The impact of bio-logging on body weight change of the Eurasian beaver

Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell

1 Faculty of Technology, Natural Sciences and Maritime Sciences, Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Notodden, Norway, 2 Department of Bioscience, Aarhus University, Rønde, Denmark

‡ These authors contributed equally and joint first authors on this work.
* christian.a.robstad@usn.no

Abstract

Bio-logging is a common method to collect ecological data on wild animals, but might also induce stress, reduce body condition, and alter behavior. Eurasian beavers (Castor fiber) are a semi-aquatic and nocturnal species that are challenging to observe in the wild. Bio-loggers are hence useful tools to study their behaviour and movements, but this raises concerns of potential negative impacts of tagging. To investigate the potential negative impacts of glue-on tags, we compared body weight change for tagged and untagged Eurasian beavers. We hypothesized that tagged beavers would gain less body weight compared to untagged beavers, and that weight change might be affected by tagging length, tag weight, water temperature and the season of tagging. Daily percentage body weight change in relation to initial body weight during the first capture was compared during 57 tagging periods (18 ± 7 days) and 32 controls periods (64 ± 47 days). Body weight change varied between the two groups, with untagged beavers on average gaining daily weight whilst tagged beavers on average lost weight daily, indicating a negative effect of tagging. The average reduction in percentage body weight change per day for tagged beavers was small (0.1 ± 0.3%), and with large individual variation. Neither tag weight, number of tagging days, nor season were important in explaining body weight change of tagged animals. In other words, we found that tagging reduced daily body weight during the tagging period but were unable to determine the mechanism(s) responsible for this decline. Detrimental effects of tagging have important implications for animal welfare and can introduce bias in data that are collected. This calls for careful consideration in the use of tags. We conclude that studies investigating the effects of tagging should consider individual variation in the effects of tagging and, where possible, compare tagged animals with a control group.

Introduction

Bio-logging studies, i.e. using animal-borne devices to gather information on animal behavior, movement, physiology, and environmental conditions, are key to increasing our
understanding of animal behavior and ecology [1, 2]. However, negative impacts of attaching instruments to animals can be substantial, yet are not always considered [3]. Generally speaking, the impact of tag weight is a primary concern, and contemporary guidelines endorse continued miniaturization of tags [4]. The total weight of a tag should not exceed 0.7–10% of body weight depending on the species and recommendations from different authors [5–9]. Moreover, negative effects from bio-logging can be caused by capture stress [8, 10] and vary depending on the attachment method [11]. For example, increased drag from external tags affects energy expenditure, locomotion, and swimming speed [12], especially for aquatic and semi-aquatic species [13–16]. Tagging may negatively impact both body condition and life history traits such as reproduction, parental care, and survival [17, 18]. Such detrimental impacts raise concerns around animal welfare and ethics. In addition, if the body condition, energy expenditure or activity patterns of animals are affected, this can produce biased data that does not reflect the true behaviour of the species [19, 20]. The effects of tag attachment vary among species, individuals [16], and geographic regions [21], and require species-specific adaptations [22]. Impacts from tagging and capture may also vary according to the sex and age of an animal [14, 23]. Assessments should therefore be made to the extent of the tag impact through species-specific studies using different tag types [18]. Importantly, the effects of tagging on animal behaviour and body condition are often not fully understood due to the difficulty in comparing tagged animals with a control group of untagged individuals [24]. This should be investigated and assessed whenever possible [25]. External attachment mechanisms for bio-logging devices such as harnesses, backpacks, collars, and glue-on tags have been used for scientific studies of numerous taxa from invertebrates to mammals [26–29]. The glue-on method is commonly used on animals that are unsuitable to tag with a collar, and involves gluing the tag directly onto the fur or skin of the animal with fast-curing adhesives [30, 31]. However, several studies have found that such tags may impact animals negatively. For example, glue-on tags affected swimming speed due to increased drag in Hawaiian monk seals (*Monachus schauinslandi*) [32], increased trip duration in Antarctic fur seals (*Arctocephalus gazella*) [33], changed foraging behavior in harbour seals (*Phoca vitulina*) [34], and caused skin abrasions on Weddell seals (*Leptonychotes weddellii*) and southern elephant seals (*Mirounga leonina*) [35]. Gluing tags onto the fur is a common method for tagging semi-aquatic mammals. For animals that are insulated by blubber, such as pinnipeds, glue-on tags are expected to have limited impact on body temperature, despite potential heat leakage at the site of tag attachment (e.g. in grey seals) [36]. However, semi-aquatic species that rely on a water-resistant fur for insulation [37] may be more vulnerable to heat loss from glue-on tags that impair the insulating properties of their pelage [38, 39].

The Eurasian beaver (*Castor fiber*) together with the closely related North American beaver (*C. canadensis*) are semi-aquatic and nocturnal, which makes it challenging to observe their behavior and habitat use [40, 41]. Therefore, bio-logging is a powerful tool to study their secret lives [42–44]. As ecosystem engineers that have large impacts on their surrounding ecosystems [45, 46], they are often the focus of ecological studies in which bio-loggers are a valuable tool. However, beavers have fusiform body shapes and thick necks with small heads that render the common tagging method of collaring impossible [41, 47, 48]. Other methods to collect data on beavers include surgically implanted transmitters [47, 49, 50], and securing devices using a hole made in the beaver’s tail [51–55]. However, implants can cause extended recovery and surgical complications [56], while tail mounting may cause tail injuries and reduce body weight gain during winter [55]. Due to these challenges, glue-on tags have been utilized as an alternative method for beaver bio-logging by the Norwegian Beaver Project (NBP) [42, 44, 57].

A study investigating short-term changes in post-tagging behaviour of beavers following tagging with glue-on tags, found only minor alterations in behaviour through reduced activity.
levels of individuals, and four beavers remained in their lodge until the next day following
attachment of glue-on tags [58]. Another long-term study within the same population found
that the number of captures and handling events negatively affected beaver reproduction
during the first years of monitoring, but this effect subsided during the later years of the study,
possibly due to habituation of older beavers captured several times throughout their life [59].
The same study found no long-term effects related to whether a beaver had carried a tag in its
lifetime on body condition, survival or reproduction [59].

Changes to body condition or body weight in beavers as a result of glue-on tags have not
yet been studied during the tagging period. Beavers usually gain body weight from spring to
fall and decrease body weight in winter when food availability is scarce [60, 61]. Young beavers
tend to gain more body weight than adults, with the weight of beavers peaking at around 10
years of age, and adult females tend to have larger body masses than males in spring and sum-
mer [59]. The aim of this study was to investigate potential negative impacts of tagging on the
body weight change of beavers by comparing tagged and untagged (control) individuals. We
also aimed to identify variables related to tagging that could influence weight change, while
controlling for potential effects of year, age, and sex. We hypothesized that glue-on tags would
reduce the rate of body weight gain in beavers and predicted that tagged beavers would gain
less body weight during the tagging period compared to untagged beavers. Secondly, we
hypothesized that negative impacts of tagging on beaver body weight would be exaggerated
during the colder months in spring and fall, and at colder water temperatures when beavers
spend more energy on thermoregulation, and have lower food access compared to the warmer
summer months [45]. Lastly, we hypothesized that the negative effect of tagging on body
weight change might be exaggerated by the increased tag weight and duration of the tagging
period.

Materials and methods

Study area and beaver population

We studied beavers in the NBP study site. This site consists of three connected rivers–Gvarv
(59° 38’ N, 09° 17’ E), Straumen (59° 29’ N, 09° 15’ E), and Saur (59° 44’ N, 09° 30’ E)–
which all discharge into lake Norsjø in Vestfold and Telemark County, Norway. The mean
annual air temperature is 4.6 Celsius and annual precipitation is 790 mm [59, 62]. Human set-
tlements, semi-agricultural landscapes, and forested woodlands are scattered throughout the
study area [62]. Eurasian beavers have inhabited the area since the 1920s [63]. Hunting pres-
sure in the area is low [64], and the population is considered to be at carrying capacity [42, 62,
64]. Beaver territories border each other, so there are few unoccupied stretches of the river. In
total, 25–30 beaver families inhabit the study area and they have been continuously monitored
since 1997 [42, 65, 66].

