12206
beta[1]	-2.11	0.26	-2.63	-2.54	-2.11	-1.67	-1.59	1	22303
beta[2]	0.00	0.32	-0.59	-0.50	-0.01	0.54	0.66	1	26087
beta[3]	1.00	0.53	0.10	0.22	0.95	1.93	2.18	1	31218
beta[4]	0.00	0.00	0.00	0.00	0.00	0.00	0.00	NaN	0
beta[5]	-0.99	0.24	-1.45	-1.37	-0.99	-0.59	-0.51	1	23487
beta[6]	-2.08	0.24	-2.54	-2.47	-2.08	-1.69	-1.61	1	27145

Figure 6: **A** : Summary table of state space survival model. **B:** Forest plot of some model parameters. The model did not show a significant effect of the GPS collar on survival (coef.collarsOn) with its 95% credible interval crossing zero. An important part of the variation in survival was explained by rain on snow (coef.ros), age (beta), the annual variation (sigma.s) and the random effect of the interaction with age and year (sigma.s2).



Age_class	Control	GPS	DeltaS2
1	68.9% (55.4;80.6)	54.8% (27;81.3)	-14% (-36.9;9.5)
2	96.1% (92.9;98.3)	92.9% (83.5;98.2)	-3.1% (-11;1.4)
3	98.2% (96.1;99.5)	96.7% (91.2;99.3)	-1.5% (-5.7;0.7)
4	94.7% (92;96.8)	90.6% (81;96.9)	-4% (-12.9;2)
5	88.9% (82.8;93.9)	81.4% (62.9;93.8)	-7.5% (-23.5;3.9)
6	67.6% (55.7;78.5)	53.3% (26.6;79.7)	-14.3% (-37.3;9.9)

Figure 7: Summary of estimated survival probabilities during a year with average rain-on-snow (45.69 mm) for the different age classes. **Control:** Individuals with light plastic collars. **GPS:** GPS collared individuals. **DeltaS2:** Estimated difference in survival between control group and collared individuals. Survival is lower for GPS collared individuals, but none of the estimated decreases in survival are significant.

