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Short-term effects of bio-logging on body mass and growth of a semi-aquatic mammal, the Eurasian beaver *(Castor fiber)*

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This thesis is worth 60 study points

Abstract

Bio-logging is a popular method to collect scientific data in the field of animal ecology. The presumption is that bio-logging should allow the study of animals with only minor disturbance to their natural behaviour and thereby avoid biased data. However, tagging may be stressful and may cause deleterious effects and alter natural responses or behaviour of animals. Knowledge of negative impacts associated with the tagging of animals should be assessed when possible. Bio-logging studies often lack a control group, and the adverse effects of tagging may therefore not be observable. In this study, I investigated whether glue-on tagging affected Eurasian beavers (*Castor fiber*) body mass and growth per day. I predicted that tagged individuals would experience reduced body mass, and externally attached tags would negatively affect beavers' growth rate per day in comparison with un-tagged beavers (control group). Thirty-one adult free-ranging beavers were tagged, and 47 un-tagged beavers were used as a control group. Linear mixed models (LMM) were used to model body mass and growth per day. Analysing differences in body mass within the tagged individuals only, showed an inconclusive result where all explanatory variables were uninformative, which indicate no substantial effect from the tag. However, analysing the tagged and un-tagged beavers combined indicated that the glue-on tag negatively affected the beavers' growth per day. This result emphasised the importance of using a control-group to reveal adverse effects that might have implications for animal welfare and sampling of biased data. Whether the adverse effects were caused by extended handling time, drag or thermoregulation are unknown. The glue-on tag likely interferes with the beaver's fur and insulation, which might be a significant factor for the decrease in beavers' growth. However, this study only investigated the short-term effect of tagged individuals. Future studies are needed to test if these effects are prolonged over time.

Keywords: Beaver, *Castor fiber*, glue-on, tag, growth, body mass, tagging effects

Contents

Foreword

First, I want to thank my supervisor, Frank Rosell, together with Martin Mayer and Hanna Kavli Lodberg-Holm, for giving me guidance on writing and advising on the statistics during my Masters. Also, thank you to Frank Rosell for all our fieldwork, trips abroad and social happenings. I hope our paths will keep us working together in animal ecology also in the future.

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1 Introduction

The knowledge produced by bio-logging studies is highly valuable to increase our understanding of animal ecology (McIntyre 2015, Neumann et al. 2015). Instrumentation of animal-borne devices, often referred to as bio-logging, are used to gather information on the behaviour, movements, physiology of animals, and environmental data (Rutz and Hays 2009). Secretive animals that move through their habitat undetected by human observers can make data collection challenging (Balmori 2016). In animal research, the presumption is that bio-logging should allow the study of animals with only minor disturbance to their behaviour (Boyd et al. 2004, Ropert-Coudert and Wilson 2005). However, knowledge of the negative impacts associated with attaching instruments to animals has not been given substantial consideration (Kays et al. 2015). Guidelines recommend that the total weight of a tag should be less than 3-10%, relative to body mass (Wilson et al. 1996, Casper 2009, Sikes and Gannon 2011, Sikes et al. 2016). Other researchers suggest tag weights between 0.7% and 9% depending on the species (Brooks et al. 2008). Adding weight to the animals is of primary concern, and the contemporary guidelines endorse continued miniaturisation of tag weight (Vandenabeele 2013).

The effects on animals can occur independently or associated with capture stress (Baylis et al. 2015), e.g. via increased drag from external tags on flying and aquatic animals (energy expenditure and locomotion) (Tudorache et al. 2014), behavioural modifications (van der Hoop et al. 2014) and effects of different attachment methods (Vandenabeele 2013). The effects of tag mount vary between species, individuals, and geographic region (White and Garrot 1990), and always require individual adaptations to particular species. Still, adverse effects caused by the instrumentations of animals cannot be avoided entirely (Saraux et al. 2011). Thus, to minimise the impacts of tags on animals, continued refinement of attachment methods and continuous improvements of animal mounted sensors should be stressed (Bridge et al. 2011, Vandenabeele et al. 2015). There are concerns about the potentially biased data they may produce, which may not reflect the true behaviour of the species (Murray and Fuller 2000, Grogan et al. 2011). Attaching tags also raises concerns for ethical and animal welfare issues. Research has shown that the adverse effects of tagged animals are generally low, although results ranging from negligible to substantial (Murray and Fuller 2000, McIntyre 2015). Thus, assessing these effects should be investigated when possible (Bank et al. 2000), and should receive increased research interest in the future (McIntyre 2015).