Capture and handling, and details of study individuals

We studied 57 beavers that had been captured as part of ongoing research. Specifically, every
year between March and November, beavers were captured as part of a long-term capture-
mark-recapture study and for tagging purposes [65, 67]. The NBP has studied beavers for over
20 years with 1,560 live captures. We attempted to reduce capture-related stress by not captur-
ing the same beaver several times a year, which resulted in a lower sample size of untagged bea-
viers (control group) compared to tagged beavers. Beavers were caught at night with nets from
a boat or onshore [68], and transferred into a cloth bag for handling. All beavers included in
this study were handled while awake with no use of anesthesia. Captured animals were micro-
chipped and ear-tagged for identification [69]. Each beaver was sexed, based on the color and
viscosity of the anal-gland secretion [70], weighed (tagged beavers were weighed with the tag during attachment, and without the tag after removal) and measured for body size, tail length, and tail thickness [65, 71]. Beavers were subsequently released back to the place of capture after 20–40 minutes. Age was assigned based on body weight if not captured for the first time as a kit or yearling. Individuals captured for the first time weighing between >17 and <19.5 kg were assigned a minimum age of two years and a minimum age of three years when over >19.5 kg [72]. We classified the beavers into age groups based on prior knowledge of rate of body weight change for different ages. Beavers aged between 2–3 years were defined as ‘young’ (i.e. individuals that are still growing), those between 4–10 were classified as ‘adult’ (fully grown with a lower body weight gain compared to young beavers). Beavers aged 11–17 were classified as ‘old’ (showing signs of senescence, such as loss of body weight). The average age when beavers in our study population tend to die or disappear is 9–10 years independent of their sex [67], but beavers in the wild can live up to 20–24 years of age [73–75]. We have had several beavers older than 10 years in our study area, with a maximum age of 17 included in the dataset [65, 76].

Tagging procedure

Since 2009, glue-on tags have been the main attachment method under the NBP. From 2009 to 2020, beavers were equipped with tags sized approximately 12 × 12 × 1.2 cm with tag weight varying according to logger weight and the materials used (total logger weight: 159 ± 36 g, range: 124–267 g). Every tag unit consisted of a VHF transmitter (18 × 35 mm, 10 g; Reptile glue-on series R1910; Advanced Telemetry Systems, Isanti, MN, USA) in combination with a global positioning system (GPS) device–model G1G 134A; Sirtrack, Havelock North, NZ (50 × 70 mm, 24 g), or model Gipsy 5 GPS; TechnoSmart, Rome, Italy, (48×21 mm, 27.8 g). Most beavers were also equipped with triaxial accelerometers (15 × 90 mm, 62 g; JUV Elektronik, Schleswig-Holstein, GER) or a Daily Diary (52 × 29 × 22 mm, 62 g with waterproof casing) developed by the SLAM lab at Swansea University, UK. During a few tagging sessions, a time-depth recorder (67 × 17 mm, 30 g; model MK9 Archival Tag, Wildlife Computers Inc, Redmond, WA, USA) was used instead of a GPS or accelerometer. The loggers were attached to a piece of coarse polyester, secured with cable ties and glue (both to the polyester and to each other), to assure all parts remained in one unit until retrieval of the tag.

The tag was glued onto the lower back of the beaver, 15 cm above the base of the tail irrespective of beaver body size, using a two-component epoxy resin (System Three Resins, Auburn WA, USA) [58] (Fig 1). Note that tags were covered with a 4.5 mm mesh net (Morenot Fishery AS, Møre and Romsdal) on both sides to prevent the glue from reaching the skin of the beaver which may cause heat or chemical burns (Fig 1). After attaching the tag to the beaver, we waited for the glue to harden, and rinsed the beaver and tag with cold water if we registered a rise in temperature that may harm the beaver. Temperatures above 50 °C cause damage to the skin of animals [77], but laboratory analysis using similar glues as we applied, showed that three types of epoxy glue never reached temperatures above 34 °C [35]. We monitored the temperature of the glue with our hands while wearing latex gloves. The whole capture, handling and attachment process took between 20–40 minutes. Tagged beavers were usually recaptured after 2–3 weeks, and the tag was cut out of the fur using a scalpel, which took approximately 10–40 minutes. We defined the tagging period from the time the tag was attached on the beaver until the beaver was recaptured and the tag removed. If the tag fell off by itself, the beaver was not recaptured, and the body weight difference from the beginning to the end of the tagging period could not be estimated. These tagging events were therefore not included in the analysis. The weight of each tag was estimated by adding together the weights
of the individual loggers and an average weight of the materials used for attachment. We weighed 21 tags post-removal (and after having removed the data loggers) to estimate the average weight of the glue and materials used for attachment; this was $90 \pm 27$ g, and we therefore added this as a constant to each tag weight.

**Ethical statement**

Ethical committees within the Norwegian Food Safety Authority (most recent authorization FOTS ID 15947) and the Norwegian Directorate for Nature Management (most recent authorization 2014/14415 ART-VI-ID) approved this study, including all handling and tagging procedures. To our knowledge, none of the beavers in this study were injured due to capture and handling. Unfortunately, one beaver was found deceased in the entrance of the lodge during the tagging period but cause of death and whether it was related to tagging could not be determined based on a necropsy by the Norwegian Veterinary Institute. The study complied with the ASAB/ABS Guidelines for the treatment of animals in behavioral research and teaching [78]. The study was also carried out in compliance with the ARRIVE guidelines [79].

**Data preparation**

We used percentage body weight change between initial and the subsequent capture of tagged and untagged beavers as an indicator of change in body condition. Tagged beavers were included if their body weight was measured both when the tag was attached (capture) and removed (recapture). Untagged beavers were only included in the control group if captured twice between March–November in a given year, in order to calculate their daily body weight.
change between the two captures. We first estimated total body weight change (%) between
the two captures, and then divided this by the number of days between capture and recapture
to obtain daily body weight change (%) in relation to the initial body weight (at first capture).
The percentage weight of the tag in relation to the initial beaver body weight was also calcu-
lated, which we hereby refer to as relative tag weight (%).

Glue-on tags were only used on beavers after 2009, so we only included observations of
tagged beavers during or following that year (2009–2020), while observations of untagged bea-
vers were included from 2006–2020. Prior to 2006, the beavers were weighed with less accu-
tract, and these observations were therefore not included. Four of the female territory owners
included in the study were pregnant in the period between captures. We conducted our analy-
sis both with and without these individuals included, and because they did not impact the
model selection or model estimates, they were retained in the dataset. Similarly, four tagged
beavers were older than the maximum age of the untagged beavers (13 years old), which
increased the average age of the tagged beavers. We also tried to exclude these older tagged
beavers from the analysis, but this did not influence model selection or model estimates, and
they were therefore retained in the dataset. Most of the study beavers have been monitored
over many years, and some were included several times in the dataset, either as tagged or
untagged (S1 File).

We defined season according to the months in which the majority of the days between cap-
tures fell within. Observations with the majority of days during March–May were defined as
spring, June–August as summer, and September–November as fall. We obtained average water
temperature measurements in Celsius from the Norwegian Water Resources and Energy
Directorate (NVE) for each river system during the periods beavers carried the tags. Water
temperatures were not monitored within the study area itself, and we therefore had to rely on
data from the same watershed to indicate water temperature. For Sauer, we used water temper-
ature data from Kirkvoll located on the Tinnåa river that runs into Heddal lake, which repre-
sents the start of Sauer river. For Straumen, we obtained water temperatures from Kilen in the
Kilåi river than runs into Flåvatn, which represents the start of the Straumen river. For Gvarv,
we used water temperature information from the Hørte river, which merges with the Gvarv
river just above the study area.