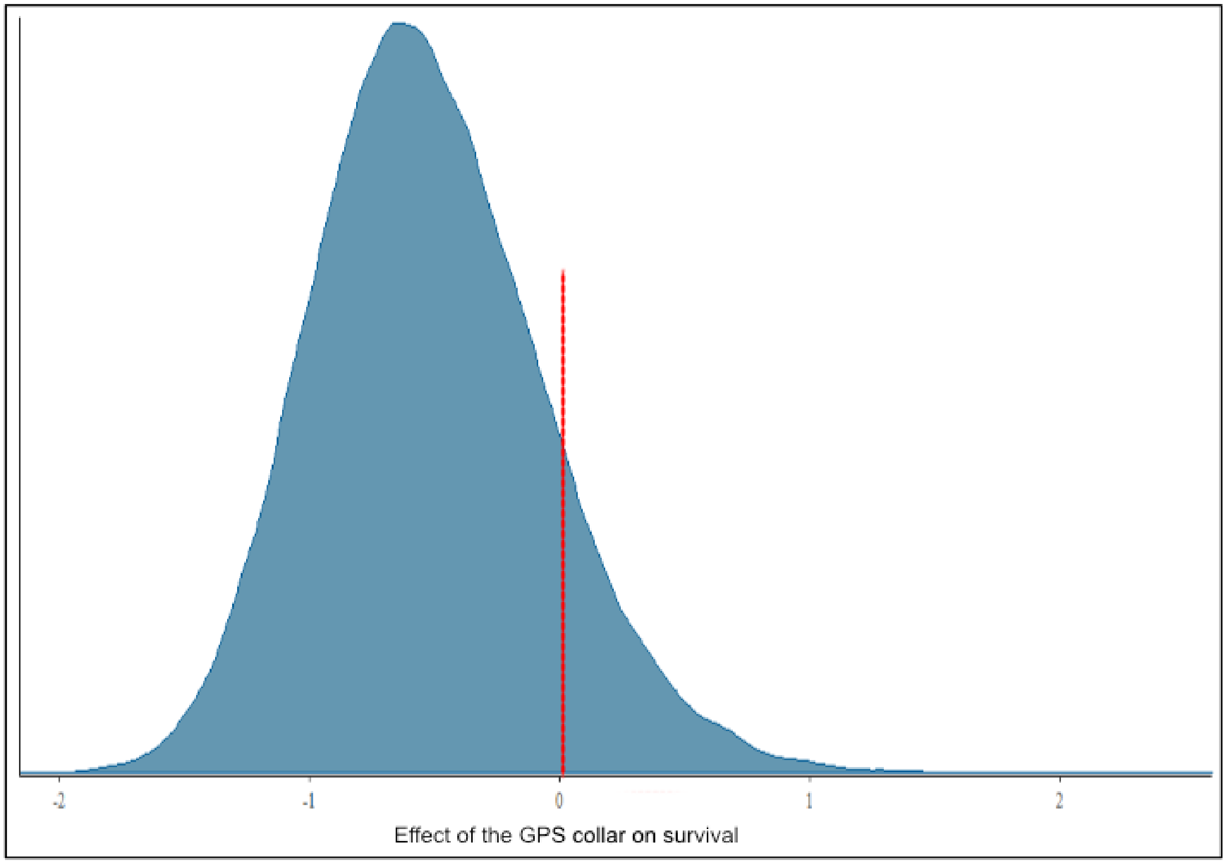


Figure 8: Posterior density of the parameter for the effect of GPS collar on survival. *Red dotted line:* Null effect. The effect is not significant, but a large part of the probability density is on the negative side

Effects of GPS-collars on Svalbard reindeer survival and body condition - Appendix B

Guillaume Borquet

Back fat thickness tobit model

Model validation

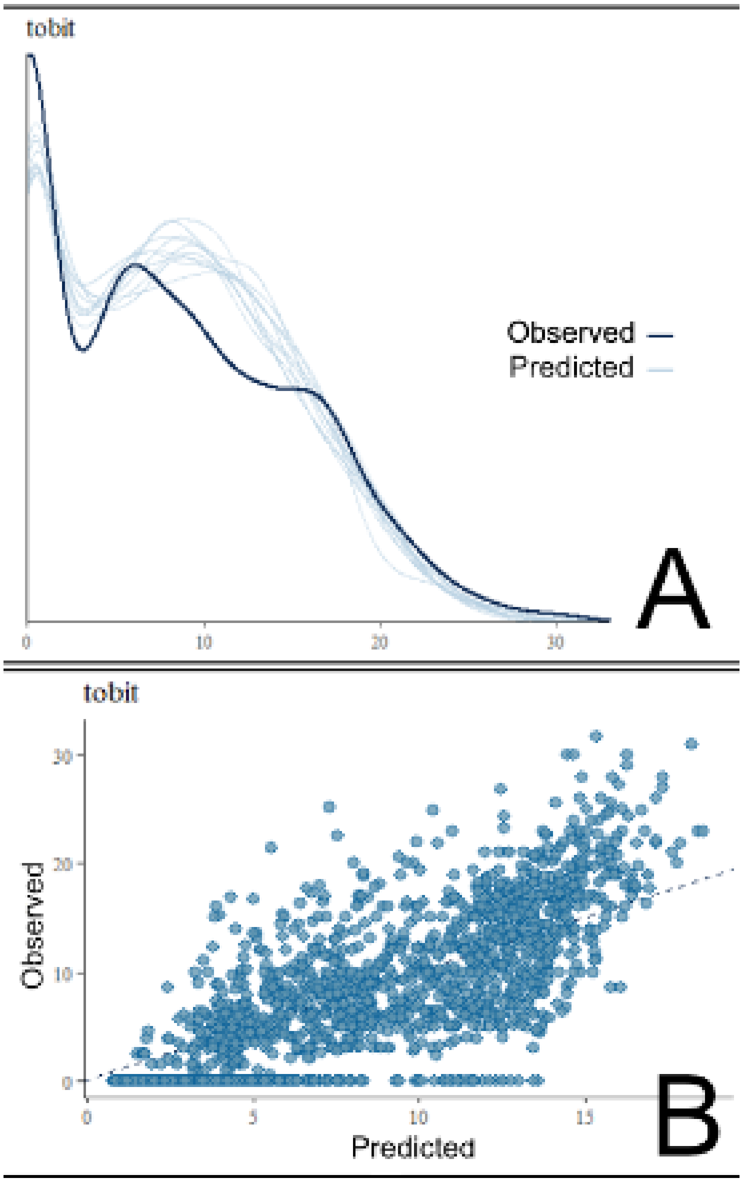


Figure 1: Goodness of fit and predictive ability of the fat thickness obit model. Pannel A is the posterior predictive check plot and pannel B is a posterior predictive scatterplot of the observed and predicted values for fat thickness. The model shows a correct fit and predictive ability.