Externally attached bio-logging devices such as harness, backpack, collar and glue-on have been used for scientific studies of numerous taxa, including terrestrial mammals (Hetem et al. 2012, McFarland et al. 2013), birds (Dean et al. 2013, Phipps et al. 2013), reptiles (Dubois et al. 2009, Watanabe et al. 2013), fish (Bonfil et al. 2005, Yasuda et al. 2013) and invertebrates (Stewart et al. 2012; Watts et al. 2012). However, the cause and effects on animal behaviour and physical condition are not entirely understood, due to the difficulty to compare with un-tagged free-living animals (Baker and Johanos 2002). However, several studies have indicated that tags might impact animals negatively. Flipper-bands attached to king penguins (*Aptenodytes patagonicus*) caused a 39% lower breeding success and 16% lower survival rate (Saraux et al. 2011). In a similar species, adélie penguins (*Pygoscelis adeliae*) using the same type of flipper band reported a 24% increase in energy expenditure (Culik et al. 1993), which might explain the devastating effect on the king penguin (Sauraux et al. 2011). Moose (*Alces alces*) that were equipped with ear-tag transmitters had higher mortality than moose equipped with ear tags only (Swenson et al. 1999). Meadow voles (*Microtus pennsylvanicus*) carrying very high frequencies (VHF) collars had a higher mortality rate than individuals not wearing a tag (Webster and Brooks 1980). Similarly, migratory caribou (*Rangifer tarandus*) experienced a lower survival of individuals equipped with more massive satellite collars than those with lighter VHF collars (Rasiulis et al. 2014). Other studies have found no evidence for adverse effects due to the instrumentation of animals (McMahon et al. 2011). Such adverse effects of tagging often appear only anecdotal, since it is rarely the main research question.

In aquatic pinnipeds, the glue-on method is often preferred since considered non-invasive, and tags are glued directly on the fur with fast-curing adhesives (e.g. epoxies, urethanes or cyanoacrylates) (Fedak et al. 1983). The attachment method itself and the placement of a tag can cause negative effects. For example, in Antarctic fur seals (*Arctocephalus gazella*) and Harbour seals (*Phoca vitulina*), glue-on tags affected the seals swimming speed (increased drag) (Littnan et al. 2004), foraging and trip duration (Boyd et al. 1991, Boyd 1997), foraging behaviour (Bowen et al. 2002), as well as causing abrasions (Field et al. 2012).

In contrast to aquatic mammals using a layer of blubber, semi-aquatic mammals carry a dense, water-resistant fur for insulation (Fish 2000), which may be vulnerable to glue-on tags. Tagging may have a more significant impact on semi-aquatic mammals since water conducts heat better than air, and the likely impaired pelage has a greater potential for heat loss (Hartung 1967, Jenssen 1994). Semi-aquatic mammals such as the European mole (*Talpa europaea*) (Stone et al. 1985), Eurasian otter (*Lutra lutra*) (Néill et al. 2008) and the platypuses (*Ornithorhynchus anatinus*) (Bethge et al. 2009) have been tagged using glue-on tags, but no adverse effects were documented. However, it is unclear if the effects have been assessed thoroughly since no details of the assessment were described in these studies. Twelve glue-on tags used on nutria (*Myocastor coypus*) showed incidents of sloughing of the skin in two individuals, and cause of death was uncertain for one other individual. However, the authors acknowledge problems with skin irritation but no increased morbidity (Merino et al. 2007). Another study involving neck-collard American mink (*Musela vison*) only recorded a brief visual observation on body condition; hence, no measurement recorded and only anecdotally commented (Hays et al. 2007).

Many bio-logging studies, including those summarised above, lack a control group when investigating for adverse effects. In other research disciplines, a control group is an essential part of the research design, used as a baseline allowing researchers to minimise the effect of all confounding variables except the explanatory variable to allow meaningful comparison to be drawn. This lack of a control group is often caused by the shortage of research animals, which longitudinal data or a long-term research project could provide (Clutton-Brock and Sheldon 2010). The Norwegian Beaver Project (NBP) represents a long-term research project on Eurasian beavers ongoing since 1997, and provides an excellent opportunity to study negative effects of tag deployment on a semi-aquatic animal for short- (Graf et al. 2016), and long- (Mortensen and Rosell 2020, submitted) term effects.

The Eurasian beaver (*Castor fiber*) and the North American beaver (*C. canadensis*) are large semi-aquatic mammals (Wilsson 1971, Novak 1987). Both species are considered socially monogamous and live as a family group, usually consisting of a dominant pair and their offsprings (Sun et al. 2003). The dominant pair are territorial and scent-mark and defend their territory from intruders (Rosell and Nolet 1997). Beavers are primarily confined to their lodge during daytime and are only active between dusk and dawn, which makes direct visual observations difficult (Barnes and Dibble 1988, Wheatley 1997a). Therefore, beavers are perfect targets for bio-logging studies to reveal their secretive lifestyles. There are, however, risks involved in placing external tags on beavers due to a unique way of life and the environments they utilise. In addition to lodges, beavers use burrows and dens and often move through narrow openings and dense vegetation, which creates a risk for entanglement by the externally attached tag (Davis et al. 1984, Guynn et al. 1987, Wheatley 1997b, Gurnell 1998). Further, beavers insulate their bodies with dense fur (Novak 1987), which function as a thermal barrier in both air and water and might be compromised by glue-on tags (Irving 1973). Adult beavers usually gain weight during the spring and autumn and decrease body weight in winter when food availability is scarce (Smith and Jenkins 1997, Campbell 2010). Beavers have a fusiform body shape and tapered necks that may create a challenge to use conventional tagging procedures (Rothmeyer et al. 2002) and has led to the development of new tagging methods for the species. Conventional collar transmitters have proven to be ineffective and potentially hazardous (Davis et al. 1984, Guynn et al. 1987, Wheatley 1997b). Several implant studies have been conducted on beavers (Davis et al. 1984, McKinstry et al. 2003, Ranheim et al. 2004). However, implantation and surgery are expensive (anaesthetics and veterinarians) and invasive with an extended recovery period and the probability of surgical complications (Wheatly 1997b).