**Statistical analysis**

We divided the analysis into two parts. First, we modelled the daily body weight change (%) as
a function of tagging status (tagged or untagged), including age group, season and sex as possi-
ble confounding variables. Second, for tagged beavers, we modelled total body weight change
(%) in relation to initial weight as a function of tagging season, relative tag weight (%), average
water temperature during the tagging period, sex, age group, and the duration of tagging. We
excluded the six tagged beavers for which we could not obtain water temperature data in this
analysis. For both analyses, we used linear mixed models (LMM) with a Gaussian distribution
and the R package lme4 [80]. Beaver ID and year were included as crossed random effects on
the intercept in both analyses to account for pseudoreplication of repeated sampling of the
same individual and yearly variations. In part one of the analysis we included interactions
between the tagging status of the beaver (tagged or untagged) and its sex, age group and the
season of tagging. The recommended steps from Zuur, Ieno and Elphick [81] were followed
for data exploration. All numerical variables were tested for collinearity and were found not to
be correlated (Pearson r coefficient <0.6) and with a cut-off of variance inflation factor (VIF)
< 3 [82]. We visually assessed collinearity between numerical and categorical variables using
boxplots. The beavers’ social status was collinear with age and was therefore excluded from the
analysis. Season of tagging and water temperature were also collinear, so we included them both in different models.

We constructed a set of candidate models with separate combinations of the explanatory variables for both parts of the analysis. Model selection was based on Akaike’s Information Criterion (AICc) values for small sample sizes [83, 84], and carried out with the R package MuMln using the “model.sel” function [85]. To avoid selecting complex models that add little additional information compared to a similar nested model, we selected the most parsimonious model among the candidate models separated with less than $<2 \Delta \text{AICc}$ from the top model [86, 87]. For each explanatory variable included in the most parsimonious model, we calculated the 95% confidence interval, and if it overlapped with zero, the variable was considered uninformative. We plotted the Pearson residuals of the most parsimonious model against fitted values to inspect for non-normality and heterogeneity [88]. We also plotted the model residuals against each variable included and not included in the most parsimonious model, and fitted a smoother to check for potential non-linear patterns in the residuals. Lastly, we simulated residuals from the model using the package DHARMa and plotted the residuals against expected and fitted values to observe deviations from the expected distribution [89]. All data analyses were performed with R version 4.0.3 (R Development Core Team 2020).

Results

We analyzed beaver body weight change across 89 periods (tagging periods or between captures of untagged beavers) of 57 individual beavers (S1 File). We included 57 tagging periods (20 females, 22 males), and 32 control periods (14 females, 13 males). Of these, 11 beavers were tagged more than once, while 13 were included with more than one control period, and 13 beavers were included as both tagged and controls at different times (S1 File). The mean age of the two groups differed by 1.8 years, and the mean number of days between captures was $18 \pm 7$ days for tagged beavers and $64 \pm 47$ days for untagged (Table 1). Water temperature varied among tagging periods between 1.29 to 15.87 Celsius. The relative tag weight (%) constituted $0.8 \pm 0.2\%$ (range, 0.5–1.4%) of the initial body weight of the beavers. Between captures, untagged beavers gained an average of 23 g per day, while body weight of the tagged beavers declined by 13.7 g daily (Table 1). Percentage daily body weight change was on average 0.1% for untagged and -0.1% for tagged beavers, but with considerable individual variation (Fig 2). The largest decline in body weight among the tagged beavers was for an individual that lost 2,333 g (11.5% reduction) over a 14-day tagging period; this constituted 0.8% daily weight loss. Amongst the tagged beavers, 57% of the tagging periods caused a decline in body weight, but 42% of the tagged beavers gained body weight. Two (7%) of the untagged beavers declined in body weight between captures, while 93% gained body weight. Visual observations during tag removal indicated that the amount of fur remaining post-tagging varied. The extent was not documented consistently, but we believe it had a negligible impact on measured body weight.

Table 1. Overview of the two Eurasian beaver (Castor fiber) groups (tagged and untagged) in relation to number of days between captures, and total and daily body weight change between the captures in southeastern Norway 2006–2020. Each variable is presented as the mean with standard deviation and the total range within the parenthesis.

|                  | Tagged                              | Untagged                            |
|------------------|-------------------------------------|-------------------------------------|
| Days between captures | 18 ± 6.6 days (8–43)               | 64 ± 46.8 (5–139)                   |
| Age              | 6.7 ± 3.5 years (2–17)              | 4.9 ± 3.0 years (2–13)              |
| Average total body weight change | -220.7 ± 953.5 g (-2,333–2,077.8) | 1,156.9 ± 953.5 g (-500–3,500)       |
| Average daily body weight change | -13.7 ± 59.4 g (-166.64–115.43)   | 23 ± 3.0 g (-66.67–149.63)           |
| Average daily body weight change % | -0.1 ± 0.3% (-0.82–0.57)       | 0.1 ± 0.2% (-0.27–0.75)             |

https://doi.org/10.1371/journal.pone.0261453.t001
For some beavers, underfur appeared intact, while others had open patches with no underfur remaining.

**Daily weight change (%) in tagged versus untagged beavers**

The most supported model retained tag presence and age group as fixed effects (Table 2). Predicted daily body weight change of tagged beavers was -0.04 g (CI: -0.18–0.09), while predicted daily body weight change of untagged beavers was 0.20 g (CI: 0.07–0.32; Fig 3 & Table 3). Age group was uninformative (95% confidence intervals overlapped zero) in explaining daily body weight change for tagged and untagged beavers (Table 3). The interactions between tag presence and either sex or season were unsupported. The diagnostic plots indicated acceptable model fit using a Gaussian distribution (S1 File).
Table 2. The model selection results investigating the percentage daily body weight change between two subsequent captures of Eurasian beavers (Castor fiber) in southeastern Norway (2006–2020). Each model represents a linear mixed effect model with year and beaver ID included as random effects. Potential fixed effects included in each candidate model are age group of the beaver, season of tagging, sex of the beaver, and whether the beaver was tagged or not. The plus signs indicate which variables were included in each candidate model. Degrees of freedom (df), log likelihood (logLik) and model AIC weight (w) are provided for each candidate model. Results for the best supported model are shown in bold.

| Intercept | AgeG | Season | Sex | Tag | AgeG*Tag | Season*Tag | Sex*Tag | df | logLik | AICc | AICcΔ | w  |
|-----------|------|--------|-----|-----|---------|-----------|---------|----|--------|------|-------|----|
| -0.04     | +    |        |     | +   |         |           |         |  7 | 4.36   | 6.66 | 0.00  | 0.90|
| 0.00      |      |        |     |     |         |           |         |  4 | -2.27  | 13.01| 6.35  | 0.04|
| 0.08      | +    |        |     |     |         |           |         |  6 | -0.47  | 13.96| 7.30  | 0.02|
| -0.09     | +    | +      |     | +   | +       |           |         | 12 | 6.55   | 15.01| 8.34  | 0.01|
| 0.09      | +    |        |     |     |         |           |         |  7 | -0.39  | 16.16| 9.49  | 0.01|
| 0.03      | +    |        |     |     |         |           |         |  8 | 0.48   | 16.83| 10.17 | 0.01|
| -0.08     | +    | +      |     | +   | +       |           |         | 13 | 6.57   | 17.72| 11.06 | 0.00|
| -0.08     | +    | +      |     | +   | +       |           |         | 13 | 6.57   | 17.72| 11.06 | 0.00|
| -0.11     | +    | +      |     | +   | +       |           |         | 14 | 6.76   | 20.15| 13.49 | 0.00|
| -0.11     | +    | +      |     | +   | +       |           |         | 15 | 6.76   | 23.05| 16.39 | 0.00|

Fig 3. Estimated daily weight change (%) between captures for tagged and untagged Eurasian beavers (Castor fiber) in southeastern Norway (2006–2020). The prediction is based on a linear mixed effects model using percent daily body weight change as the response variable. The horizontal lines represent the 95% confidence intervals around each mean.

https://doi.org/10.1371/journal.pone.0261453.g003
The null model was the most supported model; none of the explanatory variables (relative weight of tag (%), average water temperature during the tagging period, sex, age group, season, and length of the tagging period) were retained in the model selection to explain total body weight change (%) (Table 4).