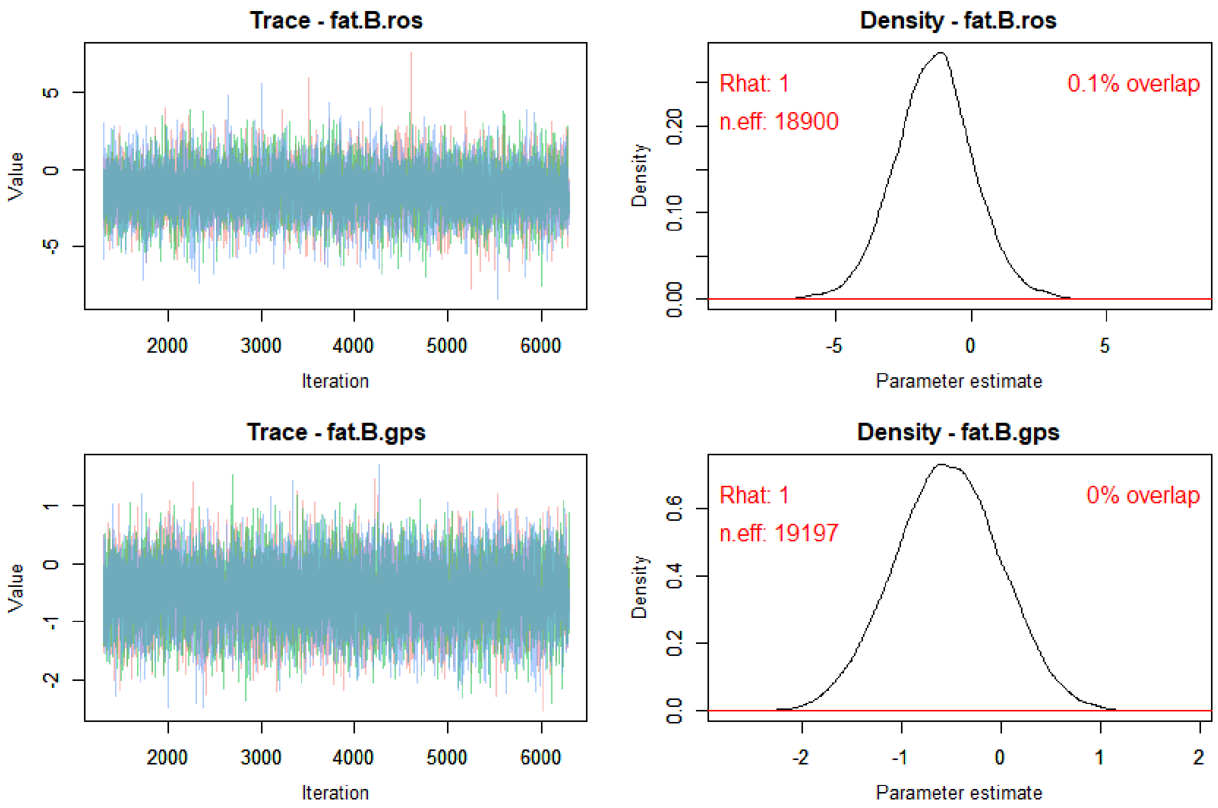
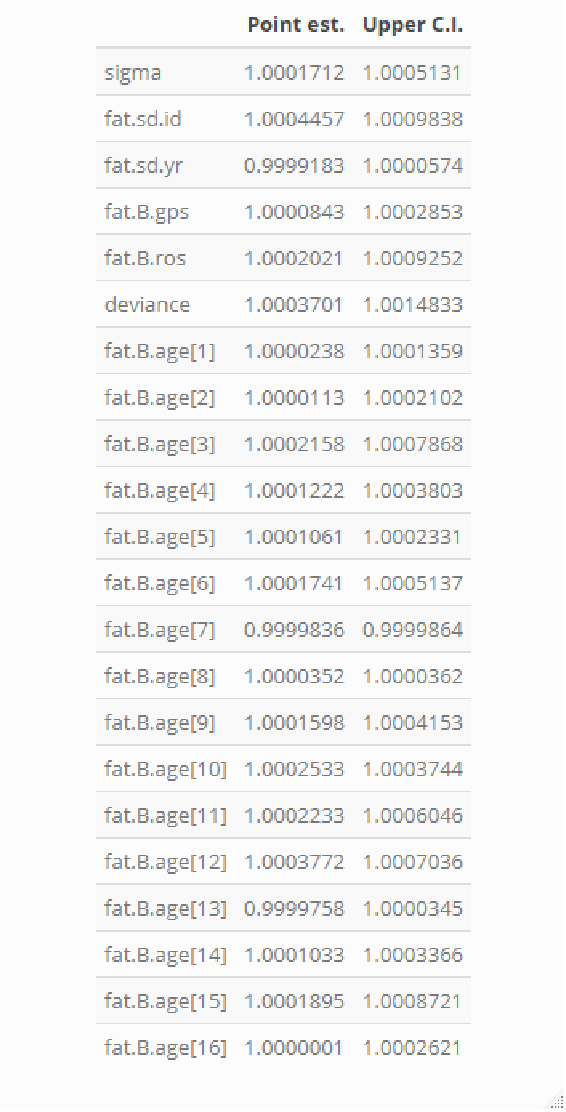


