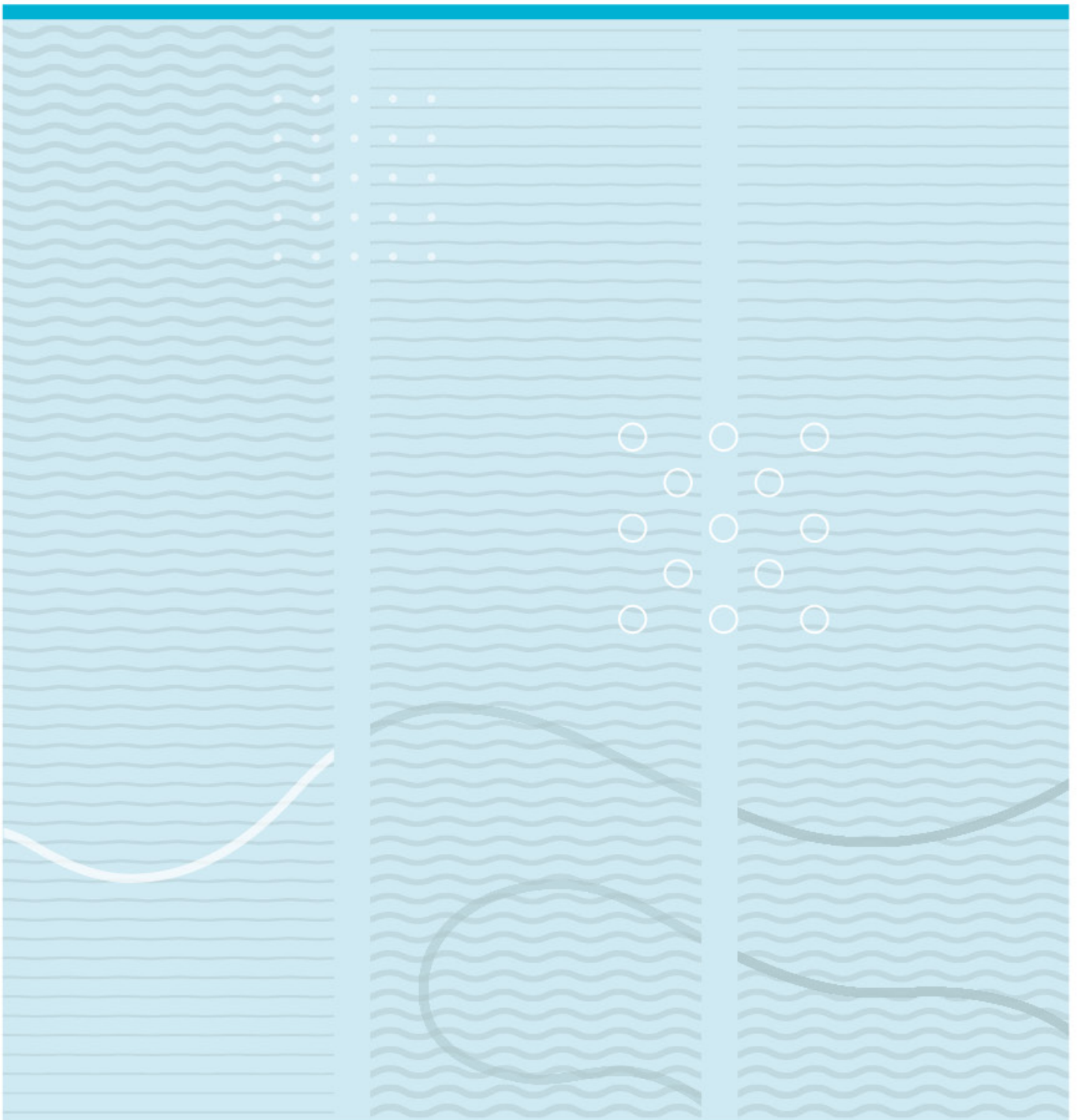Mie Prik Arnberg

The importance of vegetation availability in three scales on body condition, reproduction and territory size of the Eurasian beaver

This thesis is worth 60 study points

Table of content

Abstract

Availability of food resources can affect body condition and reproduction in animal populations as low food availability can lead to decreasing body condition and constrain reproduction. At the same time, spatial distribution and abundance of vegetation can affect movement and space use of animals thus affecting territory size. I quantified territory-specific composition of habitat types and availability of tree and plant (i.e. herbs, grasses and saplings) communities in ten beaver (*Castor fiber*) territories along two rivers in Telemark county, Norway during the summer of 2018. Further, I investigate the effect of vegetation availability within territories on body condition, reproduction and territory size of the beavers. Males and females showed a sex-dependent response in body condition to availability of vegetation. The body condition of females was positively influenced by increasing forest cover and abundance of deciduous trees and negatively influences by increasing grassland cover within a territory while males remained largely unaffected. No scale of vegetation availability impacted reproduction of the beavers and reproduction were rather influenced by previous reproduction, maternal age, and family density. Beavers adjusted territory size to avoid resource depletion as they had increasing territory size when abundance of larger deciduous trees increased. Sex-dependent differences in food selection by monomorphic species, such as the beavers, have been little explored. Further, beaver's capital breeder behavior and the impact of temporal nutrient variation in forage species, deserves more attention in the future to better understand factors controlling body condition and reproduction in beavers.

Keywords: Body condition, reproduction, territory size, vegetation availability, beaver, *Castor fiber*

Acknowledgements

Introduction

All animals require food as a source of energy. Optimal foraging theory dictates that animals choose an optimal diet to maximize their net energy intake per unit of time (Emlen, 1966; MacArthur & Pianka, 1966). An animal's optimal diet is dependent on factors such as searching time, handling time, eating expenses, and digestive constraints and animals adopts a foraging strategy that provides the most energy for the lowest cost (Schoener, 1971; Collier & Rovee-Collier, 1981). For instance, variation in food availability affect a forager's decision to be selective or opportunistic to maximize their net energy intake creating a continuum from broadly-generalist to highly-specialized species (Rosenzweig, 1981; Stephens et al., 2008; Shipley et al., 2009).

According to optimal foraging theory, animals can be described as energy maximizers if their fitness increases with greater resource consumption (Schoener, 1971; Pyke et al., 1977). Energy maximizers can go beyond daily satiation needs, such that the excess energy and nutrients obtained from foraging can positively affect body condition and reproductive success (Kotler et al., 2007; Gallant et al., 2016). For example, brown bears (*Ursus arctos*) display a positive correlation between bilberry (*Vaccinium myrtillu*s) abundance and both autumn weights of female bears and spring weights of yearling bears (Hertel et al., 2018). Contrarily, animal body condition and reproduction may decrease when faced with foraging constraints and nutritional stress (Kaji et al., 1988; Kitaysky et al., 2007; Tveraa et al., 2013). Kitaysky et al. (2010) found that restricted food availability negatively affected reproduction in black-legged kittiwakes (*Rissa tridactyla*). One strategy to ensure a stable access to sufficient food resources is to establish a territory (Maher & Lott, 1995).

Territorial animals defend areas to gain exclusive access to benefits such as food resources, shelter, or water bodies (Gill & Wolf, 1975; Maher & Lott, 1995). Defending a territory is energetically costly as it is associated with patrolling, risk of injury, and missed opportunities of foraging (Amsler, 2010; Mares et al., 2012). Thus, territory size can be negatively correlated with food abundance and competitor density (Hixon, 1980; Brown, 1964; Dunk & Cooper, 1994; Owen-Smith et al., 2010). In addition, when the temporal variation in food availability is predictable, animals can adjust their territory boundaries to account for seasonal food resources, which can ultimately result in smaller average territories (Owen-Smith et al., 2010; McClintic et al., 2014;). The inverse relationship between food abundance and temporal variability ensures territories are as large as necessary, but as small as possible, creating an optimal territory size. At the same time, the heterogeneous spatial distribution or patchiness of food resources may also effect movement and space use of animals (Mueller & Fagan, 2008).

The resource dispersion hypothesis (RDH) suggest that the negative correlation between food abundance and territory size may be invalid because larger areas are needed to include the spatial variability of resources (Johnson et al., 2002). For instance, habitat fragmentation has been shown to increase average home range sizes of eastern wild turkeys (*Meleagris gallapovo silvestris*) (Marable et al., 2012) and male meadow voles (*Microtus pennsylvanicus*) (Collins & Barrett, 1997). Variation in territory size may also lead to an unequal distribution of resources among territories with consequences for differential rates of growth and reproduction, disregarding the driver of territory size (Adams, 2001). Beavers (*Castor* spp.) are highly territorial energy maximizers (Gallant et al., 2016) that are appropriate study animals to examine how resource availability within a territory affects body condition, reproduction and territory size in a population.

The beaver genus consists of the North American beaver (*C. canadensis*) and Eurasian beaver (*C. fiber*). The two species have a nearly complete niche overlap (Parker et al., 2012) with very similar life history, ecology and behavioral traits (Danilov et al., 2011a, 2011b; Parker et al., 2012; Danilov & Fyodorov, 2015). Both are obligate monogamous (but see Crawford et al. (2008)) and form long-lasting bonds between breeding pairs (Wilsson, 1971; Svendsen, 1989; Mayer et al., 2017). They live in family groups consisting of one breeding pair, kits, yearlings, and possibly one or more sub-adults (Wilsson, 1971; Müller-Schwarze & Schulte, 1999; Campbell et al., 2005). Family groups maintain their territories through scent marking (Rosell, 2002) and direct aggression against intruders, making beavers highly territorial group-living animals (Aleksiuk, 1968; Graf et al., 2016a). Beavers display little sexual dimorphism and adults of both sexes exhibit similar behavior (Sharpe & Rosell, 2003; Steyaert et al., 2015) though differences exist. For instance, males tend to defend slightly larger territories (Herr & Rosell, 2004) and more frequently deposit scent mounts (Rosell & Thomsen, 2006).

Beavers are central place foragers and alter their foraging intensity and preference with distance from their central place (i.e. the water or their lodge) (Orians & Pearson, 1979; Haarberg & Rosell, 2006; Raffel et al., 2009). Beaver travelling and handling time of forage items increase with increasing distance from their central place (Fryxell & Doucet, 1991), which affects the beaver's choice of foraging patch as well as species and size of forage items (Belovsky, 1984; ; McGinley & Whitham, 1985; Gallant et al., 2004; Haarberg & Rosell, 2006). Central place foraging combined with territoriality means beavers are relatively sessile when searching for food, such that they rarely travel farther than 50 meters from the water when foraging on land (Graf et al., 2016a).

Beavers prefer to forage in forests with high availability of deciduous trees (Hartman, 1994; Pinto et al., 2009; Steyaert et al., 2015), mires, and vegetation patches along roadsides (Steyaert et al., 2015) and avoid anthropogenic lands (i.e., fallow land, arable land, pastures, and urban area

(Hartman, 1996; Zwolicki et al., 2019). Though some studies have examined habitat selection by beavers across heterogeneous landscapes (Steyaert et al., 2015; Zwolicki et al., 2019) most studies have focused on single ecosystem types like the riparian zone (Nolet et al., 1994; Haarberg & Rosell, 2006) or deciduous forest (Breck et al., 2001; Pinto et al., 2009). Thus, only describing narrow ranges of food availability and habitat selection. Hartman (1996) highlights that habitat selection by beavers in populations near carrying capacity may give little information about quality or preference of habitat. Instead, it can yield information on the full range of potential habitats beavers use and which habitats are usable for long-term occupation. Potential habitats are important to consider as beavers in high density populations will expand into suboptimal anthropogenic influenced habitats (Nolet & Rosell, 1998; John et al., 2010; Zwolicki et al., 2019).

Being a generalist herbivore, beavers use a wide variety of plant types (e.g. trees, shrubs, herbaceous plants like grasses, forbs and ferns and aquatic vegetation) and consume many different species within these groups (Svendsen, 1980; Ganzhorn & Harthun, 2000; Krojerová-Prokešová et al., 2010; Bełżecki et al., 2018). Beavers are considered opportunistic as their foraging behavior varies with availability, nutrient content and digestibility of foraging items (Doucet & Fryxell, 1993). They will choose the food item or foraging patch providing them the highest energy intake over time (Belovsky, 1984; Doucet & Fryxell, 1993; Gallant et al., 2016). The diet also varies throughout the year as beavers during the winter rely on woody vegetation and supplement their diet with herbaceous and aquatic vegetation through the summer (Svendsen, 1980; Elmeros et al., 2003; Gallant et al., 2016; Bełżecki et al., 2018).