Table 3. Effect size (β), adjusted standard error (SE), lower (LCI), and upper (UCI) 95% confidence interval of explanatory variables in the most parsimonious model analyzing percentage daily body weight change between two subsequent captures of Eurasian beavers (Castor fiber) in southeastern Norway (2006–2020). The intercept includes the ‘young’ age group of beavers. The informative parameters are shown in bold, and the marginal (R²m) and conditional (R²c) R squared is given for the model overall.

| Parameter                  | β      | SE   | LCI  | UCI  | R²m  | R²c  |
|----------------------------|--------|------|------|------|------|------|
| Intercept (Tagged)         | −0.04  | 0.07 | −0.18| 0.09 | 0.16 | 0.40 |
| Tag Unattached             | 0.20   | 0.06 | 0.07 | 0.32 |      |      |
| Age Group (Adult)          | −0.05  | 0.06 | −0.16| 0.07 |      |      |
| Age Group (Old)            | 0.00   | 0.09 | −0.18| 0.18 |      |      |

Total weight change (%) in tagged beavers between tag attachment and removal

The null model was the most supported model; none of the explanatory variables (relative weight of tag (%), average water temperature during the tagging period, sex, age group, season, and length of the tagging period) were retained in the model selection to explain total body weight change (%) (Table 4).

Discussion

We investigated the effects of glue-on tags on body weight change of Eurasian beavers. We found support for our first hypothesis that tagging reduced beaver body weight gain during the tagging period (and actually led to body weight loss) compared to untagged beavers that generally gained body weight. Our hypothesis that tagged beavers should gain less body weight during the colder months of the year or with colder water temperature was unsupported. Moreover, we found no evidence that relative tag weight or the number of tagging days affected beaver body weight. The tagged beavers did, however, display individual variation

Table 4. The model selection result, investigating percentage body weight change during tagging of Eurasian beavers (Castor fiber) in South-Eastern Norway (2009–2020). Each model represents a linear mixed effects model with beaver ID included as a random effect. Potential fixed effects included in each candidate model are tag weight as a percent of initial beaver body mass (tag weight %), age group of the beaver, number of days tagged, season of tagging, sex, and average water temperature during the tagging period. The plus signs indicate the categorical variables included, and values are given for numerical variables that were included in each candidate model. The intercept includes the ‘young’ age group of beavers. Candidate models were ranked based on AICc, and the range of ΔAICc < 2 are shown in bold. Degrees of freedom (df), log likelihood (logLik) and AIC weight (w) is provided for each candidate model.

| Intercept | Age group | Relative tag weight % | Tagging days | Season | Sex | Average water temperature | df | logLik | AICc | delta | w   |
|-----------|-----------|-----------------------|--------------|--------|-----|---------------------------|----|--------|------|-------|-----|
| −1.44     |           |                       |              |        |     |                           |    | −144.08| 297.03| 0.00  | 0.78|
| −1.59     |           |                       |              |        |     |                           |    | 6.00   | −143.96| 301.83| 4.80 | 0.07|
| −3.22     |           |                       |              |        |     |                           |    | 7.00   | −143.37| 303.35| 6.32 | 0.03|
| −0.37     |           |                       |              |        |     |                           |    | 7.00   | −143.47| 303.53| 6.50 | 0.03|
| −0.14     |           | −2.12                 |              |        |     |                           |    | 7.00   | −143.75| 304.10| 7.07 | 0.02|
| −1.40     |           |                       |              |        |     |                           |    | 7.00   | −143.89| 304.39| 7.36 | 0.02|
| −2.05     |           |                       |              |        |     |                           |    | 8.00   | −142.79| 305.01| 7.98 | 0.01|
| −1.54     |           |                       |              |        |     |                           |    | 8.00   | −143.22| 305.88| 8.85 | 0.01|
| −1.90     |           | −1.75                 |              |        |     |                           |    | 8.00   | −143.23| 305.88| 8.85 | 0.01|
| −3.36     |           |                       |              |        |     |                           |    | 9.00   | −142.66| 307.70| 10.67| 0.00|
| −1.93     |           |                       |              |        |     |                           |    | 9.00   | −142.73| 307.86| 10.83| 0.00|
| −1.79     |           | −1.65                 |              |        |     |                           |    | 9.00   | −143.15| 308.70| 11.66| 0.00|
| −1.81     |           | −2.10                 |              |        |     |                           |    | 10.00  | −144.24| 310.39| 13.36| 0.00|
| 0.07      |           | −2.46                 |              |        |     |                           |    | 10.00  | −142.46| 310.42| 13.39| 0.00|
| −1.79     |           | −2.00                 |              |        |     |                           |    | 11.00  | −142.41| 313.59| 16.56| 0.00|

https://doi.org/10.1371/journal.pone.0261453.t004
with some tagged beavers gaining body weight, while most lost body weight during tagging. The average daily weight loss in tagged beavers of 13 g (0.1%) appears small, but importantly indicates that tagged beavers were (on average) unable to gain weight compared to untagged beavers that gained 23 g (0.1%) daily. This difference between the two groups, as well as some tagged beavers displaying considerable declines in body weight, indicates that tagging can have a negative impact on beavers.

Control groups

We included a control group of untagged beavers in our study, who mostly increased daily body weight between captures in line with previous studies [61]. Comparing tagged animals with a control group may help quantify the impact of tagging and avoid conclusions based on statistical artifacts that may arise without one [90]. While the weight loss of tagged beavers in our study was small on average, this was in direct contrast to untagged beavers who saw a small increase in body weight. Many bio-logging studies lack a control group due to the challenges with monitoring wild animals that are not tagged, which may influence the conclusions of these studies. Other semi-aquatic mammals such as the Eurasian otter (Lutra lutra) [91] and platypus (Ornithorhynchus anatinus) [92] tagged with glue-on tags displayed no apparent adverse effects. However, the authors did not compare the tagged animals with an untagged control group, which may impact the results.

Defining a true control group to include in wildlife studies can bring additional challenges. In the current study, there was a large difference in the number of days between the captures in the control group (mean = 64 days) and the tagged individuals (mean = 18 days). This could potentially lead to biases, requiring a careful interpretation of the results. In wild populations, it can be challenging to capture a sufficient number of individuals (both for logistic and economic reasons) to have a control group that is directly comparable to the tagged animals. Here, we accounted for confounding variables such as age group, sex, season, year and individual variation. Despite controlling for these, we failed to identify any variables related to the tagging process aside from the presence of a tag that drove the observed negative effects, suggesting further investigation is needed.

Relative tag weight and drag

The decline in body weight of tagged beavers was not exaggerated by the relative weight of the tag. If added weight was the main cause for the lower body weight gain, we would expect beavers that carried heavier tags, or carried the tag over a longer period to display the strongest decline in body weight. The tags made up between 0.5–1.3% of the initial body weight of the tagged beaver, which is well below both the 3% and 5% limits suggested by several studies [7]. A meta-analysis reviewing 214 studies of birds tagged using various tag types and attachment methods, found that negative effects of tagging were only apparent when tags weighed more than 1% of the bird’s body weight [17]. As most of our tags were below this 1% threshold, we would not expect to observe a strong effect due to relative tag weight.