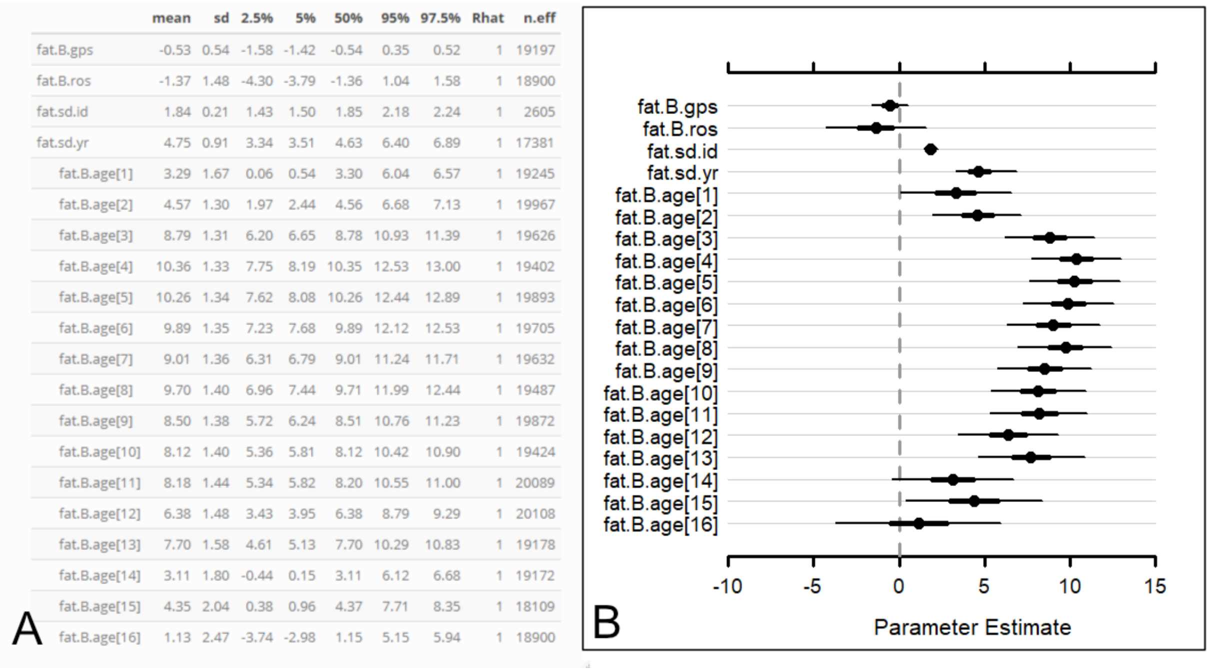
Figure 2: Trace plots and posterior density plots for two main parameters of the fat thickness model. “fat.B.ros” is the effect of rain on snow on fat thickness and “fat.B.gps” is the effect of GPS collar on fat thickness. Trace plots represent MCMC chain mixing and convergence. “n.eff” is the effective sample size and the red line along with the percentage in the upper right corner of the density plots represent the overlap between prior and posterior density. Both the parameters of rain on snow and GPS converged without problem, had sufficient effective sample size and were not influenced by their prior. The parameter of age is not displayed in this graph, but it was also not influenced by its prior.



	Point est.	Upper C.I.
sigma	1.0001712	1.0005131
fat.sd.id	1.0004457	1.0009838
fat.sd.yr	0.9999183	1.0000574
fat.B.gps	1.0000843	1.0002853
fat.B.ros	1.0002021	1.0009252
deviance	1.0003701	1.0014833
fat.B.age[1]	1.0000238	1.0001359
fat.B.age[2]	1.0000113	1.0002102
fat.B.age[3]	1.0002158	1.0007868
fat.B.age[4]	1.0001222	1.0003803
fat.B.age[5]	1.0001061	1.0002331
fat.B.age[6]	1.0001741	1.0005137
fat.B.age[7]	0.9999836	0.9999864
fat.B.age[8]	1.0000352	1.0000362
fat.B.age[9]	1.0001598	1.0004153
fat.B.age[10]	1.0002533	1.0003744
fat.B.age[11]	1.0002233	1.0006046
fat.B.age[12]	1.0003772	1.0007036
fat.B.age[13]	0.9999758	1.0000345
fat.B.age[14]	1.0001033	1.0003366
fat.B.age[15]	1.0001895	1.0008721
fat.B.age[16]	1.0000001	1.0002621

Figure 3: Gelman test values for the fat-thickness model. All parameters had Gelman test values of 1, showing a good convergence of the model.