The majority of research on beaver foraging has emphasized their use of woody species (shrubs and trees) because foraging on woody plants leaves unmistakable marks such as gnawed bark and stumps (Haarberg & Rosell, 2006). Trees are often rich in energy content, and beavers generally prefer deciduous trees such as willows (*Salix spp.*), aspen (*Populus sp.*), rowan (*Sorbus aucuparia*) and birches (*Betula spp.*), and generally avoid coniferous trees (Nolet et al., 1994; Fustec et al., 2001; Haarberg & Rosell, 2006; Vorel et al., 2015). Despite the biased focus on beavers' use of woody plants, herbaceous plants are also a vital part of the beaver diet as they provide a substantial source nutrients (Nolet et al., 1995),

Body mass and tail size are used as body condition indicators in beavers and varies as a result of seasonal deposition and depletion of fat (Aleksiuk, 1970; Smith & Jenkins, 1997). Beavers body condition generally decreases during winter and spring when foraging options are restricted and increases during autumn (Aleksiuk & Cowan, 1969). Body condition also varies between years and families which have been suggested to occur as a consequence of differences in food availability

(Smith & Jenkins, 1997; Breck et al., 2001). Fat accumulated during summer and autumn prior to winter breeding is an important determinant of reproduction (Wigley et al., 1983; Parker et al., 2017).

At northern latitudes, beavers mate from late January to early March, peaking around mid-February (Wilson, 1971). Gestation time is 104–111 days (Hediger, 1970; Doboszynska & Zurowski, 1983) with parturition peaking usually around mid-May (Doboszynska & Zurowski, 1983; Parker & Rosell, 2001; Parker et al., 2017). The lactation period lasts approximately three months (Zurowski et al., 1974). High food availability and quality have shown to positively impact on reproductive success (Campbell et al., 2012; Campbell et al., 2013) (but see Campbell et al. (2005)).

Though a growing body of research has explored beaver demography in relation to food availability, many studies have used climatic variables as a proxy for food availability or assessed territory quality on a coarse scale as cover or density of deciduous trees. Further insight is needed regarding how habitat and food availability affects beaver demography in a heterogeneous landscape (Gallant et al., 2016). Food availability and spatial distribution of resources might also influence territory size as beavers in areas dominated by less preferred forage items and poorer quality habitats tend to hold larger territories (Fustec et al., 2001; Havens et al., 2013). However, in populations at carrying capacity, beavers have been found to hold lager territories with increasing habitat quality independent of family size (Bergerud & Miller, 1977; Campbell et al., 2005).

Here I examine changes in adult body condition of male and female beavers, and changes in reproductive probability and success (litter size) in relation to territory-specific composition of habitat types and availability vegetative communities. Further, I explore how territory sizes are affected by the abundance, temporal variability, and heterogeneous spatial distribution of vegetation.

Materials and methods

Study area

This study was conducted within ten established beaver territories along the Gvarv and Straumen river systems in Sauherad and Nome municipalities in South-Eastern Norway. The Straumen river is a part of the Telemark canal and the section used in this study is bound at each end by channel locks and weirs. The Gvarv river is less restricted, and the study area is located at the lower part of the river and includes the northwestern portion of Lake Nordsjø. Channel width varies from 10 - 100 m and both rivers have regulated water regimes (Haarberg & Rosell, 2006; Graf et al., 2016a). There

are no beaver dams in the study area as both rivers are either too large for beavers to dam or are already deep enough to make damming unnecessary (Hartman & Törnlöv, 2006), though there are some dam building activities in smaller side rivers.

The meandering rivers run through an alternating landscape comprised mainly of agricultural land and boreal forest communities, generally either deciduous communities dominated by birch, grey alder (*Alnus incana*), and aspen (*P. tremula*), or coniferous communities dominated by Scots pine (*Pinus sylvestris*) and Norwegian spruce (*Picea abies).* The forests and agricultural habitats are interspersed with rural human development areas, grass-dominated meadows, mires and pastures, and riparian woodlands comprised of black alder (*Alnus glutinosa*)*,* bird cherry (*Prunus padus),* and willow. The area has a mean annual temperature of 4.6 °C and annual precipitation of 790 mm (Campbell et al., 2012).

Beavers have been in the area since the 1920s (Olstad, 1937) and have been at carrying capacity for the last 13 years (Campbell et al., 2005; Steyaert et al., 2015) with low risk of predation (Rosell & Sanda, 2006) and hunting (Graf et al., 2016a).

Data collection

Study animals

The ten territories, used in this study, have been monitored on a yearly basis as part of an extensive live-trapping research program on-going since 1997 (Campbell et al., 2012; Campbell et al., 2017). Beavers were caught on a regular basis from motorboats using hand-nets following the capture and handling protocol of Rosell and Hovde (2001). At each capture, they were measured, weighed and sampled to track known individuals; new additions were microchipped and ear-tagged for individual identification. A subset of beavers was equipped with VHF transmitters, GPS devices and tri-axial accelerometers to track movement patterns (Herr & Rosell, 2004; Steyaert et al., 2015; Graf et al., 2016a; Graf et al., 2016b; Mayer, et al., 2017). I used territory-specific reproductive observations and individual measurements of morphometric data (e.g. body size, tail length and thickness) in addition to movement patterns, age, sex, and social status of adult beavers (> 3 years) collected between 2010 and 2018 by the monitoring program.

Body condition

I used data from 113 beavers (53 females and 60 males). Most beavers were captured in the spring (n = 70), but I also used captures from the summer (n = 21) and autumn (n = 22) (Table 1). Of the 53

females, 38 were dominant and 16 of those had a successful reproduction in the year they were sampled. It is possible that some of the other 22 dominant females were pregnant but reabsorbed their fetuses or had kits that did not survive long.

The tail fat index developed by Parker et al. (2006) was used as an index of beaver body condition. The index is the ratio of tail size (seasonally variable) to body length (seasonally stable) and was calculated using the formula:

$$I = \frac{(A \times B)}{C}$$

where A was tail length (measured midline from the tail tip forward to the hair line), B was tail width (measured at tail length midpoint with a caliper), and C was body length (measured ventrally from nose tip to tail base). Larger I values indicated higher tail fat content and better body condition.

Reproduction

I estimated yearly reproduction in the timespan of 2010 – 2017 for the Gvarv and Straumen river (n = 80) as kits trapped within the sampling year in addition to yearlings trapped in the following year not trapped as kits previously as those yearlings were part of the litter from the previous year. Observations of reproduction were used as a binary response to estimate probability of reproduction i.e. the reproductive probability of a dominant pair in a given year. To elaborate on the reproduction response to vegetation availability, I further used annual observations of reproductive success (litter size) for dominant pairs (Campbell et al., 2013; Campbell et al., 2017).

Territory size

Territory size was estimated using 4856 GPS positions from 18 adult beavers (11 females and 7 males) during May to September in 2014 – 2018 (Table 2). Territory size was estimated using movement patterns determined by GPS positions from tracked beavers. All positions with horizontal dilution of precision (HDOP) values >5 were removed as well as any positions fixed with fewer than four satellites to improve spatial accuracy. Extreme outliers of more than 100 m to other positions (indicating expeditions into other territories) were removed as well. Using the GPS positions, I estimated the 95% kernel home range with the *R* package adehabitatHR (Calenge, 2011). I used the same territory estimates for all years as territory borders in the study area change little over time and dominant individuals tend to stay within the same area (Campbell et al., 2005).

Vegetation sampling

I estimated vegetation availability within each territory from late July until mid-September 2018. The survey area was restricted to each territory and within a buffer zone of 50 meters perpendicular to the shoreline, in which only terrestrial vegetation was sampled. In ArcMap, a list of 300 random sampling locations with a minimum of 20 m from each other were generated within each territory. The first 40 sampling locations listed for each territory were located with a handheld GPS (Garmin Etrex 30x) down to the 0-point. At the sampling locations vegetation was recorded in three scales;

Habitat type: At each sampling location, a circular main plot with a 10-meter diameter was placed out with the center in the 0-point. I recorded the percent cover of several habitat types (forest, agricultural land, mire, meadow, pasture, garden, rural development, and fallow land) within the main plot.

Tree layer: Tree species > 2 m in height and > 2 cm in diameter present within the main plot were counted and diameter at breast height (dbh) measured.

Field layer: At the center of the main plot a subplot of 1x1 m was placed out with the left corner facing north. Within the subplot, I recorded the percent cover of vascular plants species (i.e. trees < 2 m in height and herbaceous plants).

Consumption of aquatic plants vary between populations as it is infrequently utilized in some areas (Krojerová-Prokešová et al., 2010; Bełżecki et al., 2018) while being heavily utilized in others (Simonsen, 1973; Milligan & Humphries, 2010; Severud et al., 2013). The discrepancy is presumably caused by their availability in an area. I did not include aquatic vegetation in this study as amount aquatic vegetation was relatively low in all territories within the study area.

Habitat composition was sampled within 378 main plots across the ten territories with a mean ± SD of 37.80 ± 1.62 plots per territory (range: 35 – 40). All values are given hereafter are mean ± SD unless otherwise stated. Trees were present in 166 of the main plots meaning the tree layer was sampled in 16.60 ± 8.15 plots per territory (range: 7 – 32), while the field layer was present in 339 subplots, 33.90 ± 8.15 plots per territory (range: 29 – 39).

Data analysis

Vegetation availability

Greater land cover diversity within territories indicates greater patchiness and often greater levels of habitat fragmentation (McClintic et al., 2014). Habitat type diversity within beaver territories was

calculated using the Shannon diversity index formula:

$$SH = \sum_{i=1}^{n=8} -p_i \ln p_i$$

where p_i is the proportion of the ith habitat type in a territory (McClintic et al., 2014; Tramer, 1969). Greater Shannon diversity index values indicated more vegetation patches within beaver territories. The habitat types shrub and fallow land generally had low occurrence and showed little variation between territories, and were therefor excluded from further analysis on vegetation availability. Mire, meadow, and garden also showed little variation between territories, but since those were grass-dominated habitats they were combined into the habitat type grassland (Figure A1).

I divided trees into two groups (deciduous trees and coniferous trees), which have frequently been used to estimate habitat quality for beavers (Steyaert et al., 2015; Gallant et al., 2016; Campbell et al., 2017). The tree layer thus summarized abundance and size of deciduous and coniferous trees.

Plant species are spatially aggregated in communities in response to environmental gradients (Gentry, 1988; Santoro et al., 2012), and herbivores generally encounter food within these patches of clustered plants (Owen-Smith et al., 2010). To identify important plant communities in the field layer, environmental gradients were examined from the presence and absence of species in sampled field layer plots using non-metric multidimensional scaling (NMDS) with three axes, applying the *R* package Vegan 2.5-3 (Oksanen et al., 2018). All plots in agricultural land and plots with < 3 species present along with rare species occurring < 3 times in the whole data set, were removed to avoid total separation of agricultural plots from natural plots and to obtain model convergence. When agricultural plots and rare species had been excluded the NMDS included 175 plots comprising 104 different plant species. Each plot and species was assigned three NMDS scores (i.e. environmental gradient value) which could be retraced to the plants registered within them.

Body condition

I investigated the relationship between body condition (i.e. tail fat index) and vegetation availability across the three scales habitat type, tree layer and field layer with linear mixed effect models (LMMs) using the *lmer* function in the *R* package *lme4* (Bates et al., 2015). I constructed a separate global model for habitat type, tree layer and field layer to assess the most important predictors in each. Some beavers were sampled multiple times (2.26 ± 1.48) over the study period and seven beavers were measured twice in the same year. I accounted for variations between years and possible

pseudoreplication by including year as a random variable. Beaver ID could not be included as a random variable without overfitting the models. To control for differences between sex and seasons, both were included as fixed effects and as interactions with each of the vegetation predictors. Family size and age were included as control variables, with a potential for a quadratic (non-linear) relationship between body condition and age (Table 3). Due to collinearity between the habitat types forest and agriculture (r = 0.756), I modelled the impact of these two habitat types in separate global models in which habitat type 1 contained cover of agricultural land and habitat type 2 contained cover of forest (Table 3).