Another common way to tag beavers during the past 20 years has been tail tagging by puncturing a hole in the tail (Rothmeyer et al. 2002, Baker 2006, Arjo et al. 2008, Bloomquist et al. 2012, Smith et al. 2016). However, this method caused some tail injuries and reductions in body condition (Smith et al. 2016). Eurasian beavers have also been a subject for glue-on tags (Steyeart et al. 2015, Graf et al. 2018, Mayer et al. 2020). No injuries or adverse effects were observed (anecdotally mentioned). In a study investigating short-term changes in post-capture behaviour; beavers showed only minor alterations in their behaviour, and due to the small effect size, resulting in an inconclusive conclusion (Graf et al. 2016). Long-term monitoring of Eurasian beavers indicated that tagging, capturing and handling had no effect on adult beavers` body condition and survival. Thus a negative effect off captures where shown on reproduction in the early years of the project (Mortensen and Rosell 2020, submitted). However, the short term-effect on beavers' body mass from carrying a glue-on is to my knowledge not investigated.

This present study aims to identify the potential change and difference in beaver body mass pre and post tagging caused by external glue-on tags (1) and compare growth rates in body mass between tagged and un-tagged individuals (control group) (2). I predicted that tagged individuals would experience reduced body mass between attaching and removal of the tag, and the negative effect would increase with the number of days tagged, which the un-tagged beavers would not display.

2. Methods

2.1. Study area and animals

The study site consists of three connected rivers, Gvarv (59 386 N, 09 179 E), Straumen (59 29 N, 09 153 E) and Sauar (59 444 N, 09 307 E) in Vestfold and Telemark County, Norway (Figure 1) and discharges into Lake Norsjø. The mean annual air temperature is 4.6 Celsius and has an annual precipitation of 790 mm (Campbell et al. 2012). Human settlements, semi-agricultural landscapes and forested woodland are scattered throughout the study area (Pinto et al. 2009). Eurasian beavers have inhabited the study area since the 1920s (Olstad 1937). Hunting pressure is low (Parker et al. 2002), and the population are considered to be at carrying capacity (Pinto et al. 2009; Steyaert et al. 2015) since beaver territories border each other, with few unoccupied stretches of the river. The study area inhabited of 25-30 beaver families with 1246 live captured beavers in the last 20 years.

2.2. Capture and handling

The NBP has monitored beavers in this study site since 1997 (Campbell et al. 2005, 2013, Steyeart et al. 2015). Every year between March and November, beavers have been captured, as part of a long-term capture-mark-recapture study (Campbell et al. 2013, Mayer et al. 2017). Live captured beavers were caught at night with nets from a boat or onshore (Rosell and Hovde 2001) and transferred into a cloth bag for handling. Beavers were handled while awake with no anesthesia. Captured animals were microchipped and ear-tagged for identification (Sharpe and Rosell 2003). All individuals were sexed, based on the anal-gland (Rosell and Sun 1999), weighed and measured for body size, tail length and tail thickness (Campbell et al. 2012, 2013; Mayer et al. 2017), and released at the place of capture after 20-30 minutes. The age was assigned based on bodyweight 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 an age at least of two years and a minimum three years when over >19.5 kg (Rosell et al. 2010). An additional year was added to the age every year following the initial capture. This method has shown to be an acceptable estimate for beaver age (Rosell et al. 2010, Mayer et al. 2017).

2.3. Tagging procedure

From 2009-2016, beavers were equipped with tags sized 130 × 10 mm and weights at approximately (due to amount of glue) 130 g or 200 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 positions system (GPS) (50 × 70 mm, 24 g; model G1G 134A; Sirtrack, Havelock North, NZ), and/or a tri-axial accelerometer (TAA) (15 × 90 mm, 62 g; JUV Elektronik, Schleswig-Hollstein, GER). In a few tagging session, a time-depth recorder (TDR) (67 x 17 mm, 30 g; model MK9 Archival Tag, Wildlife computers Inc, Redmond, WA, USA) was used instead of a GPS or TAA. Tag units were covered with 4.5 mm mesh net (Mørenot Fishery AS, Møre and Romsdal) to increase the surface area of attachment and prevent glue reaching the skin to avoid heat or chemical burns. The unit was secured with cable ties to assure all parts remained in one unit until retrieval of the tag. The unit was glued on the lower back, 15 cm above the base of the tail, using a two-component epoxy-resin (System Three Resins, Auburn WA, USA (Graft et al. 2016) and the attachment process took approximately 20 minutes. Beavers were later re-captured, and tags were cut off by a scalpel, which took approximately ten minutes (Figure 2a-d). The procedure to assemble the units remained reasonable equivalent but varied slightly during the study period in relation to weight and shape of the different loggers, and due to different students and staff working on the project.