Results



	mean	sd	2.5%	5%	50%	95%	97.5%	Rhat	n.eff
fat.B.gps	-0.53	0.54	-1.58	-1.42	-0.54	0.35	0.52	1	19197
fat.B.ros	-1.37	1.48	-4.30	-3.79	-1.36	1.04	1.58	1	18900
fat.sd.id	1.84	0.21	1.43	1.50	1.85	2.18	2.24	1	2605
fat.sd.yr	4.75	0.91	3.34	3.51	4.63	6.40	6.89	1	17381
fat.B.age[1]	3.29	1.67	0.06	0.54	3.30	6.04	6.57	1	19245
fat.B.age[2]	4.57	1.30	1.97	2.44	4.56	6.68	7.13	1	19967
fat.B.age[3]	8.79	1.31	6.20	6.65	8.78	10.93	11.39	1	19626
fat.B.age[4]	10.36	1.33	7.75	8.19	10.35	12.53	13.00	1	19402
fat.B.age[5]	10.26	1.34	7.62	8.08	10.26	12.44	12.89	1	19893
fat.B.age[6]	9.89	1.35	7.23	7.68	9.89	12.12	12.53	1	19705
fat.B.age[7]	9.01	1.36	6.31	6.79	9.01	11.24	11.71	1	19632
fat.B.age[8]	9.70	1.40	6.96	7.44	9.71	11.99	12.44	1	19487
fat.B.age[9]	8.50	1.38	5.72	6.24	8.51	10.76	11.23	1	19872
fat.B.age[10]	8.12	1.40	5.36	5.81	8.12	10.42	10.90	1	19424
fat.B.age[11]	8.18	1.44	5.34	5.82	8.20	10.55	11.00	1	20089
fat.B.age[12]	6.38	1.48	3.43	3.95	6.38	8.79	9.29	1	20108
fat.B.age[13]	7.70	1.58	4.61	5.13	7.70	10.29	10.83	1	19178
fat.B.age[14]	3.11	1.80	-0.44	0.15	3.11	6.12	6.68	1	19172
fat.B.age[15]	4.35	2.04	0.38	0.96	4.37	7.71	8.35	1	18109
fat.B.age[16]	1.13	2.47	-3.74	-2.98	1.15	5.15	5.94	1	18900

Figure 4: **A:** Summary table of the tobit model. **B:** Forest plot of the model parameters. The model did not show a significant effect of the GPS collar (fat.B.gps) or rain on snow (fat.B.ros) on the amount of back fat measured at capture (in millimeters), with 90% and 95% credible intervals crossing zero. Most of the variation in back fat was explained by age (fat.B.age) and random effect of year (fat.sd.yr).