Reproduction

Reproductive probability

The probability that the dominant pair in a given territory and year would reproduce was modelled in global models for habitat type, tree layer, and field layer using generalized linear mixed effects models (GLMMs), with a binomial error structure using the *glmer* function in the *R* package *lme4* (Bates et al., 2015). To account for variation between territories and between years, both were included as random variables. Reproduction in the previous year (yes/no), study site (the Gvarv and Straumen river), family size and maternal age elevated model performance, and were included as control variables (Table 3).

Reproductive success

The modeling process for evaluating the reproductive success (litter size) of dominant beaver pairs in a given year resembled that of reproductive probability. The response variable reproductive probability was replaced with reproductive success, and the control variable reproduction in the previous year was replaced with reproductive success in the previous year (Table 3). Litter size ranged from 0 – 4 and GLMMs with Poisson error structures were used with the *glmer* function in the *R* package *lme4* (Bates et al., 2015).

Territory size

Although I used multiple plots to describe vegetation availability across the three vegetation scales, I only had one measure of territory size for each territory, which caused problems for developing models. To have a working, validated model I averaged the vegetation data from the surveyed plots (cover of habitat types, abundance and diameter of coniferous and deciduous trees, and field layer gradients) for each territory, resulting in one estimate per predictor. Harrell Jr (2015) states that to

adequately detect effect sizes with reasonable power, one needs 10-20 observations of the response variable per parameter (covariate) estimated. To comply with this recommendation, I fit the averaged vegetation availability predictors and the habitat type diversity index values individually as separate candidate models, and included a null model for each scale of vegetation availability. Due to the low sample size I included no random or control variables and ran the candidate models as linear regressions (LMs) using the *lm* function from the *R* package *lme4* (Bates et al., 2015).

Model selection

I explored which explanatory variables across the three scales of vegetation availability were the best predictors of body condition and reproduction by using the *dredge* function from the *R* package MuMIn (Bartoń, 2018). The dredge fit all possible combinations of the explanatory models including a null model and ranked them according to Akaike information criterion controlling for small sample sizes (AICc). I retained only models within ΔAICc < 2 of the single most supported model (lowest AICc) in the top model sets, as these are considered equally supported by the data (Burnham & Anderson, 2002). To combine the two global models for habitat type into one top model set, I used the best models (ΔAICc < 2) from habitat type 1 and habitat type 2. I then evaluated the best models using the *model.sel* function from the *R* package MuMIn (Bartoń, 2018), and retained only models with a ΔAICc < 2 from the most supported model. The candidate models predicting territory size from across three scales of vegetation availability and habitat diversity were evaluated according to AICc using the *model.sel* function from the *R* package MuMIn (Bartoń, 2018).

I used Akaike weight-based averaging to average the estimates for the top model sets separately for the analysis of body condition, reproduction and territory size. Then I calculated the 95 % confidence intervals (CIs) for the retained predictors. Predictors that included zero within their 95 % CIs were considered uninformative (Arnold, 2010). All data analysis was performed in R version 3.4.1(R Core Team, 2017).

Results

Vegetation availability

Habitat types varied greatly between territories. Three territories were highly influenced by anthropogenic use and were comprised of more than 50 % agricultural land, while agricultural land was absent in two territories. Forest cover tended to increase with a decreasing amount of agricultural land

cover. Forest cover and could account for over 75 % of a territory in territories without agricultural land, but only constitute 10.50 % when agricultural land was present (Figure 1).

Abundance of deciduous trees varied from 2.28 ± 7.60 to 0.44 ± 0.96 trees per plot while abundance of coniferous trees varied from 6.38 ± 8.18 to 0 trees per plot (Figure 2A). The size of available deciduous and coniferous trees also differed among territories. The largest mean diameter of coniferous trees was 16.43 ± 7.66 cm in contrast to 6.84 ± 7.45 cm as the smallest (Figure 2B).

Plant species in the field layer were ordered along the three axes NMDS 1-3. NMDS 1 illustrated a soil moisture gradient, from very moist to dry soil conditions (Figure A2). The NMDS 2 was gradient displayed the human impact (or disturbance) on the vegetation from activities such as pasture cultivation. The undisturbed end of the gradient retained shaded conditions with canopy cover and natural soil conditions, which decreased towards the disturbed end where sun exposure with heavily processed soil conditions prevailed (Figure A2). NMDS 3 had a wet flushing gradient, which is characterized by a high water content in the soil. It differs from the soil moisture gradient by supplying a constant seepage of water at a relatively stable temperature, and has greater oxygen, mineral, and nutrient concentration that ultimately support different plant comminutes (Økland & Eilertsen, 1993) (Figure A2).

Body condition

Males had a higher average tail fat index than females (4.24 ± 0.30 and 3.99 ± 0.28, respectively). For both sexes the tail fat index varied seasonally with the highest values in autumn (4.24 ± 0.33), lowest in the summer (4.02 ± 0.27), and intermediate values in spring (4.12 ± 0.31) (Table 1; Figure 3).

For the models evaluating tail fat index in relation to habitat type availability, the interaction of forest and grasslands with sex were important predictor variables (Table A1). Increasing forest cover had a negative effect on male tail fat index, but had a positive effect on female tail fat index (Table 4, Figure 4A). The tail fat index response to grassland cover was reversed, where greater grassland cover was negatively correlated with female tail fat index but had no effect on males (Table 4, Figure 4B).

When predicting body condition from vegetation availability in the tree layer, the top models included the interaction between abundance of deciduous trees and beaver sex as a highly-supported predictor variable (Table A2). Increased abundance of deciduous trees was correlated with greater female tail fat index, but correlated with a lower tail fat index for males (Table 4, Figure 5). The abundance of coniferous trees, and diameter of coniferous and deciduous trees were also included in

the top model set, but were less supported predictor variables (Table A2) and had no effect on tail fat index (Table 4).

None of the explanatory vegetation variables from the field layer had an impact on tail fat index in beavers. The NMDS 3 gradient was not included in the top model set, and while both NMDS 1 and 2 and their interactions with sex and season were included in the top model set, all 95 % CIs spanned zero (Table A3, Table 4). Rather, the control variables explained most of the variation in beaver tail fat index (Table 4).

Variation in tail fat index was not dependent on family size in any models but the quadratic effect of age showed an increase in tail fat index until the age of nine, and decreased thereafter (Table 4). Sex and season both influenced tail fat index in models linking tail fat index to vegetation availability in the tree layer and field layer. Males had higher tail fat index than females and was higher in the autumn compared to spring and summer but were uninformative when linking availability of habitat types to tail fat index (Table 4). Variation in tail fat index was best explained by availability of habitat types as the top model for tree layer and field layer had a ΔAICc > 9.735 from the top model of habitat type (Table A1-A3). Thus, the superior predictor habitat type might have masked the effect of sex and season.

Reproduction

The dominant pairs reproduced in an average of 3.50 $\pm$ 1.18 years (range: 2 – 5 years), and territories in the Gvarv and Straumen river had a similar yearly reproductive probability (0.63 $\pm$ 0.91 and 0.63 $\pm$ 0.89 kits per year, respectively). The probability of reproduction in a year averaged 0.41 $\pm$ 0.16 (range: 0.25 – 0.63) while the reproductive success (litter size) averaged 2.10 $\pm$ 0.99 kits (range: 0 – 4) (Table 5).

Reproductive probability

Vegetation availability in the three scales habitat type, tree and field layer had no effect on reproductive probability after controlling for reproduction in the previous year, family size, and maternal age (Table 6). From the global models, only grassland and forest habitat types were retained in the top model sets, but both had low support as predictors of reproductive probability (Table A4) and were uninformative (Table 6). Within the top model sets for habitat type, tree and field layer, the control variables were strong predictors of reproduction probability (Tables A4 – A6). Reproduction during the previous year reduced the probability that a beaver pair would reproduce again the following

year, while increasing family size and maternal age increased the probability of reproduction (Table 6).

Reproductive success

Modeling reproductive success from vegetation availability yielded similar trends as reproductive probability. None of the vegetation predictors influenced reproductive success after controlling for reproduction in the previous year, family size, and maternal age (Table 7). From the top model sets, predicting reproduction success only diameter of coniferous trees was retained with low support as a predictor (Table A5), and were uninformative (Table 7).

The control variables (reproductive success in the previous year, family size, and maternal age were highly supported predictors of reproductive success at all three vegetation scales (Table A4 – A6). Reproductive success in the previous year was correlated with smaller litter sizes the following year, similar to the effect on reproductive probability. However, litter sized tended to decrease with greater maternal age and larger family size (Table 7).

Territory size

Territory size varied greatly between territories (0.85 ± 0.52 km^2). Nordsjø 1 (1.69 km^2) was the largest territory, and was approximately 6 times larger than Lunde 3 (0.28 km^2), the smallest territory (Table 2). Regarding habitat types, agricultural land cover was the most supported predictor variable (Table A7). However, it only had a marginal negative effect on territory size (Table 8). Diversity of habitat types within a territory and the field layer communities were not important predictors of beaver's territory size, with the greatest support for the null models (Table A7). Rather, a greater variation in territory size was explained when modeled using explanatory variables from the tree layer.

From the candidate models including the tree layer predictors, diameter of deciduous was the most supported model (Table A7) and was a better predictor of territory size than agricultural land cover (ΔAICc = 5.83). Territory size was positively correlated with average deciduous tree diameter in a territory (Table 8, Figure 6).

Discussion

Food availability may impact body condition and constrain reproduction in animal populations as low food abundance can induce nutritional stress and low energy gain (Massei et al., 1996; Kotler et

al., 2007; Kitaysky et al., 2010;). At the same time, spatial distribution and abundance of vegetation can affect territory size as animals encompass needed food resources within their territory (Owen-Smith et al., 2010; McClintic et al., 2014). I found that vegetation availability affected body condition and territory size of beavers. Habitat type and tree abundance were the most important predictors while vegetation in the field layer had no effect. Reproduction in the study area was not affected on vegetation availability, but was rather dictated by past reproduction, maternal age and family size.

Body condition

The seasonal fluctuations of body condition in this study were similar to previous studies on beavers (Aleksiuk & Cowan, 1969; Aleksiuk, 1970). However, body condition increased until the age of nine and decreased hereafter, showing signs of senescence which is commonly seen in other mammals (Proffitt et al., 2007; Nussey et al., 2011; Tafani et al., 2013). Increasing forest cover had a negative effect on body condition of males, while it had a positive effect on females. Females had better body condition with increasing abundance of deciduous trees within their territory, while males remained unaffected. At the same time, increasing grassland cover had a negative effect on body condition of females while males were unaffected. The sex-dependent response in body condition suggests that male and female beavers need or prefer different food items, despite displaying similar habitat selection (Steyaert et al., 2015).

No previous studies on beavers have found that forage availability affect body condition of beavers (Campbell et al., 2012; Severud et al., 2013). Possibly because of a too course division of forage vegetation and not considering sex-specific effects. Bełżecki et al. (2018) found that male and female beavers select different food items as stomach content varied between the sexes. Although both sexes favor deciduous tree species, females ate more deciduous shoots and tree leaves during summer and autumn compared to males (Bełżecki et al., 2018). The increased dependence of deciduous trees is congruent with the findings in this study as females benefitted from increased abundance of deciduous trees. However, other studies have found the diet of both sexes to consist mainly of the same vegetation with no discernable differences (Roberts & Arner, 1984; Krojerová-Prokešová et al., 2010).

Beavers often select against the habitat type grassland (Hacker & Coblentz, 1993; Francis et al., 2017). Possibly because beavers have a reduced ability to digest grasses (Krojerová-Prokešová et al., 2010). Beavers vary their diet depending on nutrient content and digestibility (Doucet & Fryxell, 1993) selecting food items that give them the greatest return of energy (Gallant et al., 2016).

Ganzhorn and Harthun (2000) found that beavers preferable foraged on vegetation with a lower concentration of fiber compared to surrounding vegetation. The grass species included in their analysis, had a higher fiber content than average fiber content of non-food items. Further, grasses contained a high amount of fiber compared to the fiber content in bark and tree leaves of preferred tree species measured in other studies (Nolet et al., 1994).