The shape of the tag and its location on the body of an animal may be more important than tag weight, as these factors directly impact tag-induced drag; something that is essential for animals moving in fluid media [12, 93]. For example, drag created by an external tag might increase energy expenditure, thereby increasing foraging time [94, 95]. A simulation study on grey seals (Halichoerus grypus) showed that shape of a tag is much more important than its size, e.g. a larger but more streamlined tag can reduce drag by 22% in swimming seals compared to a smaller but conventionally shaped tag [93]. We did not record the size or shape of the tag attached to beavers, and can therefore not directly analyze the drag impact. However,
the relatively slow swimming speed of Eurasian beavers compared to other aquatic or semi-aquatic species may make them less susceptible to negative impacts from tag-induced drag. Indeed, drag is influenced by the speed and acceleration of the tagged animal, with slower moving animals not relying on high acceleration to capture prey being less impacted [9]. Great cormorants (Phalacrocorax carbo) were only negatively affected by drag from a tag at swimming speeds >1.4 m/s [4]. Beavers rarely swim faster than 0.8 m/s when swimming at the surface [96], and 0.6 m/s when diving [97]. The tags used on beavers here are usually above the surface of the water when beavers are swimming, and the beavers spend only 3% of their active time diving [57]. Thus, we speculate that the tag-induced drag impact of the glue-on tags used here may have been relatively small. However, we cannot make certain conclusions regarding drag in tagged beavers, and future studies should attempt to address this.

Tagging season and tag removal

The season of tagging did not impact body weight change of the beavers, and neither did water temperature in the river. A study of the impacts of tags on North American beavers in Minnesota, USA, that used different tagging methods (tail tags and implants) found no difference in body weight between tagged and untagged individuals during summer, but tagged animals lost more body weight in winter [55]. We did not tag beavers during the winter months, which might partly explain why we did not observe a seasonal effect. Beavers may be more susceptible to negative tagging effects during winter due to the colder winter temperatures and lower access to green plants during this time. In ice free areas beavers may even increase their active time and time spent foraging during winter, and tagging during this time may represent an additional stressor [96]. Semi-aquatic species are in an especially energetic precarious position due to changing temperature conditions in water and on land [37]. A major concern with attaching a tag to the fur of a semi-aquatic animal is how it impacts the thermal insulation properties of the fur [36]. Beaver fur consists of a protective overlayer of coarse guard hairs and an underlayer of fur-wool [98], functioning as a thermal barrier in both air and water [99]. Beavers groom regularly to maintain the waterproof properties of the fur [100, 101] and a glued patch will impair their ability to groom that patch, which might cause heat loss. Additionally epoxy used to attach the tag has a higher thermal conductivity than fur, and therefore may act as a source of increased energy expenditure [36]. Grey seals tagged with glue-on tags displayed no apparent heat loss when wet, but heat loss was clear when animals were dry [36]. We would recommend that future studies apply thermal imaging to measure differences in surface temperature of tagged beavers both when they are wet and dry.

Following tag removal, we observed cases in which the underfur was left intact, but also occasions where patches with no underfur were left on the beaver. Fur loss may be exaggerated by excessive amounts of glue and attachment too close to the skin. The damaged patch left after tagging beavers with glue on tags usually takes 3 to 4 months to be restored [58]. Thus, the open patch may be a source of heat loss until the fur is regrown, further reducing body weight because resources are invested into thermoregulation. Future studies should explore whether the negative effects on body weight continues after tag removal. Skin irritation or major wounds following tagging has not previously been documented with glue-on tags on beavers, with the exception of one beaver included in our study with a small wound underneath the logger. Tagging of nutria (Myocastor coypus) using glue-on tags on the tail caused sloughing of the skin [102], which we did not observe in our beavers. There is always a trade-off between minimizing the amount of glue in order to reduce damage to the beaver fur, and so minimize the compromise to thermal insulation and using sufficient amounts to ensure that the tag remains attached to the beaver for the required duration.
**Tagging length, handling and individual variation**

The length of the tagging periods varied between 8 to 43 days. While we attempted to recapture beavers after 2–3 weeks for tag removal, some were retrieved earlier due to different battery capacities of the loggers. Some beavers also evaded capture and carried the tag for longer time periods. Despite the considerable variation, we did not find that tagging length affected body weight change. A comprehensive long-term study in the same population of Eurasian beavers found that beaver body mass and litter size (in old individuals only) decreased with increasing number of captures [59]. However, this effect was less clear during the later years of the project, indicating possible habituation towards capture and handling [59]. A previous tagging study from the same area also found that tagged beavers tend to spend more time in the lodge during the night they were tagged compared to later in the tagging period [58]. Upon capture, tagged beavers are typically handled for longer time periods than non-tagged beavers, due to the extra time required to attach and remove the tag. However, as we cannot monitor the spatial movements of untagged beavers, we cannot conclude on whether this behavior is driven by the capture itself or related to carrying the tag. Future tagging studies should attempt to reduce handling time during tagging as much as possible to mitigate any potential negative impacts.

We found considerable individual variation among the tagged beavers, and while the majority lost body weight during tagging, some tagged beavers also gained body weight. In comparison only two of the untagged beavers lost body weight between captures. This indicates that it is unusual for beavers to lose body weight between spring and autumn (March and November). Thus, body weight loss in 57% of the tagged beavers is a cause for concern. Habituation to both capture and tagging could go some way to explain why some tagged beavers gained body weight, and this would be interesting to explore in future studies with additional data on body weight gain of the same individuals during several tagging periods.

**Conclusion**

Our study emphasizes the importance of using a control group to investigate tagging effects on wildlife. We found a negative effect on beaver body weight change during the tagging period, but with considerable individual variation amongst tagged individuals. These findings might have implications regarding animal welfare and the validity of data collected [103, 104]. The large variation among tagged beavers illustrates how effects of tagging should not only be studied by comparing averages among tagged and untagged individuals, but also by analyzing individual impacts. The negative effect of tagging did not vary as a function of the confounding variables (sex, age, relative tag weight, tagging duration, season, water temperature) we examined. This means we found no support for our hypothesis that relative tag weight would negatively impact tagged beavers, but the drivers of the observed body weight loss should be investigated further. The observed changes in body weight might be caused by stress associated with capture [105, 106] as tagging usually requires longer handling time, and such impacts on body condition do not necessarily mean that the beavers change their activity patterns or spatial movements [58], or prolonged effects after tag removal, but this should be investigated further. Especially the duration of weight loss in tagged beavers remains uncertain, and this should be explored in relation to environmental conditions and food availability that may exaggerate negative effects during tagging. Glue-on tags are used as a relatively short-term tagging method on beavers, and the cumulative body weight loss observed was not extensive in comparison to their total body weight. Nevertheless, any decrease in body weight gain during tagging may be important in terms of individual animal welfare especially considering that untagged animals by comparison tended to increase their body weight. Assessing potential...
negative impacts of tagging on both a population and individual level should therefore be a priority for all research projects applying tags on wild animals.

Supporting information
S1 File. This file contains all the supporting tables and figures.

Acknowledgments
This study was conducted by the Norwegian Beaver Project at the University of South-Eastern Norway. We thank all staff, students, and volunteers who have participated in collecting the data. Thanks to Rasmus M. Mortensen and Andreas Zedrosser for advice on the statistical analysis, and to Roisin Campbell-Palmer and Tess Espey for proofreading the manuscript.

Author Contributions
Conceptualization: Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell.
Data curation: Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell.
Formal analysis: Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell.
Funding acquisition: Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell.
Investigation: Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell.
Methodology: Christian Andre Robstad, Hanna Kavli Lodberg-Holm, Martin Mayer, Frank Rosell.
Project administration: Frank Rosell.
Resources: Frank Rosell.
Supervision: Martin Mayer, Frank Rosell.
Validation: Hanna Kavli Lodberg-Holm.
Writing – original draft: Christian Andre Robstad, Hanna Kavli Lodberg-Holm.
Writing – review & editing: Martin Mayer, Frank Rosell.