2.4. Ethical statement

The Norwegian Food Safety Authority (most recent authorisation FOTS ID 15947) and The Norwegian Directorate for Nature Management (most recent authorisation 2014/14415 ART-VI-ID) have approved this study and granted our permission to conduct fieldwork in our study area, including all handling and tagging procedures. To our knowledge, none of the beavers in this study was injured due to capture and handling.

2.5. Data preparation

I explored changes in body weight between subsequent captures of tagged and un-tagged beavers. For this analysis, only individuals that were >two years old and assigned as an adult were included, because these were the only individuals that were tagged. Pregnant beavers were excluded from the analysis during spring to avoid the effect of weight change due to pregnancy. Because some beavers were missing tail measurements, the weight (body mass) was used as the single indicator of body condition. Tagged beavers were included in this study if the weight was measured both during attachment (capture) and removal of the tag (re-capture). Un-tagged beavers only captured and measured (not tagged) were captured between 1999 and 2015 and included as a control group. An un-tagged beaver was only considered if captured twice between March –November in a given year, in order to calculate their growth rate. Adult beavers usually gain mass from spring (March) to autumn (November) (Campbell et al. 2012). The growth rate was calculated by dividing the difference in weights from captured (captured once in a given year) and re-captured (later in a given year) by days.

2.6. Statistical analysis

To analyse changes in body weight either per day or throughout the period between capture events, I used linear mixed models (LMM) and the R package lme4 (Bates et al. 2015) and accounted for Beaver ID as a random factor to account for pseudoreplication of repeated sampling of the same individual.

I investigated whether beaver body mass was affected by glue-on tags using two different analyses. First, I investigated body weight before tag attachment and after the tag was removed in the "tagged beaves only". Secondly, I analysed the difference in "growth rate per day" between the tagged beavers and a control group (un-tagged beavers). For the first analysis, I modelled how total body mass changed from attachment to removal of the tag using body mass (weight) as the response variable. Measure (attachment or removal of the tag), sex, age, season (spring: March-July, autumn: July-November), days (number of days carrying a tag) and tag weight (130g or 200g) were included as potential explanatory variables. For the second analysis, I analysed how the growth rate in body mass per day, differentiated between the two groups. The growth per day was used as a response variable and tagged (yes or no), sex, and age was included as explanatory variables. All numerical variables were tested for collinearity and were not correlated (Pearson r coefficient <0.6) and with a cut-off of variance inflation factor (VIF) < 3 (Zuur et al. 2009, 2010).

Model selection was based on Akaike's Information Criterion (AICc) values for small sample sizes (Burnham and Andersen 2002, Arnold 2010), and carried out with the R package MuMln by using the ''dredge' function, which performs an automated model selection of the global model (Barton 2019). Models with ΔAICc < 6 were selected as the top models (Harrison et al. 2018). If several models were within this range, I carried out model averaging to estimate the effect sizes (Burnham and Anderson 2002). For each explanatory variable, I calculated the 95% confidence interval, and if it overlapped with zero, the variable was considered uninformative (Arnold 2010). To check for model validity, I plotted model residuals against fitted values to inspect for non-normality and heterogeneity (Zuur et al. 2009). All data analyses were performed with R version 3.5.2 (R Development Core Team 2018).

3. Results

3.1. Tag attachment and body condition

We tagged 31 individuals consisting of 16 males (two were tagged multiple times) and 15 females (two were tagged twice). The average weight of the tagged beavers at the time of tagging was (mean ± SD) 22.04 ± 2.23 kg and 21.68 ± 2.44 kg at re-capture. Beavers were on average 6.03 ± 3.20 (range, 2 - 14) years old. Tags were deployed on average 19.32 ± 7.82 (range, 8 - 44) days, and the tag means weight constituted 0.52 ± 0.16 (range, 0.5 – 1.0) % of the beaver body mass.

The un-tagged beavers consisted of 47 individuals, 27 males (six were captured multiple times) and 20 females (three were captured twice). The average control beaver weight at the time of capture was 21.01 ± 2.11 kg and 22.21 ± 1.96 kg at re-capture and aged 4.57 ± 1.70 (range, 3 - 10) years old. The mean number of days between capture and re-capture was 80.74 ± 43.41 (range, 8 - 200).

Visual observations indicated the amount of fur left after removal of the tag varied but were not documented consistently. For some beavers, underfur appeared intact, while others had open patches with no underfur remaining (Figure 3a-b).