The majority of studies on sex-dependent differences in habitat use and forage selection have concerned sexually dimorphic species such as ungulates (King & Smith, 1980; Mooring et al., 2005; Loe et al., 2006). Larger bodied males with proportionally larger digestive tracts might be better equipped to digest forage as a larger digestive tract prolongs retention time and increases digestive capacity, making males highly efficient at extracting energy from fiber. At the same time, a large digestive tract is poorly equipped to digest forage of too high a quality. Hence, food quantity is expected to be favored over food quality for sexually dimorphic males. Smaller females with proportionally smaller digestive tracts may therefore be less efficient in digesting forage. Thus, selecting food quality over quantity (Barboza & Bowyer, 2000; Main et al., 1996; Ruckstuhl & Neuhaus, 2002; Bowyer, 2004). Sex differences in the foraging ecology of monomorphic species such as the beaver, on the other hand, are poorly understood (Ruckstuhl & Neuhaus, 2000; Kwieciński et al., 2017). Ruckstuhl and Neuhaus (2002) suggested that in monomorphic species, males and non-reproductive females should select the same quality forage as they have similar energetic needs and digestive capacity. Bełżecki et al. (2018) also found the digestive tract to be similar between male and female beavers. Still, I found different response in body condition to vegetation availability for males and females, which could suggest that differences still exist between the sexes.

Beavers behavior are in accordance with the behavioral theory of monogamous species (Kleiman, 1977), but certain sex differences persist (Magurran & Garcia, 2000) related to the cost of reproduction. Reproduction is energetically costly as both gestation and lactation exert substantial energy demands on the mother (Gittleman & Thompson, 1988; Oftedal, 2008). Capital breeders, such as the beaver, acquire resources in advance and depend upon stored reserves for reproduction (Jönsson, 1997). It may take them one non-breeding season or more to store the resources needed for future reproduction in the form of body fat (McNamara & Houston, 2008). Indeed, reproduction in this study was negatively influenced by reproduction in the previous year, similar to findings by Ruusila et al. (2000) and intermittent years of non-breeding occurred in all territories within the study area. Due to reproduction in the current or previous years, female beavers might require more food resources than males and therefore be more vulnerable to digestive constraints of plants. For females, grassland may not hold energy sufficient to build body reserves after reproduction while deciduous

forest does. This study has shown that sex dependent factors controlling body condition in beaver's merits further attention.

Reproduction

I found that probability of reproduction increased with age of the female while the litter size decreased with increasing age, indicating senescence. Mayer et al. (2017) found similar results where reproductive success in beavers decreased with increasing age of both parents. However, the effect of senescence on reproductive success is somewhat unclear. Wigley et al. (1983) found maternal age was positively correlated with litter size, while others found litter size to increase to a certain age and decrease thereafter (Payne, 1984; Campbell et al., 2017), or being unrelated to age (Ruusila et al., 2000). Contrary to previous research my results were obtained from a wider age range as maternal age in this study varied from $2 - 17$ years (8.2 ± 4.17 years), which represents a wider age range considering that beavers in the wild can reach 23 years of age (Gorbunova et al., 2008). Further, I found that larger family groups promoted higher probability of reproduction and bigger litter sizes in contrast to findings of Payne (1984) where bigger family groups decreased fecundity in beavers. When considering that sub adults and yearlings in a family group will assist in feeding, grooming and defending the kits (Patenaude, 1983) my findings are, however, not surprising.

Though energy requirements of female beavers during reproduction have not been estimated, Parker et al. (2002) suggested that pregnant females are more active in their search for food as they were more likely to be shot during spring hunting than other family members. Further, in the North American beaver, breeding females uses 52 % of their active time during May and June on feeding, compared with 29 % for adult males (Buech, 1995). In addition, the nutrient requirements of phosphorous and sodium are estimated to be more than six times greater during lactation compared to maintenance for females (Nolet et al., 1995). With the above in mind, it seems reasonable to assume that energy requirements are elevated during reproduction for females.

No measure of vegetation availability in this study affected reproduction in beavers. Although I found a positive correlation between abundance of deciduous trees in a territory and body condition in females, it did not translate to reproduction. Neither forest cover or availability of deciduous trees had any effect on reproduction, which is in compliance with findings of Campbell et al. (2005). On the other hand, Campbell et al. (2017) found availability of deciduous saplings within a territory to affect probability of reproduction as decreasing abundance of saplings reduced the likeliness of reproduction for older females, but it did not impact litter size.

Herbaceous plants are rich in nutrients and theorized to be essential for successful reproduction in beavers (Nolet et al., 1995). I found no effect of availability of plant communities in the field layer on reproduction. However, low spring temperatures influence foraging quality of plants as it slows plant development and prolongs the early growth phase in which plants contain high concentrations of nutrients, and low concentrations of fiber and defensive compounds (Nolet et al., 1995; Campbell et al., 2013). Campbell et al. (2012) and Campbell et al. (2017) found that lower spring temperature positively correlated with litter size. Hence, high quality food should enhance reproductive success. In this study, I linked spatial availability of vegetation during the late summer to reproduction, but the above implies that temporal availability of high quality forage during the spring are more important for reproduction in beavers.

As beavers in this study display intermittent yeas between reproduction, females might asses resource levels over several years before reproducing. Indeed, body condition have been shown to positively correlate with reproduction (Parker et al., 2017), indicating that beavers must reach a certain threshold before reproducing. Availability of vegetation in one year may thus be an insufficient measure when exploring reproduction in beavers, a pattern seen in other capital breeders (Madsen & Shine, 1999).

Territory size

High productive habitats with high food abundance can facilitate smaller territories, but when habitat productivity declines, resource exploitation is extended over a wider area and territories become larger (Owen-Smith et al., 2010). My results did not support any relationship between territory size and vegetation availability in either of the three scales. Beavers have shown alteration in territory size linked to food abundance where territory size decreased with increasing abundance of deciduous trees (Fustec et al., 2001) or the reverse, a positive relationship between abundance of less preferred woody species and territory size (Havens et al., 2013). As an alternative, woody plants produce more green biomass than herbaceous plants and beavers have been observed to hold larger territories to incorporate more woody species in their territories (Campbell et al., 2005; McClintic et al., 2014). The effect vegetation availability on territory size might have been lost as this study quantified all available vegetation and did not distinguish categorically between revered food and non-food items. However, a missing link between food availability and territory size is common and in a review of 40 studies availability of food had no effect on territory size in 14 studies (Adams, 2001).

Beavers alter their diet through the year taking advantage of temporal variations in abundance of food resources to maximize their energy intake over time (Gallant et al., 2016). This ability enables them to hold smaller territories with increasing temporal variability of plant material (McClintic et al., 2014). Agricultural crops introduces temporal variability by being available in great abundance during a few months of the year in which beavers actively forage on them (Krojerová-Prokešová et al., 2010; Bełżecki et al., 2018). The habitat type agricultural land used in this study were a collective of mostly wheat and oat fields with some rye and potato fields. My results revealed a negative correlation between amount of agricultural land and territory size though the effect was marginal. However, Havens et al. (2013) showed that beavers hold smaller territories when their lodge is near agricultural land. The pooling of all agricultural crops might have diluted the effect on territory size as beavers prefer to forage on wheat and oats and generally avoid rye (Rosell & Pedersen, 1999; Bełżecki et al., 2018). To my knowledge, there are no observations of beavers foraging on potatoes. Further, following harvest agricultural fields may become a sink with limited natural foods and the effect of agricultural crops on territory size should be examined closer.

The predictions from the RDH in which larger territory size are mediated by higher habitat diversity did not hold true for beavers in this study although higher habitat diversity have been proven to cause larger territories in the North American beaver (McClintic et al., 2014; Francis et al., 2017). This discrepancy could be caused by the small sample size (n = 18) and a too course division of habitat types (n = 8) used in this study. Rather, beavers seem to adjust territory size according to size of deciduous trees.

Beavers increased territory size with increased diameter of available deciduous trees within the territories. As a central place forager, four principal factors can influence food item processing for beavers: time required cutting down an item, time required dragging the item to the central place, time spent consuming the item and time required for digestion (Fryxell, 1999). Large trees offer more edible biomass but requires more time to cut and transport (Fryxell & Doucet, 1991, 1993). Size preference of trees have been the topic of many research projects, yet no clear consensus have been reached. Beavers preferred cutting smaller trees with increasing distance from the shoreline when a broad range of tree sizes (2.5 cm - 30 cm in diameter) were present (Jenkins, 1980; Pinkowski, 1983; Belovsky, 1984; Donkor & Fryxell, 1999). In studies with predominantly smaller trees (diameter < 10 cm) available found beavers cut larger trees at increasing distance to the shore line (McGinley & Whitham, 1985; Gallant et al., 2004; Haarberg & Rosell, 2006) or lodge (Fryxell & Doucet, 1991; Raffel et al., 2009). Raffel et al. (2009) argued that conflicting results regarding tree size preferences might be due to the size ranges of trees available for beavers in study sites. They

found that beavers prefer stem diameters between 2.0 and 6.9 cm at all distances to their central place and avoid trees less than 2 cm or greater than 10 cm in diameter. Indeed, in many studies diameter of cut trees averages under 10 cm (Hall, 1960; Pinkowski, 1983; Belovsky, 1984; Haarberg & Rosell, 2006) although Donkor and Fryxell (1999) found the average stem diameter cut to be 15.1 cm. As central place foragers, beavers deplete foraging patches close to their central place before exploiting patches further away (Orians & Pearson, 1979; Goryainova et al., 2014). I suggest that beavers hold larger territories with increasing average stem diameter as a result of resource depletion close to their central place. Beavers occupy larger territories to incorporate preferred stem diameters of deciduous trees.

Conclusion

Insight into vegetation availability's role impact on body condition for beavers were improved by my models as male and female beaver showed a divergent adjustment in body condition to varying availability. However, many questions remain unanswered and future research should include sex-specific requirements of the beavers and account for female's capital breeding behavior. I have shown that vegetation availability of one year during the summer is insufficient in predicting reproduction in beavers. The capital breeding behavior along with temporal nutrient content of vegetation should also be taken into account for future exploration of vegetation's role in reproduction in beavers. Last, beaver territory size was determined by avoidance of resource depletion, but in territories with high temporal availability of agricultural beavers showed tendencies for smaller territories.

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Tables

TABLE 1. Mean tail fat index of adult (> 3 years) male and female beavers captured spring (March – May), summer (June – August) and autumn (September – November) in the Gvarv and Straumen river. The tail fat index was calculated as (tail length x tail width at midpoint)/body length. All values are presented as mean ± SD with sample size (n).

Season	Both sexes	Females	Males
Spring	4.12 ± 0.31 (70)	4.01 ± 0.27 (34)	4.23 ± 0.31 (36)
Summer	4.02 ± 0.27 (21)	3.83 ± 0.23 (8)	4.14 ± 0.23 (13)
Autumn	4.24 ± 0.33 (22)	4.06 ± 0.31 (11)	4.42 ± 0.26 (11)
All	4.13 ± 0.32 (113)	3.99 ± 0.28 (53)	4.24 ± 0.30 (60)

TABLE 2. Overview of beavers used to calculate average territory size of ten territories in Telemark county, Norway. Dominance status, days of recording, number of GPS positions, and year of monitoring are displayed along with average territory size estimated as 95 % kernel home range.