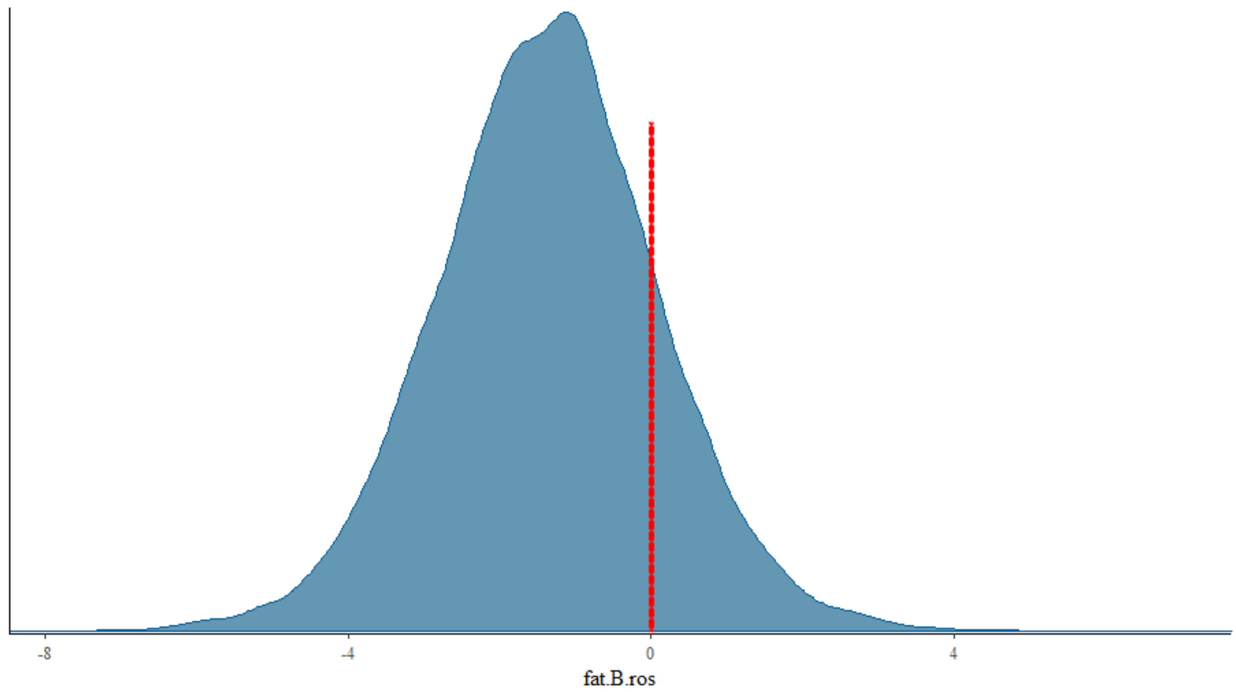


Figure 5: Posterior density plot of the effect of rain on snow on back-fat thickness. The red dotted line represents a null effect. The credible interval crosses zero. Part of the probability density is on the negative side.

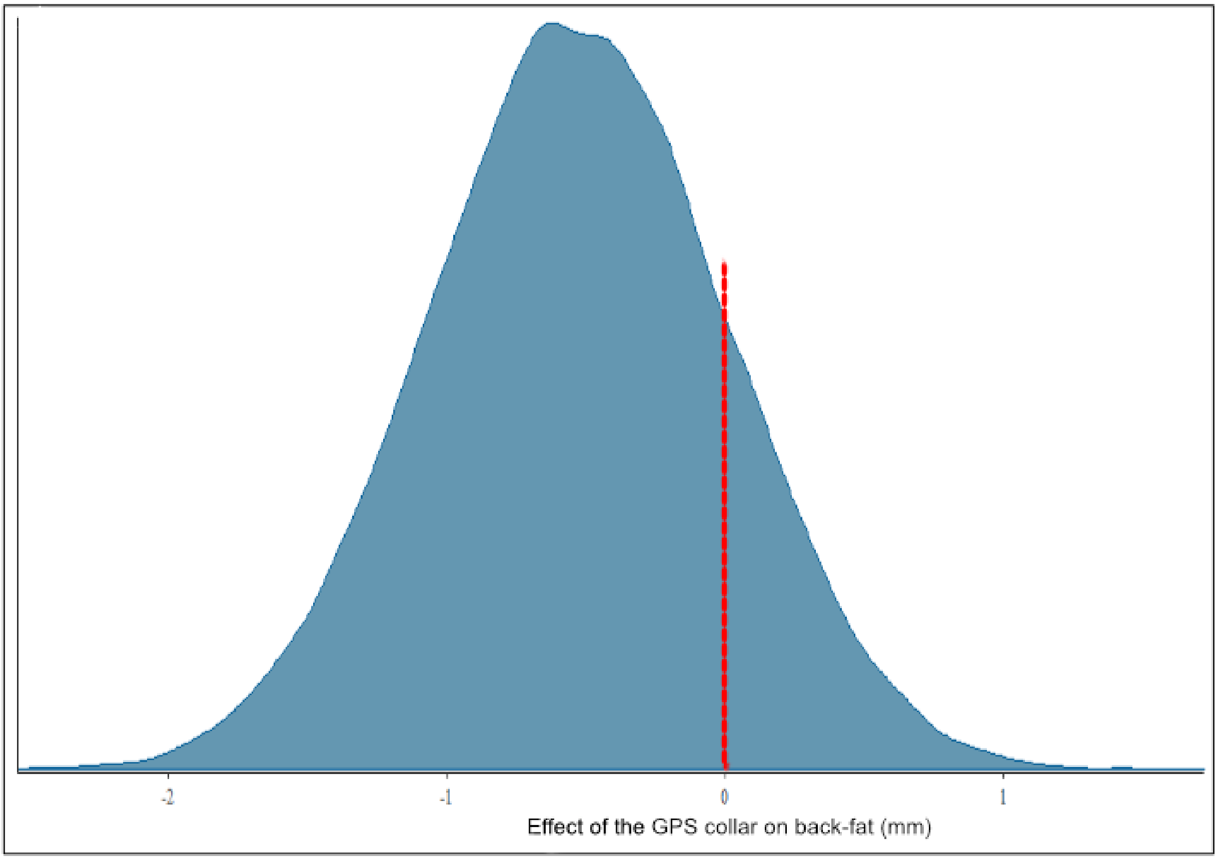


Figure 6: **Figure 8:** Posterior density of the parameter for the effect of GPS collar on fat thickness. *Red dotted line:* Null effect. The effect is not significant, but part of the probability density is on the negative side.