3.2. Differences in body mass at tag attachment and tag removal

In the first model, there were eight top-ranked models in the range ΔAICc < 6 (Table 1). After model averaging, measure, sex and season were included in the final model explaining beaver body mass. However, all variables included zero in their 95% CI and were thus considered uninformative (Table 2).

3.3. Differences in growth per day in tagged and un-tagged beavers

For the second model, only one model was within the range of ΔAICc <6, and the ΔAICc of the second-best model was 8.10 (Table 3). Tag, as the only explanatory variable included in the top model, had a negative effect on beaver growth per/day (Figure 4) and an estimated difference equal to 0.035 kg/day (Table 4). The un-tagged beavers had an estimated growth rate of 0.015 kg/day (95% confidence interval, 0.005 kg/day, to 0.025 kg/day) whereas the tagged beavers had an estimated growth rate of -0.020 kg/day (95% confidence interval, -0.050 kg/day, to -0.020 kg/day) (Table 4, Figure 4).

4. Discussion

This study aimed to highlight the potential short-term adverse effects of glue-on tags on Eurasian beavers. Investigating tagged beavers only, the top models did not reveal any major changes or effects caused by the tag, and all the explanatory variables included in the top model were considered uninformative. However, this result may be masked by the annual growth in beavers between spring and autumn (Smith and Jenkins 1997, Campbell 2010). Including a control group in the dataset showed that tagged beavers had a decreased daily growth rate compared to un-tagged individuals. No other explanatory variables were included in the top model, suggesting that the glue-on tagging drives the decrease in beaver growth per day in this study, and highlights the importance of researchers' awareness about possible deleterious effects from bio-logging studies.

In a previous study in North America, beavers were equipped with transmitters, either implanted or tail-tagged, and compared with only captured and ear-tagged individuals. They found no difference between the groups related to body condition during the summer. Despite no differences during the summer, transmitter equipped beaver lost more weight during the winter than their counterparts. Thus, transmitter or not, beavers recovered their body weight the following summer (Smith et al. 2016). Even though growth was affected by glue-on tags in my study, beavers were only equipped with a tag for a short time. Despite this, a comprehensive long-term (20 years of data) study in our area found no apparent effect on adults beavers body condition from carrying a tag or capture, nor from survival. Thus, reproduction was likely affected in the earlier years of his data due to capture and handling (not from tagging) (Mortensen and Rosell 2020, submitted). This suggests that beavers can regain their body weight post tagging, and despite a temporary weight loss, it is unlikely to affect the long-term life history.

The inconclusive result outcome from analysing only the tagged beavers may explain why several other bio-logging studies report limited effects of tags, and suggest the need for studying this subject thoroughly and with a control group. For example, Bethge et al. (2003) studied short-term mass gain before and after removal of glue-on tags on platypus found no significant difference, similar to the results I found analysing "only tagged" beavers. Generally, sampling a control group may be useful in studies to control for mass loss and to avoid conclusions based statistical artefacts that can often arise without a control group (Authier et al. 2013). Other studies and species, as in Baker and Johanos (2002) and Henderson and Johanos (1988) found no alteration in behaviour, survival or body conditions, analysing tagged versus un-tagged Hawian monk seals (*Neomonachus schauinslandi*). In my study, it was essential to account for the beavers` mass gain in the tagged period. The un-tagged beavers in this study (serving as a control group) had an estimated growth similar to findings in Campbell (2010) who found (0.012 kg/day. 95% confidence interval, 0.006 kg/day, to 0.018 kg/day) in the same study area. However, there is a large difference in the number of days between the captures in the control group (mean= 80.74 days) and the tagged individuals (mean=19.32 days). This might potentially affect the measurement error and thus lead to biases. Still, I observed that tagged beavers experienced lower estimated growth than the un-tagged, but the causes are still unknown. Capture effect, drag and thermoregulation are plausible causes described in the literature, and will, therefore, be evaluated and discussed below.

4.1. The effect of capture

Capture, restraint and handling may affect animals, and studies show how a single exposure to a stressor can induce changes in behaviour and stress levels (Armario et al. 2008). In my study, including the control group controls for the potential negative effects of regular captures procedures as all beavers have been captured, but not tagged. The handling time for tagged beavers was extended due to extra time for attaching and removal of the tag. Based on the available research and literature, it is not likely that the decrease in growth in the tagged individuals is explained by the capture or the extended handling time from tagging.

4.2. Drag

In semi and aquatic animals, body shape is crucial and externally mounted devices can increase drag in both air and water (Casper 2009). The drag of an external tag that an individual has to drag through the water creates a higher rate of energy expenditure, which might result in increased foraging time or a reduction of energy sources (Wilson et al. 1986, Culik and Wilson 1991). In studies related to the effect of drag showed a potential increased drag force of 14% in large seals (Hazekamp et al. 2010) and a 27% in green turtles (*Chelonia mydas*) (Watson and Granger 1998). However, the great cormorant's (*Phalacrocorax carbo*) who is dependent on swimming and diving was not negatively affected before swimming speed increased over 1.5 m/s (Vandeeble et al. 2015). Beavers only reach a speed of 0.8 m/s on the surface (Nolet and Rosell 1994) and 0.6 m/s when swimming underwater (Allers and Culik 1997). Additional, tags are usually above the surface of the water when beavers are swimming, and the beavers spent only 3 % of their active time diving underwater (Graf et al. 2018). In the first full model (tagged beaver only), the number of days was included as an explanatory variable, but was not included as a variable in any of the top-ranked models and was discarded from further analyses. It seems reasonable to believe if drag was an essential factor for the decrease in weight, the "number of days tagged" should be weighted heavier in the analysis. Drag is possibly not contributing largely to the negative effects on beavers. However, the force of potential drag is not investigated due to the lack of data on this matter.