References
1. Börger L, Bijleveld AI, Fayet AL, Machovsky-Capuska GE, Patrick SC, Street GM, et al. Biologging special feature. J Anim Ecol. 2020; 89:6–15. https://doi.org/10.1111/1365-2656.13163 PMID: 32091640
2. Kays R, Crofoot MC, Jetz W, Wikelski M. Terrestrial animal tracking as an eye on life and planet. Science. 2015; 348(6240):aaa2478. https://doi.org/10.1126/science.aaa2478 PMID: 26068858
3. McIntyre T, editor Animal telemetry: tagging effects 2015: American Association for the Advancement of Science.
4. Vandenabeele S, Shepard E, Grémillet D, Butler P, Martin G, Wilson R. Are bio-telemetric devices a drag? Effects of external tags on the diving behaviour of great cormorants. Mar Ecol Prog Ser. 2015; 519:239–49. https://doi.org/10.3354/meps11058
5. Brooks C, Bonyongo C, Harris S. Effects of global positioning system collar weight on zebra behavior and location error. J Wildl Manage. 2008; 72(2):527–34. https://doi.org/10.2193/2007-061

6. Casper RM. Guidelines for the instrumentation of wild birds and mammals. Anim Behav. 2009; 78(6):1477–83. https://doi.org/10.1016/j.anbehav.2009.09.023

7. Portugal SJ, White CR. Miniaturization of biologgers is not alleviating the 5% rule. Methods Ecol Evol. 2018; 9(7):1662–6. https://doi.org/10.1111/2041-210X.13013

8. Sikes RS, Gannon WL. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of mammalogy. 2011; 92(1):235–53. https://doi.org/10.1644/10-MAMM-F-355.1

9. Wilson RP, Rose KA, Gunner R, Holton MD, Marks NJ, Bennett NC, et al. Animal lifestyle changes acceptable mass limits for attached tags. bioRxiv. 2021:2021.04.27.441641. https://doi.org/10.1098/rspb.2021.2005 PMID: 34702077

10. Baylis AMM, Page B, Staniland I, Arnould JPY, McKenzie J. Taking the sting out of darting: risks, restraint drugs and procedures for the chemical restraint of Southern Hemisphere otariids. Mar Mamm Sci. 2015; 31(1):322–44. https://doi.org/10.1111/mms.12148

11. Vandenabeele SP. Avian rucksacks for science: in search for minimum-impact tagging procedures for birds: Swansea University (United Kingdom); 2013.

12. Rosen DAS, Gerlinsky CG, Trites AW. Telemetry tags increase the costs of swimming in northern fur seals, Callorhinus ursinus. Mar Mamm Sci. 2018; 34(2):385–402. https://doi.org/10.1111/mms.12460

13. Tudorache C, Burgerhout E, Brittijn S, van den Thillart G. The effect of drag and attachment site of external tags on swimming eels: experimental quantification and evaluation tool. PLoS One. 2014; 9(11):e112280. https://doi.org/10.1371/journal.pone.0112280 PMID: 25409179

14. Bouyoucos IA, Suski CD, Mandelman JW, Brooks EJ. Effect of weight and frontal area of external telemetry packages on the kinematics, activity levels and swimming performance of small-bodied sharks. J Fish Biol. 2017; 90(5):2097–110. https://doi.org/10.1111/jfbi.13290 PMID: 28239865

15. van der Hoop JM, Fahlman A, Hurst T, Rocho-Levine J, Shorter KA, Petrov V, et al. Bottlenose dolphins modify behavior to reduce metabolic effect of tag attachment. J Exp Biol. 2014; 217(23):4229–36. https://doi.org/10.1242/jeb.108225 PMID: 25324344

16. Lear KO, Gleiss AC, Whitney NM. Metabolic rates and the energetic cost of external tag attachment in juvenile blacktip sharks Carcharhinus limbatus. J Fish Biol. 2018; 90(5):2097–110. https://doi.org/10.1111/jfbi.13290 PMID: 28239865

17. Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, et al. A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. Methods Ecol Evol. 2018; 9(4):946–55. https://doi.org/10.1111/2041-210X.12934

18. Barron DG, Brawn JD, Weatherhead PJ. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods Ecol Evol. 2010; 1(2):180–7. https://doi.org/10.1111/j.2041-210X.2010.00013.x

19. Murray DL, Fuller MR. A critical review of the effects of marking on the biology of vertebrates. In: Botani L, K. FT, editors. Research techniques in animal ecology: controversies and consequences. New York: Columbia University Press; 2000. p. 15–64.

20. Saraux C, Le Bohec C, Durant JM, Viblanc VA, Gauthier-Clerc M, Beaune D, et al. Reliability of flipper-banded penguins as indicators of climate change. Nature. 2011; 469(7329):203–6. https://doi.org/10.1038/nature09630 PMID: 21228875

21. White GC, Garrott RA. Analysis of wildlife radio-tracking data: Elsevier; 2012.

22. Williams HJ, Taylor LA, Benhamou S, Bileveld AI, Clay TA, de Grissac S, et al. Optimizing the use of biologgers for movement ecology research. J Anim Ecol. 2020; 89(1):186–206. https://doi.org/10.1111/1365-2656.13094 PMID: 31424571

23. Jung TS, Konokics SM, Kukka PM, Majchrzak YN, Menzies AK, Oakley MP, et al. Short-term effect of helicopter-based capture on movements of a social ungulate. J Wildl Manage. 2019; 83(4):830–7. https://doi.org/10.1002/jwmg.21640

24. Baker JD, Johanos TC. Effects of research handling on the endangered Hawaiian monk seal. Mar Mamm Sci. 2002; 18(2):500–12. https://doi.org/10.1111/j.1748-7692.2002.tb01051.x

25. Bank MS, Franklin WL, Samo RJ. Assessing the effect of radiocollars on juvenile guanaco survival. Oecologia. 2000; 124(2):232–4. https://doi.org/10.1007/s004420050011 PMID: 28308183

26. Hetem RS, Strauss WM, Fick LG, Maloney SK, Meyer LC, Shobrack M, et al. Activity re-assignment and microclimate selection of free-living Arabian oryx: responses that could minimise the effects of climate change on homeostasis? Zoology. 2012; 115(6):411–6. https://doi.org/10.1016/j.zool.2012.04.005 PMID: 23036437
27. Stewart J, Hazen E, Foley D, Bograd S, Gilly W. Marine predator migration during range expansion: Humboldt squid *Dosidicus gigas* in the northern California Current System. Mar Ecol Prog Ser. 2012; 471:135–50. https://doi.org/10.3354/meps10022

28. McFarland R, Hetem RS, Fuller A, Mitchell D, Henzi SP, Barrett L. Assessing the reliability of biologger techniques to measure activity in a free-ranging primate. Anim Behav. 2013; 4(85):861–6. https://doi.org/10.1016/j.anbehav.2013.02.005

29. Watts C, Empson R, Thornburrow D, Rohan M. Movements, behaviour and survival of adult Cook Strait giant weta (*Deinacrida rugosa; Anostostomatidae: Orthoptera*) immediately after translocation as revealed by radiotracking. J Insect Conserv. 2012; 16(5):763–76. https://doi.org/10.1007/s10841-012-9461-8

30. Brien M, Webb G, Manolis C, Lindner G, Ottway D. A method for attaching tracking devices to crocodilians. Herpetol Rev. 2010; 41(3):305.

31. Fedak MA, Anderson SS, Curry MG. Attachment of a radio tag to the fur of seals. J Zool. 1983; 200(2):298–300. https://doi.org/10.1111/j.1469-7998.1983.tb05794.x

32. Litthnan CL, Baker JD, Parrish FA, Marshall GJ. Effects of video camera attachment on the foraging behavior of immature Hawaiian monk seals. Mar Mamm Sci. 2004; 20(2):345–52.