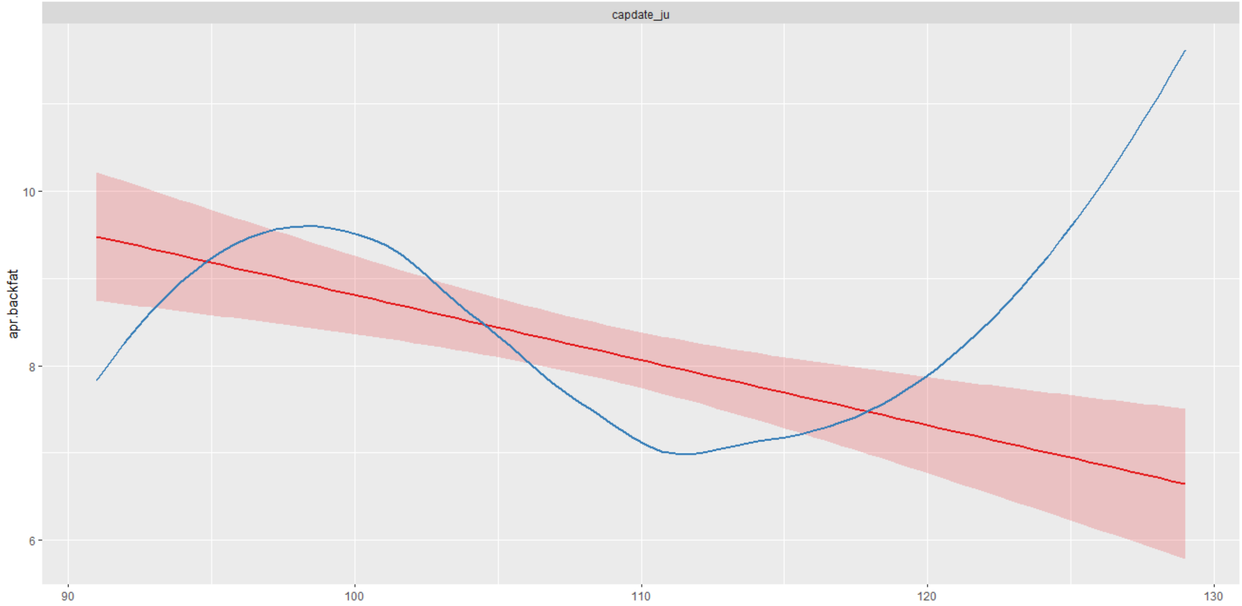


Figure 7: **Figure 9:** Linear relationship between fat thickness measured in April and capture date (Red line). Reindeer back fat thickness is not constant and decreases during captures.

Effects of GPS-collars on Svalbard reindeer survival and body condition - Appendix C

Guillaume Borquet

Loaded packages

sjPlot v2.8.2
gridExtra v2.3
kableExtra v1.1.0

MCMCvis v0.13.5
bayesplot v1.7.1
cowplot v1.0.0
boot v1.3-23
R2jags v0.5-7
rjags v4-10
coda v0.19-3
brms v2.11.1
mgcv v1.8-31
nlme v3.1-142
shinystan v2.5.0
shiny v1.4.0
rstanarm v2.19.2

Rcpp v1.0.3
DHARMa v0.2.6
lme4 v1.1-21
Matrix v1.2-18
lubridate v1.7.4
forcats v0.4.0
stringr v1.4.0
dplyr v0.8.3
purrr v0.3.3
readr v1.3.1
tidyr v1.0.0
tibble v2.1.3
ggplot2 v3.2.1
tidyverse v1.3.0