4.3. Thermal balance

Effects of tag attachment on animals' thermal balance were raised as a possibility by McCafferty et al. (2007) in seals. Beavers have to deal with both the terrestrial and aquatic environment and are in an energetically precarious position (Fish 2000). The beaver's fur consists of a protective overlayer of coarse guard hairs and an underlayer of fur-wool (Novak 1987). The fur should work as a thermal barrier in both air and water (Irwing 1973), but its thermal properties may be affected if the fur is damaged or in a poor state. Therefore, beavers groom to waterproof regularly (Wilsson 1971, Walro and Svendsen 1982) and a glued patch will impair their ability to groom that patch. The thermal conductivity of water is 25 times greater than air (Webb and King 1984), and if the glue-on tagging makes beaver fur less waterproof, it may act as a conductor of heat away from the body surface. According to Graf et al. (2016), the tagging and removal of the tag did only affect the guard hairs. However, I have observed both, with the underfur intact and also several occasions where small patches with no underfur remained. This might be associated with excessive amounts of glue, and attachment of the tag too close to the skin that may create burns or irritation. However, both the underfur and guard hair prevent water from penetrating to the skin (Novak 1987). The damaged patch left after removal of the tag regrow within 3 to 4 months (Graf et al. 2016). Thus, the open patch may be a source of further heat loss until the fur is regrown and even a further decrease in body weight. However, according to Graf et al. (2018), this open patch is mostly over the water surface when the beaver is not diving, which might reduce the negative effect compared to other potential locations on the body. Still, heat loss could be a major driving factor, with higher heat losses and energy consumption leading to a decline in beaver growth.

5. Conclusion and future perspective

In this study, I emphasised the importance of using a control group to investigate tagging effects on study animals. A control group may not often be available due to lack of research animals but should be included whenever possible. The possible adverse effect of bio-logging is essential to mitigate in the future, for animal welfare, and to ensure reliable research data. I found a short-term tagging effect, which might have implications regarding animal welfare and the possibility of biased data. These changes might be physiological (Kock et al. 1987, Meyer et al. 2008), and do not necessarily imply behavioural alterations (Graf et al. 2016) or create prolonged effects after the removal of the tag.

The length and extent of the short-term effect on growth found in this study are unknown. Revealing this, requires several re-captures after the removal of the tag the following year, for analysing if growth has normalised or continuing with a negative trend. I would also recommend testing thermal imaging to measure differences in surface temperature following hair damage associated with tag removal to see if this can explain the decline in body growth. Nevertheless, the glue-on tag is a short-term method, and the total loss of body weight is not huge as determined by comparison of total body mass proportion. These factors support the continued use of this method, until other more refined attachments, methods have been developed.

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7. List of tables and figures

Table 1. The model selection result, investigating the body mass difference before and after tagging in a Eurasian beaver population in south-eastern Norway between 2009 and 2016. Beaver ID was included as a random effect. Candidate models were ranked on AICc, and the range of ΔAICc <6 are shown in bold.

Variables*	df	log-likelihood	AICc	ΔAICc	weight
1/3	**5**	**-108.90**	**228.90**	**0.00**	**0.23**
3	**4**	**-110.14**	**229.00**	**0.11**	**0.22**
1/3/4	**6**	**-108.09**	**229.70**	**0.84**	**0.15**
3/4	**5**	**-109.33**	**229.70**	**0.86**	**0.15**
1	**4**	**-111.48**	**231.70**	**2.79**	**0.06**
0	**3**	**-112.72**	**231.90**	**2.98**	**0.05**
1/4	**5**	**-110.51**	**232.10**	**3.21**	**0.05**
4	**4**	**-111.75**	**232.20**	**3.32**	**0.04**
1/2/3	6	-110.85	235.20	6.35	0.01
2/3	5	-112.09	235.20	6.37	0.01
2/3/4	6	-111.27	236.10	7.20	0.01
1/2/3/4	7	-110.03	236.10	7.26	0.01
1/2	5	-113.18	237.40	8.56	0.00
2	4	-114.42	237.50	8.67	0.00
1/3/5	6	-112.23	238.00	9.11	0.00
3/5	5	-113.47	238.00	9.13	0.00
1/2/4	6	-112.24	238.00	9.13	0.00
2/4	5	-113.48	238.00	9.16	0.00
3/4/5	6	-112.65	238.80	9.94	0.00
1/3/4/5	7	-111.41	238.90	10.01	0.00
1/5	5	-114.64	240.40	11.48	0.00
5	4	-115.88	240.50	11.59	0.00
1/4/5	6	-113.66	240.90	11.98	0.00
4/5	5	-114.90	240.90	12.00	0.00
2/3/5	6	-115.38	244.30	15.41	0.00
1/2/3/5	7	-114.14	244.30	15.47	0.00
2/3/4/5	7	-114.55	245.20	16.30	0.00
1/2/3/4/5	8	-113.31	245.30	16.46	0.00
1/2/5	6	-116.30	246.10	17.25	0.00
2/5	5	-117.54	246.10	17.27	0.00
2/4/5	6	-116.60	246.70	17.84	0.00
1/2/4/5	7	-115.36	246.80	17.91	0.00