Territory	Beaver ID	Sex	Status	Year	# GPS days	# GPS positions	Territory size (km^2)
Håtveit	Pam	F	Dominant	2014	10	318	0.351
Gvarvbrua middle	Klumpen	M	Dominant	2014	12	427	0.330
Gvarvbrua lower	Hazel	F	Dominant	2015	6	150	0.770
	Paddy	F	Dominant	2015	6	148	
Nordsjø 1	Tina	F	Subadult	2016	13	188	1.694
	Jodie	F	Dominant	2015	8	183	
Lunde 1	Waltraut	F	Dominant	2015	13	448	0.492
Lunde 2	Gyda	F	Dominant	2015	8	152	1.359
	Lasse	M	Dominant	2015	8	240	
Lunde 3	Solveig	F	Dominant	2016	9	240	0.284
	Kyle	M	Dominant	2018	9	199	
Lunde 4	Malena	F	Dominant	2015	10	256	0.824
	Rory	M	Dominant	2015	9	185	
	Laura	F	Dominant	2015	11	310	
	Darwin	M	Dominant	2015	11	375	
Lunde 5	Yasmin	F	Dominant	2016	13	443	1.584
	Rudolf	M	Dominant	2018	10	328	
Lunde 6	Johan	M	Dominant	2016	9	266	0.798
Total	**18**				**175**	**4856**	

TABLE 3. Global models linking vegetation availability in the three scales habitat type, tree layer and field to body condition, reproduction (probability and success), and territory size in the Eurasian beaver. Tail fat index was used as a measure of body condition and calculated as (tail length × tail width at midpoint)/body. The habitat types agriculture and forest showed high collinearity (r = 0.756) and habitat type models were split into habitat type 1 containing agriculture and habitat type 2 containing forest. Dec is number of deciduous trees per plot, dec dia diameter of deciduous trees, con number of coniferous trees per plot and con dia diameter of coniferous trees. RPY is reproduction (yes/no) in the previous year and RSY reproduction success in the previous year. Maternal age could not be included in global model predicting reproduction from vegetation availability in the field layer due to overfitting.

Response	Model	Model terms	Random terms
Body condition (Tail fat index)	Habitat type	(Agriculture + forest + Grassland + Rural) * (Season + Sex) + Family size + Age + Age^2	Year
	Habitat type 1	(Agriculture + Grassland + Rural) * (Season + Sex) + Family size + Age + Age^2	Year
	Habitat type 2	(Forest + Grassland + Rural) * (Season + Sex) + Family size + Age + Age^2	Year
	Tree layer	(Dec + Dec dia + Con + Con dia) * (Season + Sex) + Family size + Age + Age^2	Year
	Field layer	(NMDS 1 + NMDS 2 + NMDS 3) * (Season + Sex) + Family size + Age + Age^2	Year
Reproduction probability	Habitat type 1	Agriculture + Grassland + Rural + Study site + RPY + Family size + Maternal age	Territory + Year
	Habitat type 2	Forest + Grassland + Rural + Study site + RPY + Family size + Maternal age	Territory + Year
	Tree layer	Dec + Dec dia + Con + Con dia + Study site + RPY + Family size + Maternal age	Territory + Year
	Field layer	NMDS 1 + NMDS 2 + NMDS 3+ Study site + RPY + Family size	Territory + Year
Reproduction success	Habitat type 1	Agriculture + Grassland + Rural + Study site + RPY + Family size + Maternal age	Territory + Year
	Habitat type 2	Forest + Grassland + Rural + Study site + RPY + Family size + Maternal age	Territory + Year
	Tree layer	Dec + Dec dia + Con + Con dia + Study site + RPY + Family size + Maternal age	Territory + Year
	Field layer	NMDS 1 + NMDS 2 + NMDS 3+ Study site + RPY + Family size	Territory + Year

Table 4. Model averaged results from the top model set (ΔAICc <2) of parameters linking tail fat index of adult (> 3 years) beavers to vegetation availability in the three scales habitat type, tree layer and field layer in Telemark county, Norway. Dec is number of deciduous trees per plot, con number of coniferous trees per plot, dec dia diameter of deciduous trees, and con dia diameter of coniferous trees. Model terms with estimates are on logit scale and standard error (SE), confidence intervals (CI) are displayed. All informative model terms (CI do not include 0) are marked with an asterisk.

		Habitat type				Tree layer				Field layer			
				95 % CI				95 % CI				95 % CI	
Predictor		**Estimate**	**SE**	**Lower**	**Upper**	**Estimate**	**SE**	**Lower**	**Upper**	**Estimate**	**SE**	**Lower**	**Upper**
Control variables	Intercept	4.307	0.115	4.082	4.532*	3.832	0.148	3.541	4.122*	4.102	0.070	3.964	4.240*
	Season (spring)	-0.114	0.060	-0.232	$3.71e^{-03}$	-0.138	0.066	-0.268	$-8.70e^{-03}$*	-0.130	0.065	-0.258	$-1.57e^{-03}$*
	Season (summer)	-0.214	0.077	-0.366	-0.062*	-0.242	0.082	-0.403	-0.080*	-0.229	0.086	-0.397	-0.062*
	Sex (male)	0.108	0.120	-0.127	0.343	0.649	0.131	0.393	0.906*	0.274	0.050	0.176	0.372*
	Age	0.080	0.028	0.025	0.136*	0.022	0.035	-0.047	0.091	0.060	0.040	-0.019	0.138
	Age^2	$-4.75e^{-03}$	$1.75e^{-03}$	$-8.17e^{-03}$	$-1.33e^{-03}$*	$-1.42e^{-03}$	$2.24e^{-03}$	$-5.81e^{-03}$	$2.96e^{-03}$	$-3.94e^{-03}$	$2.55e^{-03}$	$-8.94e^{-03}$	$1.06e^{-03}$
	Family size	$2.43e^{-03}$	$7.47e^{-03}$	-0.012	0.017								
Vegetation variables	Forest	$3.31e^{-03}$	$2.06e^{-03}$	$-7.28e^{-04}$	$7.35e^{-03}$								
	Grassland	-0.015	$2.85e^{-03}$	-0.020	$-9.13e^{-03}$*								
	Forest:Sex (male)	$-7.36e^{-03}$	$2.59e^{-03}$	-0.012	$-2.28e^{-03}$*								
	Grassland:Sex (male)	0.017	$3.57e^{-03}$	0.010	0.024*								
	Dec					0.165	0.056	0.055	0.276*				
	Con					$3.44e^{-03}$	0.024	-0.043	0.050				

					Estimate	SE	2.5%	97.5%		Estimate	SE	2.5%	97.5%
Dec dia					$-6.57e^{-03}$	0.017	-0.039	0.026					
Con dia					$-8.47e^{-04}$	0.010	-0.020	0.018					
Dec:Sex (male)					-0.242	0.079	-0.397	-0.087*					
Con:Sex (male)					-0.017	0.035	-0.086	0.052					
Dec dia:Sex (male)					$7.24e^{-03}$	0.024	-0.040	0.054					
Con dia:Sex (male)					$-8.53e^{-03}$	0.016	-0.040	0.023					
NMDS 1										$-6.03e^{-03}$	0.014	-0.033	0.021
NMDS 2										-0.120	0.115	-0.346	0.105
NMDS 1:Sex (male)										-0.011	0.021	-0.053	0.030
NMDS 2:Season (spring)										0.085	0.111	-0.132	0.302
NMDS 2:Season (summer)										0.133	0.158	-0.177	0.443

TABLE 5. Overview of reproductive probability and mean reproductive success (litter size) for dominant beaver pairs from 2010 – 2017 in the ten territories along the Gvarv and Straumen river.

Territory	Yearly probability of reproduction (0,1)	Reproduction success (litter size) Mean ± SD	Range
Håtveit	0.25	0.25 ± 0.46	0 – 1
Gvarvbrua middle	0.50	0.88 ± 1.13	0 – 3
Gvarvbrua lower	0.63	1.00 ± 1.07	0 – 3
Nordsjø 1	0.50	0.38 ± 0.74	0 – 2
Lunde 1	0.25	0.75 ± 0.89	0 – 2
Lunde 2	0.63	1.25 ± 1.39	0 – 4
Lunde 3	0.25	0.38 ± 0.74	0 – 2
Lunde 4	0.50	0.75 ± 0.89	0 – 2
Lunde 5	0.38	0.38 ± 0.52	0 – 1
Lunde 6	0.25	0.25 ± 0.46	0 – 1

TABLE 6. Model averaged results from the top model set (ΔAICc <2) of the parameters linking reproductive probability for dominant beaver pairs to vegetation availability in the three scales habitat type, tree layer, and field layer in the study area in Telemark county, Norway. RPY is reproduction (yes/no) in the previous year. Model terms with estimates on logit scale and standard error (SE), confidence intervals (CI) are displayed. All informative model terms (CI do not include 0) are marked with an asterisk.

	Predictor	Habitat type				Tree layer				Field layer			
				95 %CI				95 %CI				95 %CI	
		Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper
Control variables	Intercept	-4.645	0.483	-5.591	-3.698 *	-4.645	0.483	-5.592	-3.698*	-3.605	0.769	-5.122	-2.097*
	Maternal age	0.034	0.016	$3.24e^{-03}$	0.065 *	0.034	0.016	$3.24e^{-03}$	0.065*	$2.85e^{-03}$	0.015	-0.027	0.032
	Family size	0.816	0.042	0.732	0.899 *	0.816	0.042	0.733	0.899*	0.711	0.074	0.566	0.856*
	RPY	-1.376	0.130	-1.630	-1.122 *	-1.376	0.130	-1.630	-1.122*	-0.828	0.252	-1.321	-0.335*
	Study site (Straumen)	1.764	0.441	0.900	2.628 *	1.764	0.441	0.900	2.628*	0.984	0.801	-0.588	2.555
Vegetation	Agriculture	$-8.67e^{-04}$	0.020	-0.039	0.038								
	Grassland	$1.47e^{-03}$	0.025	-0.047	0.050								

TABLE 7. Model averaged results from the top set (ΔAICc <2) of the parameters linking reproductive success (litter size) for dominant beaver pairs to vegetation availability in the three scales habitat type, tree layer, and field layer in Telemark county, Norway. RSY is reproduction success in the previous year. Model terms with estimates on a log scale, standard error (SE), and confidence intervals (CI) are displayed. All informative model terms (CI do not include 0) are marked with an asterisk.

		Habitat type				Tree layer				Field layer			
				95 %CI				95 %CI				95 %CI	
Predictor		Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper	Estimate	SE	Lower	Upper
Control variables	Intercept	-2.202	0.386	-2.959	-1.446 *	-2.229	0.383	-2.980	-1.479 *	-1.731	0.539	-2.786	-0.675 *
	Maternal age	-0.035	$8.27e^{-03}$	-0.052	-0.019 *	-0.035	0.008	-0.052	-0.019 *	-0.075	0.016	-0.107	-0.044 *
	Family density	0.407	0.019	0.369	0.444 *	0.407	0.019	0.369	0.445 *	0.415	0.037	0.343	0.488 *
	RSY	-0.514	0.033	-0.578	-0.451 *	-0.514	0.033	-0.578	-0.451 *	-0.592	0.061	-0.712	-0.472 *
	Study site (Straumen)	0.434	0.409	-0.369	1.236	0.477	0.405	-0.316	1.271	0.335	0.509	-0.663	1.333
Vegetation variable	Con dia					$-7.55e^{-05}$	$1.43e^{-03}$	$-2.88e^{-03}$	$2.73e^{-03}$				

TABLE 8. Model averaged results from the top model sets (ΔAICc <2) linking beaver territory size to vegetation availability in the three scales habitat type and tree layer in the study area in Telemark county, Norway. Dec dia is diameter of deciduous trees. Model terms with estimates, standard error (SE), confidence intervals (CI) are displayed. All informative model terms (CI do not include 0) are marked with an asterisk.