33. Boyd IL, Lunn NJ, Barton T. Time budgets and foraging characteristics of lactating antarctic fur seals. J Anim Ecol. 1991; 60(2):577–92. https://doi.org/10.2307/5299

34. Bowen W, Tully D, Boness DJ, Bulheier B, Marshall G. Prey-dependent foraging tactics and prey profitability in a marine mammal. Mar Ecol Prog Ser. 2002; 244:235–45. https://doi.org/10.3354/meps244235

35. Field IC, Harcourt RG, Boehme L, De Bruyn PN, Charrassin J-B, McMahon CR, et al. Refining instrument attachment on phocid seals. Mar Mamm Sci. 2011. https://doi.org/10.1111/j.1748-7692.2011.00519.x

36. McCafferty DJ, Currie J, Sparling CE. The effect of instrument attachment on the surface temperature of juvenile grey seals (*Halichoerus grypus*) as measured by infrared thermography. Deep Sea Res. 2007; 54(3):424–36. https://doi.org/10.1016/j.dsr2.2006.11.019

37. McCafferty DJ, Currie J, Sparling CE. The effect of instrument attachment on the surface temperature of juvenile grey seals (*Halichoerus grypus*) as measured by infrared thermography. Deep Sea Res. 2007; 54(3):424–36. https://doi.org/10.1016/j.dsr2.2006.11.019

38. Fish FE. Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. Physiol Biochem Zool. 2000; 73(6):683–98. https://doi.org/10.1086/318108 PMID: 11121343.

39. Hartung R. Energy metabolism in oil-covered ducks. J Wildl Manage. 1967:798–804. https://doi.org/10.2307/3797987

40. Jenssen BM. Review article: Effects of oil pollution, chemically treated oil, and cleaning on thermal balance of birds. Environ Pollut. 1994; 86(2):207–15. https://doi.org/10.1016/0269-7491(94)90192-9 PMID: 15091638

41. Francis RA, Taylor JD, Dibble E, Strickland B, Petro VM, Easterwood C, et al. Restricted cross-scale habitat selection by American beavers. Curr Zool. 2017; 63(6):709–10. https://doi.org/10.1093/cz/zox059 PMID: 29492032

42. Mayer M, Frank SC, Zedrosser A, Rosell F. Causes and consequences of inverse density-dependent territorial behaviour and aggression in a monogamous mammal. J Anim Ecol. 2020; 89(2):577–88. https://doi.org/10.1111/1365-2656.13100 PMID: 31469174

43. Rosell F, Bozsér O, Collen P, Parker H. Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mamm Rev. 2005; 35(3–4):248–76. https://doi.org/10.1111/j.1365-2907.2005.00067.x

44. Wright JP, Jones CG, Flecker AS. An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia. 2002; 132(1):96–101. https://doi.org/10.1007/s00442-002-0929-1 PMID: 28947281

45. Davis JR, Von Recum AF, Smith DD, Guyrn DC. Implantable telemetry in beaver. Wildl Soc Bull. 1984; 12(3):322–4.

46. Guyrn DC Jr, Davis JR, Von Recum AF. Pathological potential of intraperitoneal transmitter implants in beavers. J Wildl Manage. 1987; 51(3):605–6. https://doi.org/10.2307/3801277
49. McKinstry MC, Anderson SH. Survival, fates, and success of transplanted beavers, *Castor canadensis*, in Wyoming. Can Field-Nat. 2002; 116(1):60–8.

50. Ranheim B, Rosell F, Haga HA, Arnemo JM. Field anaesthetic and surgical techniques for implantation of intraperitoneal radio transmitters in Eurasian beavers Castor fiber. Wildlife Biol. 2004; 10(1):11–5. https://doi.org/10.2981/wlb.2004.004

51. Rothmeyer SW, McKinstry MC, Anderson SH. Tail attachment of modified ear-tag radio transmitters on beavers. Wildl Soc Bull. 2002; 30(2):425–9.

52. Baker BW, Hill E. Beaver (*Castor canadensis*). *Beaver* (*Castor canadensis*). 2nd ed. Baltimore, MD: Johns Hopkins University Press; 2003.

53. Arjo WM, Joos RE, Kochanny CO, Harper JL, Nolte DL, Bergman DL. Assessment of transmitter models to monitor beaver *Castor canadensis* and *C. fiber* populations. Wildlife Biol. 2008; 14(3):309–17. https://doi.org/10.2981/wlb.2008.003

54. Bloomquist CK, Nielsen CK, Shew JJ. Spatial organization of unexploited beavers (*Castor canadensis*) in southern Illinois. Am Midl Nat. 2012; 167(1):188–97. https://doi.org/10.1674/0003-0031-167.1.188

55. Smith JB, Windels SK, Wolf T, Klaver RW, Belant JL. Do transmitters affect survival and body condition of American beavers *Castor canadensis*? Wildlife Biol. 2016; 22(3):117–23. https://doi.org/10.2981/wlb.00160

56. Wheatley M. A new surgical technique for implanting radio transmitters in beavers, *Castor canadensis*. Can Field-Nat. 1997; 111(4):601–6.

57. Graf PM, Wilson RP, Sanchez LG, Hackländer K, Rosell F. Diving behavior in a free-living, semi-aquatic herbivore, the Eurasian beaver *Castor fiber*. Ecol Evol. 2018; 8(2):997–1008. https://doi.org/10.1002/ece3.3726 PMID: 29375773

58. Graf PM, Hochreiter J, Hackländer K, Wilson RP, Rosell F. Short-term effects of tagging on activity and movement patterns of Eurasian beavers (*Castor fiber*). Eur J Wildl Res. 2016; 62(6):725–36. https://doi.org/10.1007/s10344-016-1051-8

59. Mortensen RM, Rosell F. Long-term capture and handling effects on body condition, reproduction and survival in a semi-aquatic mammal. Sci Rep. 2020; 10(1):17886. https://doi.org/10.1038/s41598-020-74933-w PMID: 33087816

60. Smith DW, Jenkins SH. Seasonal change in body mass and size of tail of northern beavers. J Mammal. 1997; 78(3):869–76. https://doi.org/10.2307/1382945

61. Campbell RD. Demography and life history of the Eurasian beaver *Castor fiber*. Oxford, UK: Oxford University; 2010.

62. Pinto B, Santos MJ, Rosell F. Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. Can J Zool. 2009; 87(4):317–25. https://doi.org/10.1139/Z09-015

63. Olstad O. Beverens (*Castor fiber*) utbredelse i Norge. Statens viltundersøkelser Nytt Mag Naturvidensk. 1937; 77:217–73.

64. Parker H, Rosell F, Hermansen T, Sørløkken G, Stærk M. Sex and age composition of spring-hunted Eurasian beaver in Norway. J Wildl Manag. 2002; 66(4):1164–70. https://doi.org/10.2307/3802949

65. Campbell RD, Newman C, Macdonald DW, Rosell F. Proximate weather patterns and spring green-up phenology effect Eurasian beaver (*Castor fiber*) body mass and reproductive success: the implications of climate change and topography. Glob Chang Biol. 2013; 19(4):1311–24. https://doi.org/10.1111/gcb.12114 PMID: 23504905

66. Campbell RD, Rosell F, Nolet BA, Dijkstra VAA. Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav Ecol Sociobiol. 2005; 58(6):597–607. https://doi.org/10.1007/s00265-005-0942-6

67. Mayer M, Kunzel F, Zedrosser A, Rosell F. The 7-year itch: non-adaptive mate change in the Eurasian beaver, Behav Ecol Sociobiol. 2017; 71(2):32. https://doi.org/10.1007/s00265-016-2259-z

68. Rosell F, Hovde B. Methods of aquatic and terrestrial netting to capture Eurasian beavers. Wildl Soc Bull. 2001; 29:269–74.