*0 = Intercept, 1 = Measure (removal tag), 2 = Number of days, 3 = Season, 4 = Sex, 5 = Weight of tag

Table 2. Effect size (β), adjusted standard error (SE), lower (LCI) and upper (UCI) 95 % confidence interval of explanatory variables from the analysis of the difference in body mass in tagged beavers before and after attachment of tag in south-eastern Norway between 2009 and 2016. I performed model averaging of best models (ΔAICc < 6) to estimate the effect size of each variable. The informative parameters are shown in bold.

Variables	Estimate (β)	Adjusted SE	LCI	UCI
Tagged only				
Intercept	**22.607**	**0.631**	**21.370**	**23.843**
Measure (removal tag)	-0.186	0.222	-0.620	0.249
Season (spring)	-1.250	0.987	-3.183	0.684
Sex (male)	-0.169	0.580	-1.306	0.968

Table 3. Model selection result for investigating the difference in growth per day between tagged and un-tagged beavers in south-eastern Norway between 1999 and 2016. Models are ranked based on AICc. Beaver ID was included as a random effect. Candidate models in the range of ΔAICc <6 are given in bold.

Variables*	df	log-likelihood	AICc	ΔAICc	weight
3	**4**	**154.12**	**-299.70**	**0.00**	**0.97**
0	3	148.96	-291.60	8.10	0.02
2/3	5	150.41	-290.00	9.70	0.01
1/3	5	149.16	-287.50	12.21	0.00
2	4	145.27	-282.00	17.70	0.00
1	4	143.42	-278.30	21.40	0.00
1/2/3	6	145.37	-277.60	22.13	0.00
1/2	5	139.75	-268.70	31.02	0.00

* 0 = Intercept, 1 = Age, 2 = Sex, 3 = Tagged

Table 4. Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95 % confidence interval of explanatory variables for the analysis of differences in growth rate per day between tagged and un-tagged beavers in south-eastern Norway between 1999 and 2016. The best model within (ΔAICc < 6) and the estimate of the effect size for each variable. Informative parameters are given in bold.

Variables	Estimate (β)	SE	LCI	UCI
Intercept	0.015	0.005	0.005	0.025
Tagged (Yes)	-0.035	0.007	-0.050	-0.020

Figure 1: Map of the study area in southeast Norway with rives Gvarv, Sauar and Straumen in south-eastern Norway between 1999 and 2016. Black- and grey dots represent GPS positions for some of our tagged beavers (McClanahan 2019).