Vegetation class	Model	Model term	Estimate	SE	95 % CI	
					Lower	Upper
Habitat type	H1	Intercept	1.093	0.260	0.584	1.608*
		Agriculture	-0.011	$8.77e^{+03}$	-0.028	$6.52e^{-03}$
Tree layer	T3	Intercept	-0.104	0.241	-0.661	0.453
		Dec dia	0.778	0.065	0.129	0.426*

Figures
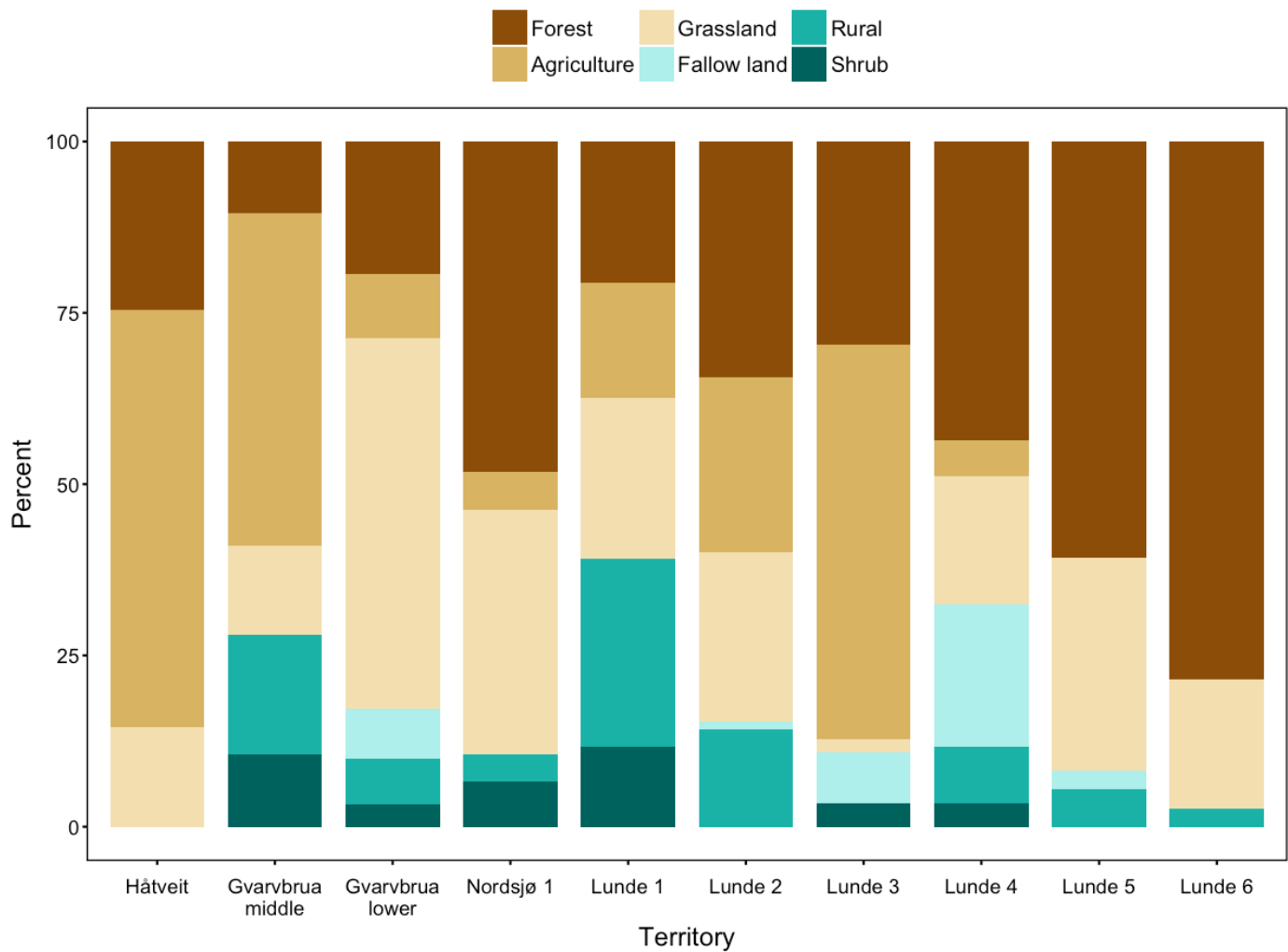
FIGURE 1. The percentage cover of the habitat types forest (dark brown), agricultural land (brown), grassland (light brown), fallow land (light blue), rural development (turquoise) and shrub vegetation (dark blue) in the ten territories along the Gvarv and Straumen river.
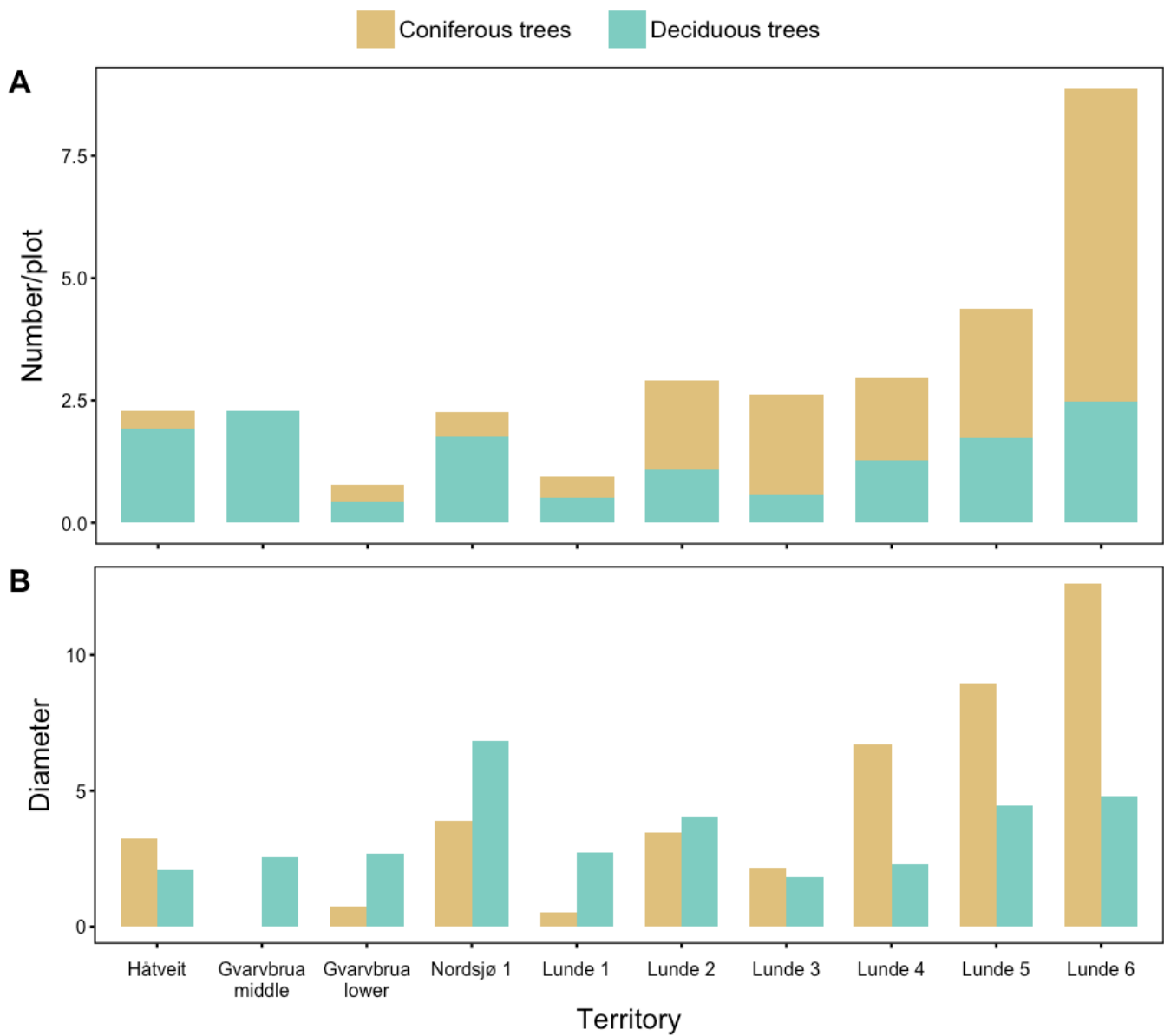
FIGURE 2. The Abundance of coniferous trees (brown) and deciduous trees (green) per plot (**A**) and Average diameter of coniferous trees (brown) and deciduous trees (green) per plot (**B**) in each of the ten territories along the Gvarv and Straumen river
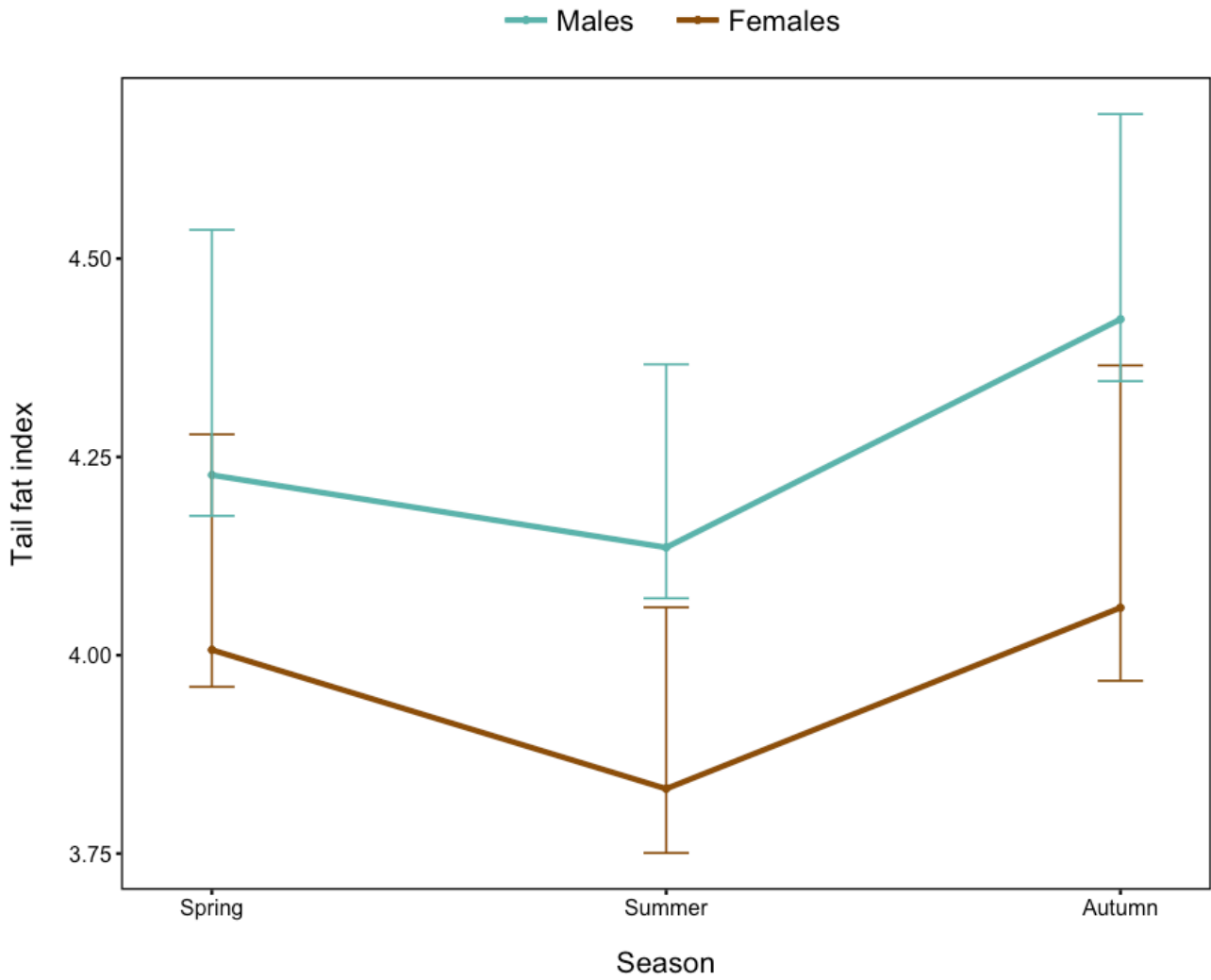
FIGURE 3. Mean tail fat index of adult (> 3 years) male and female beavers captured in the spring (March – May), summer (June – August) and autumn (September – November) in the Gvarv and Straumen river. The tail fat index was calculated as (tail length x tail width at midpoint)/body length. All values are presented as mean ± SD
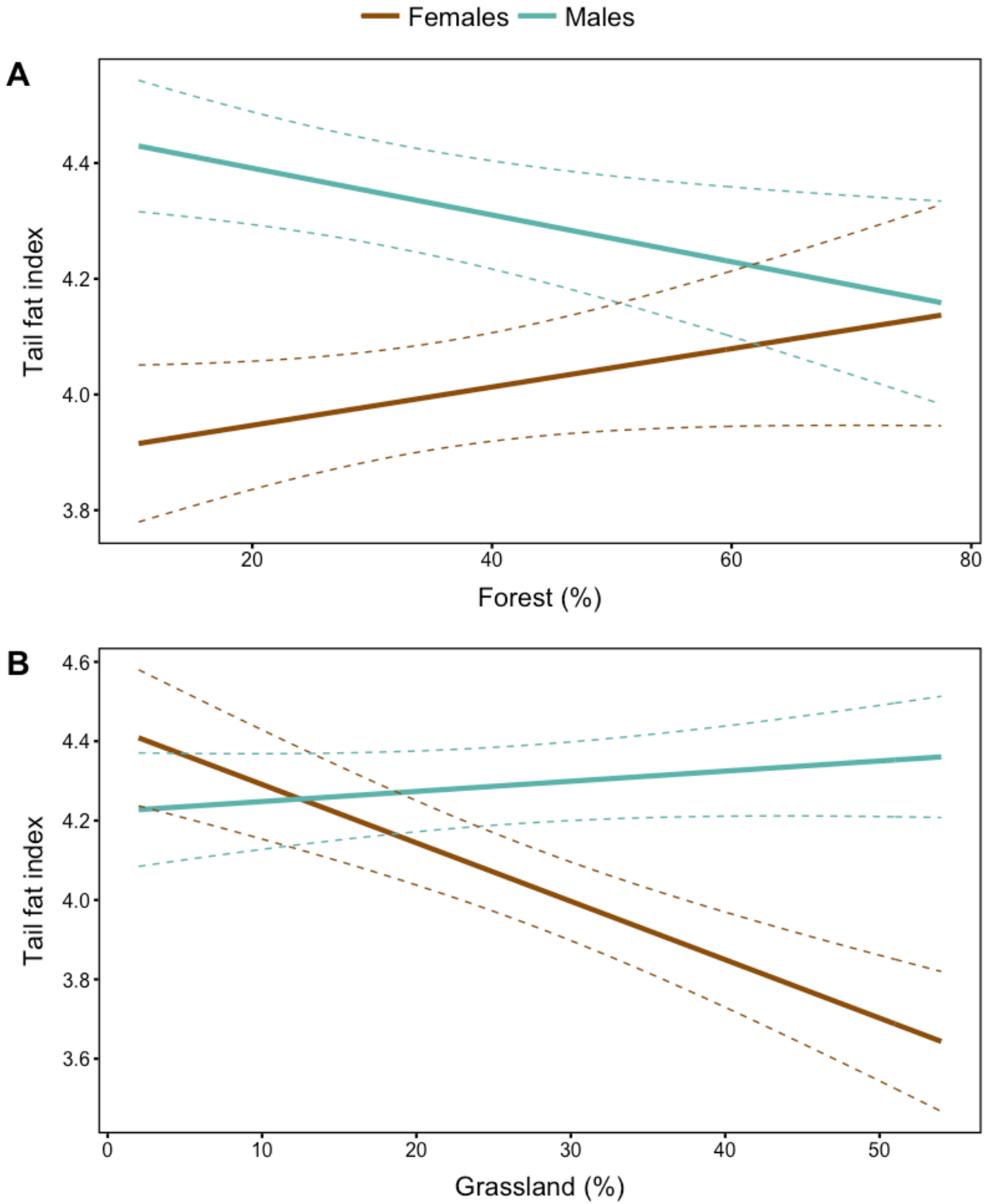
FIGURE 4. Effect on tail fat index in adult (> 3 years) female (brown) and male (blue) beavers in the study area of percentage cover forest (**A**) and grassland (**B**) territories the Gvarv and Straumen river in Telemark county, Norway. The 95 % confidence intervals are marked by dashed lines.
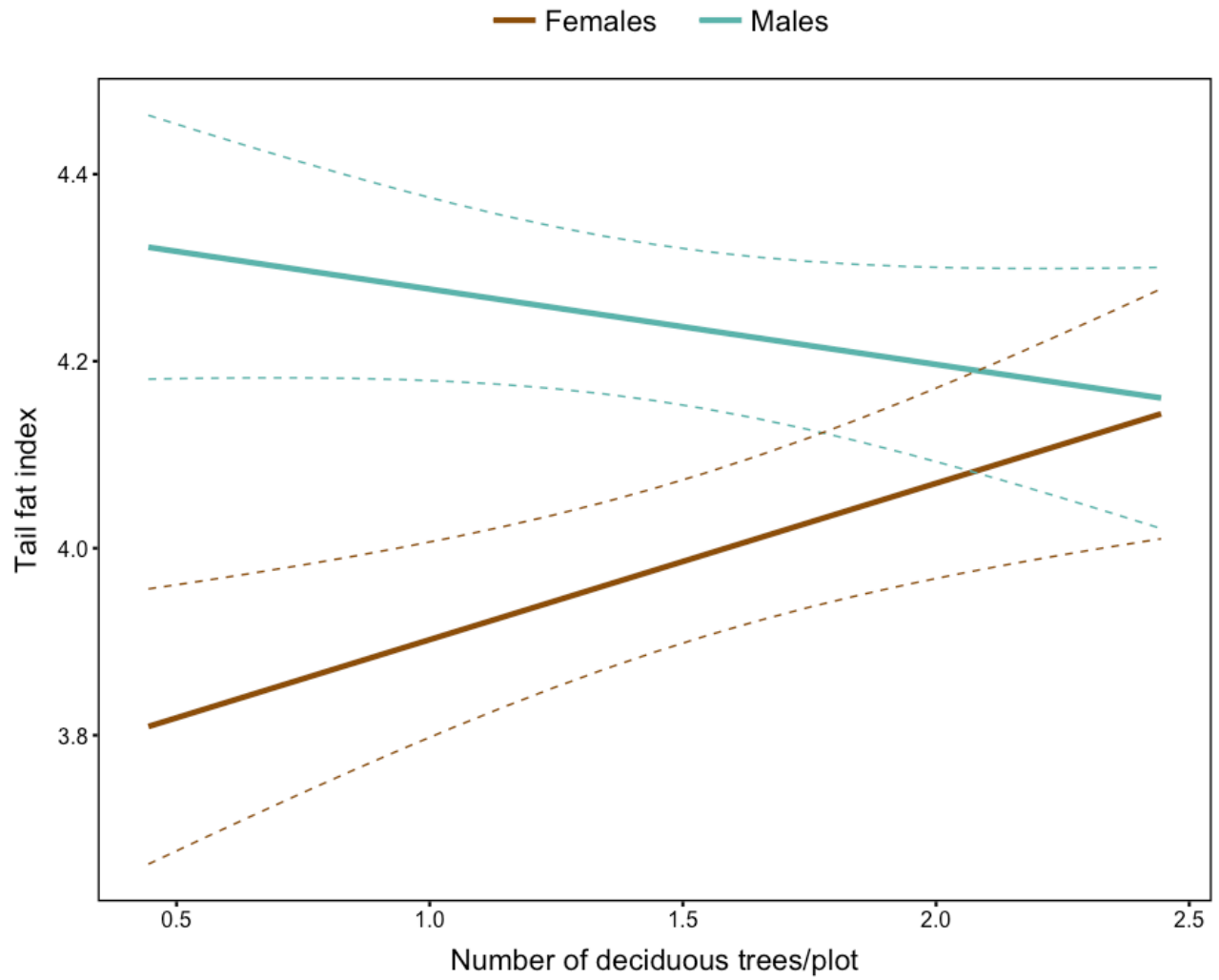
FIGURE 5. Effect of deciduous tree abundance in a territory on tail fat index in adult (> 3 years) female (brown) and male (blue) beavers in territories along the Gvarv and Straumen river in Telemark county, Norway. The 95 % confidence intervals are marked by dashed lines.
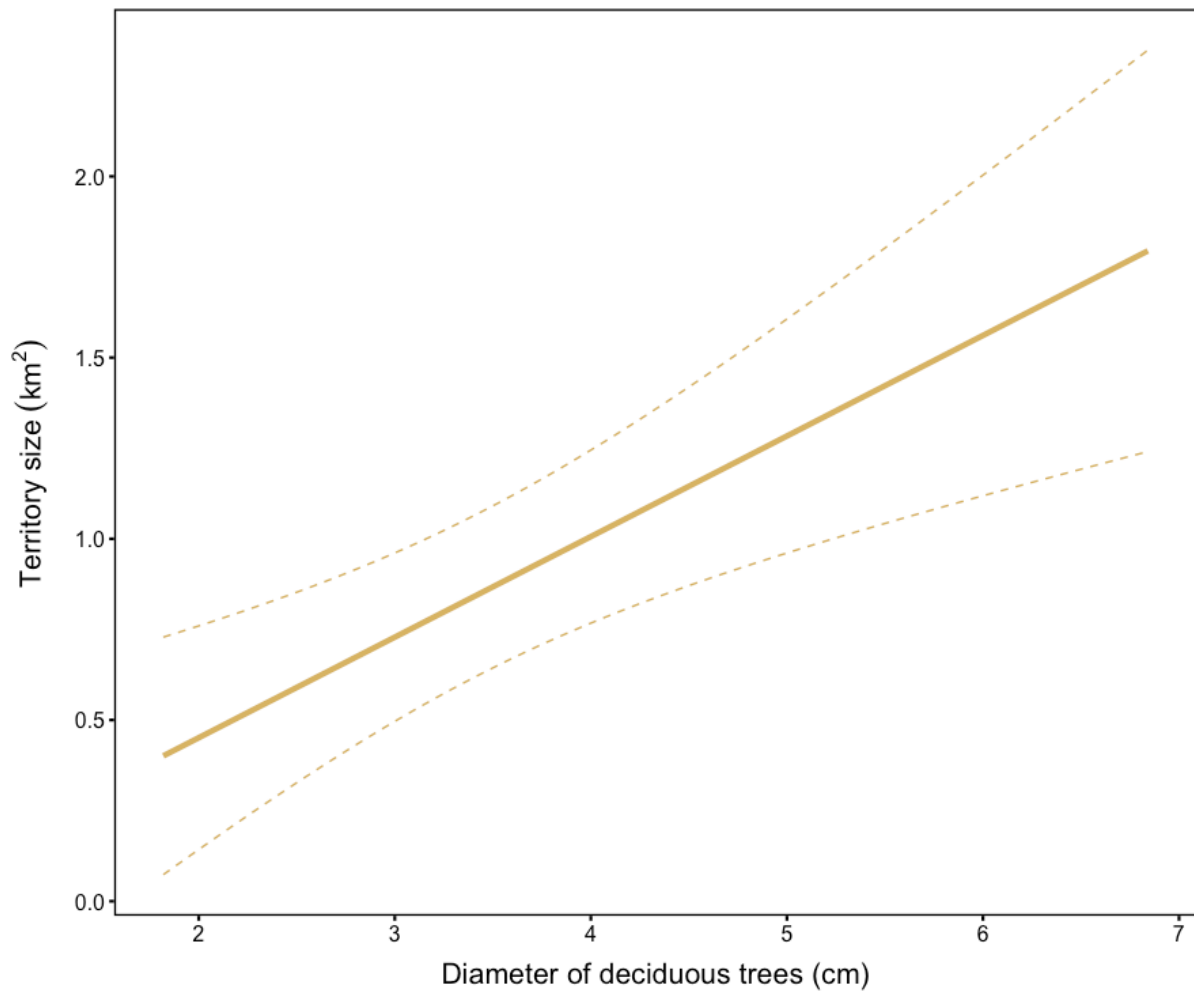
FIGURE 6. Effect of mean diameter of deciduous trees on territory size for beavers in the Gvarv and Straumen river in Telemark county, Norway. The 95 % confidence intervals are marked dashed lines.