Model Code

Survival Model

```
"
model {
    # base model (sp) + effect of env at birth and curEnv +ran.yr
    # --------------------------------------
    # 1. Survival
    # ---------------------------------------
    # 1.1 Survival function
    for (i in 1:nind){
        for (t in first[i]:(last[i]-1)){
            logit(s[i,t]) <-   int+beta[x[i,t]]+
            collarsOn[i,t]*coef.collarsOn+
            ros[t]*coef.ros+
            ros[t]*coef.ros.age[x[i,t]]+
            #season[ws[t]]+
            epsilon.s[t]+gamma[x[i,t],t]
        } #t
    } #i

    ### Priors  -------------------
    # random effects
     for (t in 1:(ntimes-1)){
         epsilon.s[t] ~ dnorm(0, tau.s)
          for(a in 1:6){
            gamma[a,t] ~ dnorm(0, tau.s2)
         }
     } #t
    tau.s <- 1 / (sigma.s * sigma.s) # Precision for epsilon.
    sigma.s ~ dunif(0,10)
    tau.s2 <- 1 / (sigma.s2 * sigma.s2) # Precision for epsilon.
    sigma.s2 ~ dunif(0,10)

    # fixed effects
    coef.collarsOn~dnorm(0, 0.001)
    coef.ros~ dnorm(0, 0.001)

    int~dnorm(0, 0.001)
    for(i in 1:3){
        beta[i]~dnorm(0, 0.001)
        coef.ros.age[i]~dnorm(0, 0.001)
    }
    beta[4]<-0
    coef.ros.age[4]<-0
    for(i in 5:6){
        beta[i]~dnorm(0, 0.001)
        coef.ros.age[i]~dnorm(0, 0.001)
    }

#    season[1] ~ dnorm(0, 0.001)
#    season[2] <- 0

    Pcoef.collarsOn~dnorm(0, 0.001)

    # ---------------------------------------
```

```
    # 2. Observation probabilities (Model section 2)
    # ---------------------------------------

    for (t in 1:ntimes){
         for(i in 1:nind){
        logit(p[i,t]) <- mu.p[ws[t]]+ collarsOn[i,t]*Pcoef.collarsOn+ eps.p[t]
        }
        eps.p[t] ~ dnorm(0, tau.p[ws[t]])
    } #t

    for(i in 1:2){
    mu.p[i] <- log(mean.p[i] / (1-mean.p[i]))
    mean.p[i] ~ dunif(0,1)
    tau.p[i] <- 1 / (sigma.p[i] * sigma.p[i])
    sigma.p[i] ~ dunif(0,10)
    }

    # -----------------------------------------------------------------------
    # 3. Likelihood of the different data sets
    # ------------------------------------------------------------------------
    # 3.1 Capture-mark-recapture data
    for (i in 1:nind){
        for (t in (first[i]+1):last[i]){
            # State process
            z[i,t] ~ dbern(mu1[i,t])
            mu1[i,t] <- s[i,t-1] * z[i,t-1]
            # Observation process
            y[i,t] ~ dbern(mu2[i,t]) #individual observations
            mu2[i,t] <- p[i,t] * z[i,t]

        } #t
    } #i

    # ------------------------------------------------------------------------
    # 4. Derived parameters
    # ------------------------------------------------------------------------

    for (i in 1:nind){
        for (t in (first[i]+1):last[i]){

        expected[i,t] <- mu2[i,t]

        y.rep[i,t]~ dbern(mu2[i,t])

        # freeman
        E.org[i,t] <- pow((pow(y[i,t],0.5)-pow(expected[i,t],0.5)),2)
        E.new[i,t] <- pow((pow(y.rep[i,t],0.5)-pow(expected[i,t],0.5)),2)

        # chi
        C.org[i,t] <- pow((y[i,t]-expected[i,t]),2) / (expected[i,t]+0.5)
        C.new[i,t] <- pow((y.rep[i,t]-expected[i,t]),2) / (expected[i,t]+0.5)

        pt.log.like[i,t]<- log(y[i,t]*mu2[i,t]+(1-y[i,t])*(1-mu2[i,t]))
```

```
        } #t
       id.loglik[i] <- sum(pt.log.like[i,(first[i]+1):last[i]])

    id.E.org[i] <- sum(E.org[i,(first[i]+1):last[i]])
    id.E.new[i] <- sum(E.new[i,(first[i]+1):last[i]])
    id.C.org[i] <- sum(C.org[i,(first[i]+1):last[i]])
    id.C.new[i] <- sum(C.new[i,(first[i]+1):last[i]])

    } #i

    sum.E.org <- sum(id.E.org[])
    sum.E.new <- sum(id.E.new[])
    sum.C.org <- sum(id.C.org[])
    sum.C.new <- sum(id.C.new[])

} #model
"
```

Fat thickness model

```
'
model{
for (j in 1:nb.row){
y.ind[j] ~ dinterval(y.censored[j], 0)
y.censored[j] ~ dnorm(y.hat[j], tau)

y.hat[j] <- fat.B.age[age[j]]+
        GPSon_num[j] *fat.B.gps +
        ros[j]*fat.B.ros +
        ranef.yr.fat[year[j]]+ranef.id.fat[id[j]]

}

# prior
for(a in 1:nb.age){
fat.B.age[a]~dnorm(0,0.0001)
}

fat.B.gps~dnorm(0,0.0001)
fat.B.ros~dnorm(0,0.0001)

for (t in 1:nb.t){
ranef.yr.fat[t]~dnorm(0,fat.tau.yr)
} #t
fat.tau.yr <- 1 / (fat.sd.yr * fat.sd.yr)
fat.sd.yr ~ dunif(0,10)

for (i in 1:nb.id){
ranef.id.fat[i]~dnorm(0,fat.tau.id)
} #t
fat.tau.id <- 1 / (fat.sd.id * fat.sd.id)
fat.sd.id ~ dunif(0,10)
```

```
tau <- pow(sigma, -2)
sigma ~ dunif(0, 100)

# derived
for(j in 1:nb.row){
    yRep.censored[j] ~ dnorm(y.hat[j], tau)
    y.Rep[j] <- yRep.censored[j]* (yRep.censored[j]>0)
}

}
'
```