69. Sharpe F, Rosell F. Time budgets and sex differences in the Eurasian beaver. Anim Behav. 2003; 66(6):1059–67. https://doi.org/10.1006/anbe.2003.2274

70. Rosell F, Sun LX. Use of anal gland secretion to distinguish the two beaver species *Castor canadensis* and *Castor fiber*. Wildlife Biol. 1999; 5(2):119–23. https://doi.org/10.2981/wlb.1999.015 WOS:000080973800006.

71. Mayer M, Zedrosser A, Rosell F. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. Animal Behaviour. 2017; 123:375–82. https://doi.org/10.1016/j.anbehav.2016.11.020
72. Rosell F, Zedrosser A, Parker H. Correlates of body measurements and age in Eurasian beaver from Norway. Eur J Wildl Res. 2010; 56(1):43–8. https://doi.org/10.1007/s10344-009-0289-9

73. Brown MK. Two old beavers from Adirondacks. N Y game fish. 1979; 26:92.

74. Gorbunova V, Bozella MJ, Seluanov A. Rodents for comparative aging studies: from mice to beavers. Age. 2008; 30(2–3):111–9. https://doi.org/10.1007/s11357-008-9053-4 PMID: 19424861

75. Larson JS. Age structure and sexual maturity within a western Maryland beaver (Castor canadensis) population. J Mammal. 1967; 48(3):408–13. https://doi.org/10.2307/1377773

76. Nimje P, Tinnesand HV, Buesching CD, Sæbø M, Senn H, Zedrosser A, et al. Almost faithful: SNP markers reveal low levels of extra-pair paternity in the Eurasian beaver. Under review Ecology and Evolution. 2019. https://doi.org/10.7287/peerj.preprints.27866v1

77. Leach E, Peters R, Rossiter R. Experimental thermal burns, especially the moderate temperature burn. Q J Exp Physiol. 1943; 32(1):67–86. https://doi.org/10.1113/expphysiol.1943.sp000875

78. ASAB/ABS. Guidelines for the treatment of animals in behavioural research and teaching. Anim Behav. 2020; 159:I–XI. https://doi.org/10.1016/j.anbehav.2019.11.002

79. Percie du Sert N, Ahluwalia A, Alam S, Avey MT, Baker M, Browne WJ, et al. Reporting animal research: Explanation and elaboration for the ARRIVE guidelines 2.0. PLOS Biol. 2020; 18(7):e3000411. https://doi.org/10.1371/journal.pbio.3000411 PMID: 32663221

80. Bates D, Mächler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. J Stat Soft. 2015; 67(1):48. Epub 2015-10-07. https://doi.org/10.18637/jss.v067.i01

81. Zuur AF, Ieno EN, Elphick CS. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol. 2010; 1(1):3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x

82. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. Mixed effects models and extensions in ecology. New York: Springer Science and Business Media; 2009.

83. Burnham KP, Anderson DR, Huyvaert KP. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol. 2011; 65(1):23–35.

84. Anderson D, Burnham K. Model selection and multi-model inference. Second ed. New York: Springer-Verlag; 2004. 10 p.

85. Barton K. MuMIn: Multi-model Inference. R package version 1.43.17. 1.43.17 ed2020.

86. Arnold TW. Uninformative parameters and model selection using Akaike's information criterion. J Wild Manage. 2010; 74(6):1175–8. https://doi.org/10.1111/j.1937-2817.2010.tb01236.x

87. Harrison XA, Donaldson L, Correa-Canó ME, Evans J, Fisher DN, Goodwin CED, et al. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ. 2018; 6:e4794. https://doi.org/10.7717/peerj.4794

88. Zuur AF, Ieno EN. A protocol for conducting and presenting results of regression-type analyses. Methods Ecol Evol. 2016; 7(6):636–45. https://doi.org/10.1111/2041-210X.12577

89. Hartig F. DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. 0.3.3.0 ed2020.

90. Authier M, Péron C, Mante A, Vidal P, Grémillet D. Designing observational biologging studies to assess the causal effect of instrumentation. Methods Ecol Evol. 2013; 4(9):802–10. https://doi.org/10.1111/2041-210X.12075

91. Néill LO, Wilson P, de Jongh A, de Jong T, Rochford J. Field techniques for handling, anaesthetising and fitting radio-transmitters to Eurasian otters (Lutra lutra). Eur J Wildl Res. 2008; 54(4):681. https://doi.org/10.1007/s10344-008-0195-5

92. Bethge P, Munka S, Otley H, Nicol S. Activity patterns and sharing of time and space of platypuses, Ornithorhynchus anatinus, in a subalpine tasmanian Lake. J Mammal. 2009; 90(6):1350–6. https://doi.org/10.1644/08-mamm-a-359r.1

93. Kay WP, Naumann DS, Bowen HU, Withers SJ, Evans BJ, Wilson RP, et al. Minimizing the impact of biologging devices: Using computational fluid dynamics for optimizing tag design and positioning. Methods Ecol Evol. 2019; 10(8):1222–33. https://doi.org/10.1111/2041-210X.13216

94. Wilson RP, Grant WS, Duffy DC. Recording devices on free-ranging marine animals: does measurement affect foraging performance? Ecology. 1986; 67(4):1091–3. https://doi.org/10.2307/1939832

95. Culling B, Wilson RP. Swimming energetics and performance of instrumented adélie penguins (Pygoscelis adeliae). J Exp Biol. 1991; 158(1):355–68. https://doi.org/10.1242/jeb.158.1.355

96. Nolet BA, Rosell F. Territoriality and time budgets in beavers during sequential settlement. Can J Zool. 1994; 72(7):1227–37. https://doi.org/10.1139/z94-164
97. Allers D, Culik Boris M. Energy requirements of beavers (Castor canadensis) swimming underwater. Physiol Zool. 1997; 70(4):456–63. https://doi.org/10.1086/515852 PMID: 9237306.

98. Novak M. Wild furbearer management and conservation in North America: Ontario Ministry of Natural Resources; 1987.

99. Irving L. Aquatic mammals. Comparative physiology of thermoregulation: Elsevier; 1973. p. 47–96.

100. Wilsson L. Observations and experiments on the ethology of the European beaver (Castor fiber L.). Viltrevy. 1971; 8(3):160–203.

101. Walro JM, Svendsen GE. Castor sacs and anal glands of the North American beaver (Castor canadensis): their histology, development, and relationship to scent communication. J Chem Ecol. 1982; 8(5):809–19. https://doi.org/10.1007/BF00994781 PMID: 24415179

102. Merino S, Carter J, Thibodeaux G. Testing tail-mounted transmitters with Myocastor coypus (nutria). Southeast Nat. 2007; 6(1):159–64. https://doi.org/10.1656/1528-7092(2007)6[159:TTTWM C]2.0.CO;2

103. Cleasby IR, Morrissey BJ, Bolton M, Owen E, Wilson L, Wischnewski S, et al. What is our power to detect device effects in animal tracking studies? Methods Ecol Evol. 2021; 12(7):1174–85. https://doi.org/10.1111/2041-210X.13598

104. Soulsbury CD, Gray HE, Smith LM, Braithwaite V, Cotter SC, Elwood RW, et al. The welfare and ethics of research involving wild animals: A primer. Methods Ecol Evol. 2020; 11(10):1164–81. https://doi.org/10.1111/2041-210X.13435

105. Kock MD, Clark RK, Franti CE, Jessup DA, Wehausen JD. Effects of capture on biological parameters in free-ranging bighorn sheep (Ovis canadensis): evaluation of normal, stressed and mortality outcomes and documentation of postcapture survival. J Wildl Dis. 1987; 23(4):652–62. https://doi.org/10.7589/0090-3558-23.4.652 PMID: 3682092.

106. Meyer LCR, Fick L, Matthee A, Mitchell D, Fuller A. Hypothermia in captured impala (Aepyceros melampus): a fright not flight response. J Wildl Dis. 2008; 44(2):404–16. https://doi.org/10.7589/0090-3558-44.2.404 PMID: 18436672.