Appendix
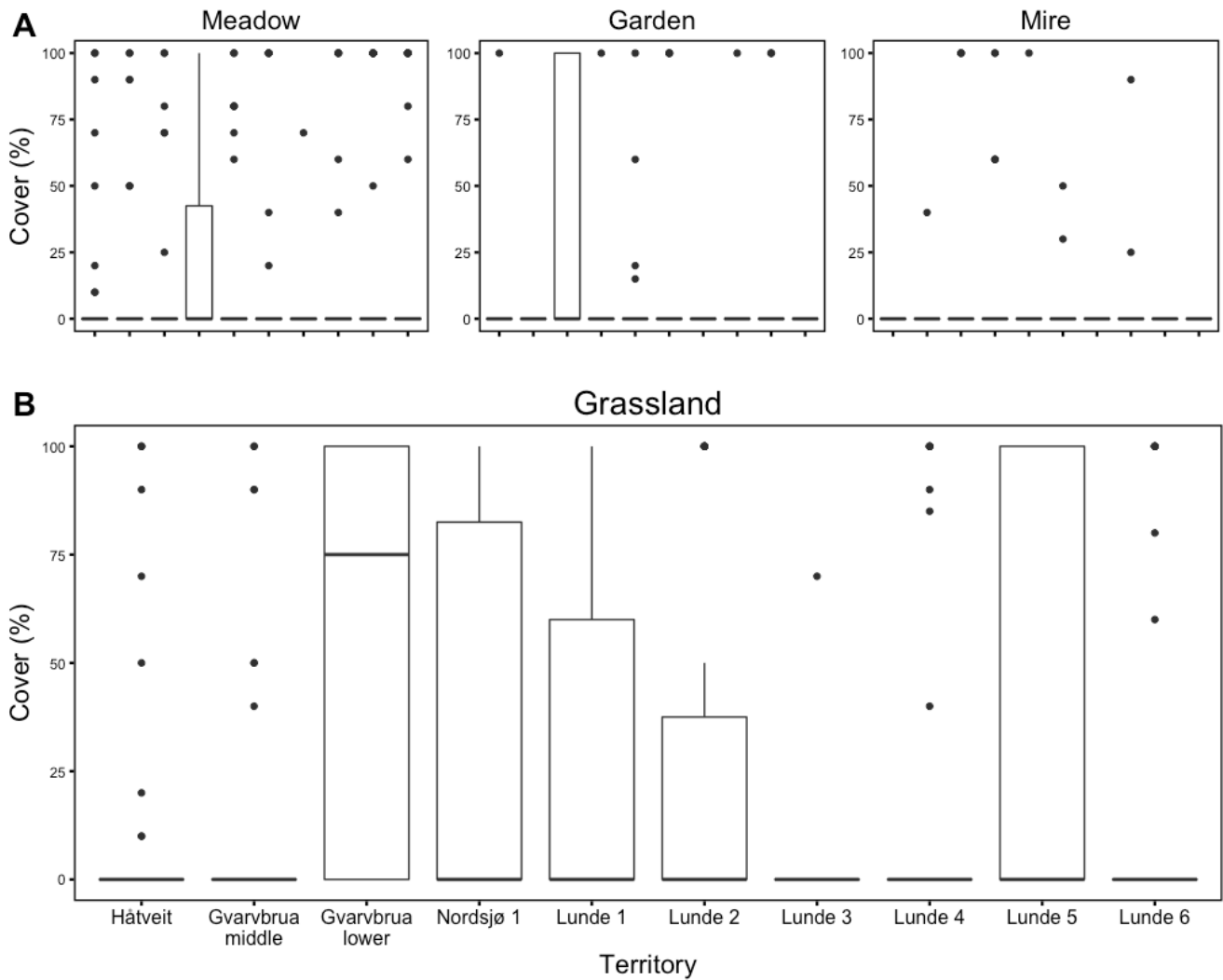
Figure A1 Percentage cover of the grass-dominated habitat types meadow, garden and mire (**A**) and percentage cover of the habitat type grassland combined from meadow, garden and mire (**B**) in the main plots within each of the ten territories along the Gvarv and Straumen river in Telemark county, Norway.
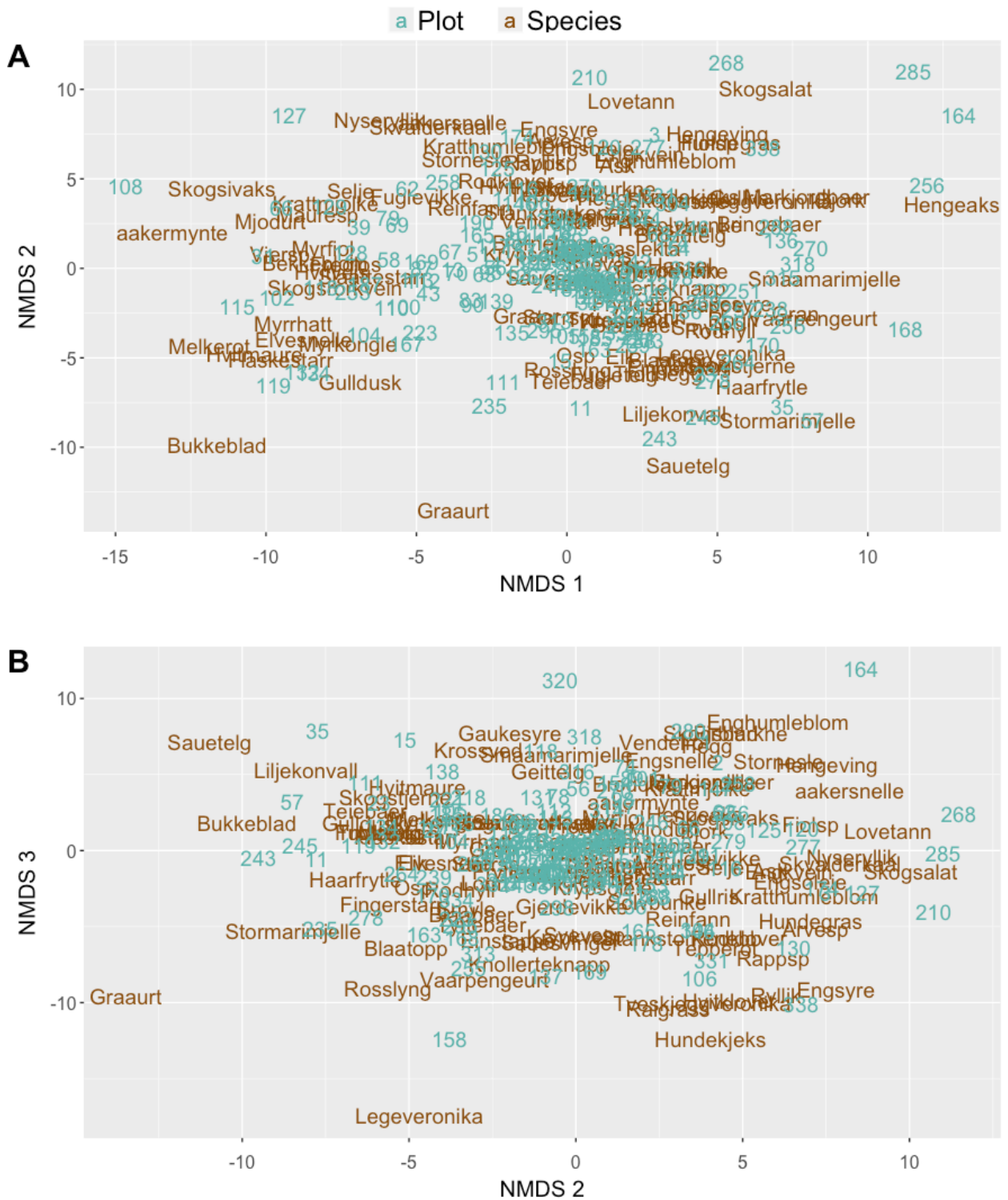
Figure A2: Results from non-metric multidimensional scaling ordination (NMDS) ordering plant species along axis one, a gradient of soil moisture (NMDS 1) and axis two, a gradient of human impact (NMDS 2) (**A**) and along axis 2 and axis 3, a gradient of wet flushing (NMDS 3) (**B**). All stress values <0.2.