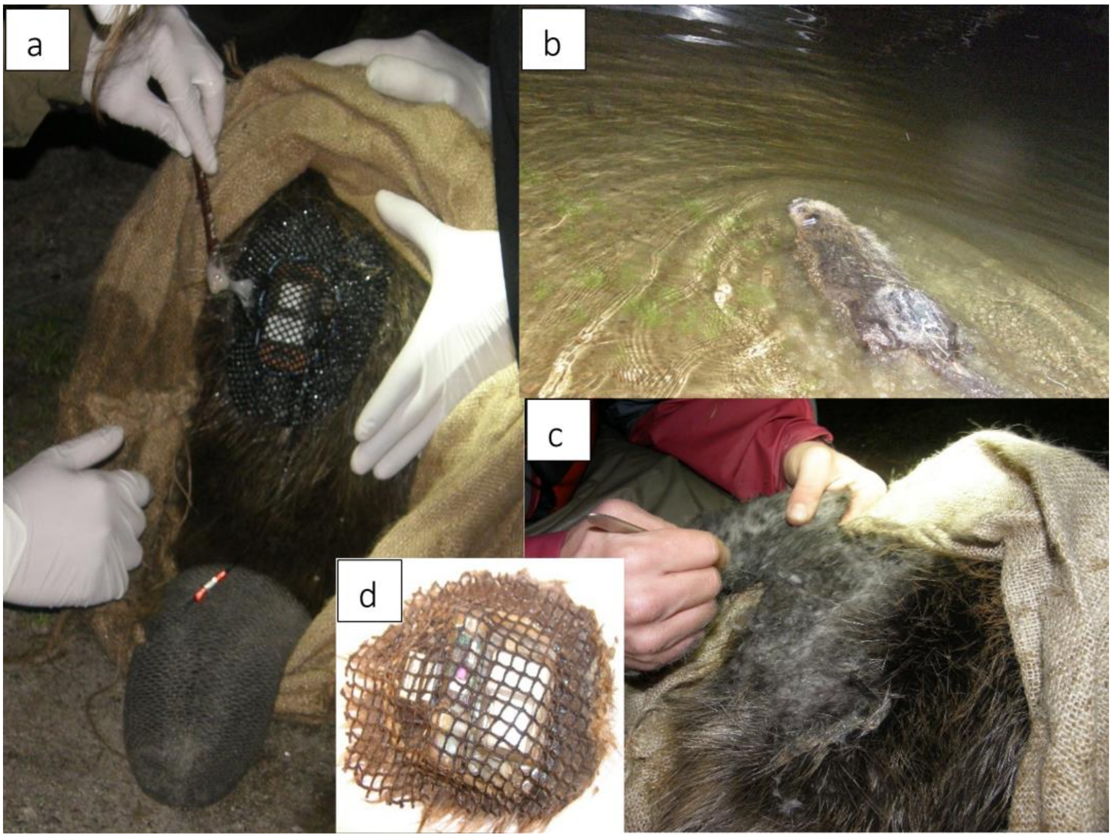

Figure 2a-d: A GPS unit being glued to a beaver's lower back (a) and released after attachment of tag (b). The tagged beaver are re-captured, and the tag was removed with a scalpel (c) and the tag unit retrieved (d) in south-eastern Norway between 2009 and 2016.

Figure 3a-b: Beaver pelt after removal of glue-on tags (a,b), with only guard hairs removed, but the underfur is still intact (a) and patches with both guard hair and underfur removed (b) in south-eastern Norway between 2009 and 2016.

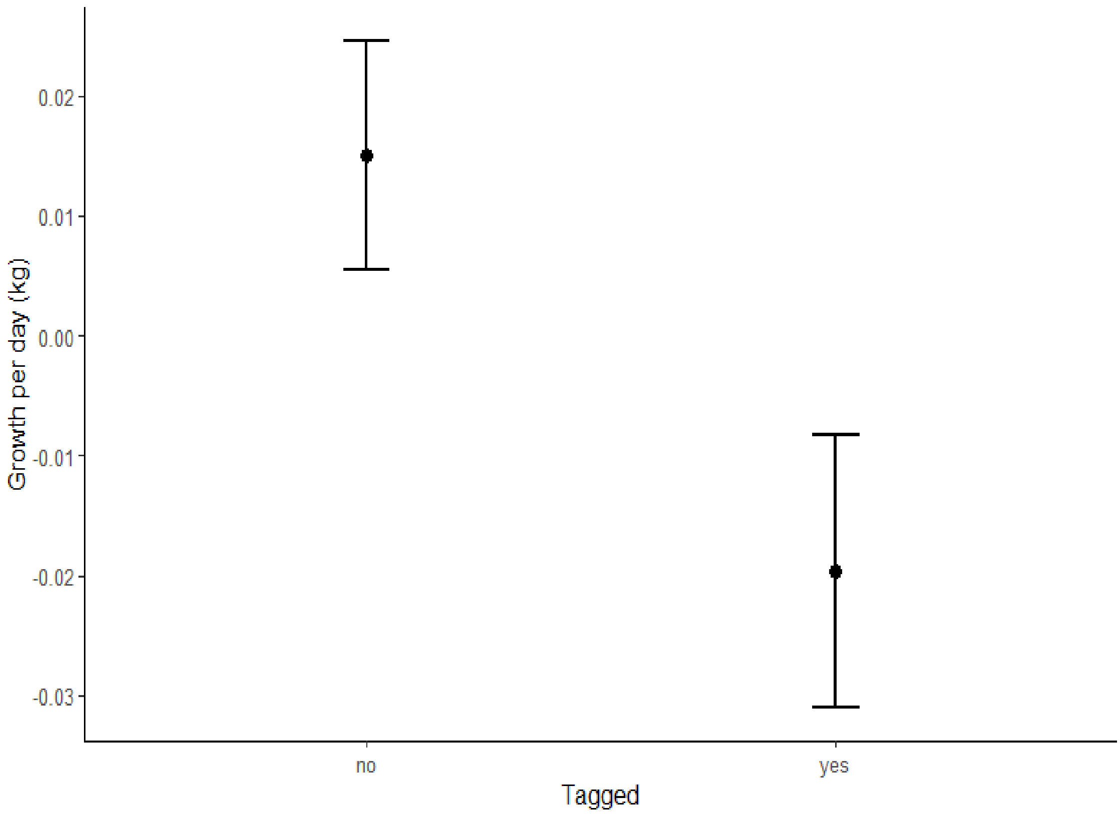

Figure 4: The estimated effect on growth per day (in kg) in tagged (yes) and un-tagged (no) Eurasian beavers in south-eastern Norway between 1999 and 2016.