Table A1. Model selection results for linear mixed effect models linking tail fat index of adult (> 3 years) beavers captured in 2010 to 2018 in spring (March - May), summer (June - August) and autumn (September – November) to availability of habitat types in the Gvarv river and the Straumen river. Model terms included in each model are displayed with estimates and the whole model with AICc, ΔAICc and Akaikes weight. Only models within ΔAICc < 2 of the top model are included.

Intercept	Age	Age^2	Grassland	Season	Sex	Grassland:Sex	Density	Forest	Forest:Sex	df	AICc	ΔAICc	Weight
4.091	0.081	$-4.79e^{-03}$	-0.015	+	+	+		$3.18e^{-03}$	+	12	17.752	0.000	0.731
4.053	0.078	$-4.64e^{-03}$	-0.015	+	+	+	$9.01e^{-03}$	$3.66e^{-03}$	+	13	19.750	1.997	0.269
												Total	*1.000*

Table A2. Model selection results for linear mixed effect models linking tail fat index of adult (> 3 years) beavers captured in 2010 to 2018 in spring (March - May), summer (June - August) and autumn (September – November) to vegetation availability in the tree layer in the Gvarv and Straumen river. Con dia symbolized diameter of coniferous trees, con abundance of coniferous trees per plot, dec dia diameter of deciduous trees and dec abundance of coniferous trees per plot. Model terms included in each model are displayed with estimates and the whole model with AICc, ΔAICc and Akaikes weight. Only models within ΔAICc < 2 of the top model are included.

Intercept	Age	Age^2	Con dia	Con	Dec dia	Dec	Season	Sex	Con dia: Sex	Con: Sex	Dec dia: Sex	Dec:Sex	df	AICc	ΔAICc	Weight
3.870			3.74e^{-03}			0.160	+	+	+			+	10	30.859	0.000	0.106
3.854				0.019		0.165	+	+		+		+	10	31.322	0.463	0.084
3.875						0.163	+	+				+	8	31.393	0.534	0.081
3.705	0.064	-4.13e^{-03}				0.159	+	+				+	10	31.458	0.599	0.079
3.728	0.064	-4.22e^{-03}	-0.012			0.170	+	+				+	11	31.515	0.655	0.076
3.676	0.064	-3.95e^{-03}		0.018		0.160	+	+		+		+	12	31.690	0.831	0.070
3.718	0.059	-3.81e^{-03}	0.001			0.160	+	+	+			+	12	31.718	0.859	0.069
3.976			0.010		-0.042	0.171	+	+	+		+	+	12	31.732	0.873	0.069
3.893			-0.011			0.171	+	+				+	9	31.757	0.897	0.068
3.898				-0.024		0.162	+	+				+	9	32.077	1.217	0.058
3.936					-0.023	0.171	+	+				+	9	32.087	1.228	0.057
3.727	0.064	-4.15e^{-03}		-0.024		0.159	+	+				+	11	32.101	1.242	0.057
3.908			6.29e^{-03}		-0.015	0.164	+	+	+			+	11	32.603	1.744	0.044
3.954				0.029	-0.040	0.181	+	+		+	+	+	12	32.667	1.808	0.043
3.846			-0.015	0.052		0.177	+	+		+		+	11	32.850	1.991	0.039
															Total	*1.000*

Table A3. Model selection results for linear mixed effect models linking tail fat index of adult (> 3 years) beavers captured in 2010 to 2018 in spring (March - May), summer (June - August) and autumn (September – November) to vegetation availability in the field layer as the gradients NMDS 1 (soil moisture), NMDS2 (human disturbance) and NMDS 3 (wet flushing). Model terms included in each model are displayed with estimates and the whole model with AICc, ΔAICc and Akaikes weight. Only models within ΔAICc < 2 of the top model are included.

Intercept	Age	Age^2	NMDS 1	NMDS 2	Season	Sex	NMDS 1 :Sex	NMDS 2 :Season	df	AICc	ΔAICc	Weight
3.889	0.077	-4.95e^{-03}		-0.225	+	+		+	11	37.278	0.000	0.194
3.901	0.074	-4.92e^{-03}	-0.016	-0.214	+	+		+	12	38.091	0.813	0.129
3.891	0.078	-5.04e^{-03}			+	+			8	38.519	1.241	0.104
4.112			1.48e^{-03}	-0.067	+	+	+		9	38.799	1.521	0.091
3.900	0.076	-5.13e^{-03}	-0.017		+	+			9	38.891	1.614	0.086
4.107				-0.228	+	+		+	9	38.944	1.666	0.084
3.932	0.067	-4.52e^{-03}	-1.45e^{-03}		+	+	+		10	39.012	1.734	0.081
3.921	0.068	-4.66e^{-03}	-0.021	-0.056	+	+			10	39.036	1.758	0.080
3.927	0.067	-4.43e^{-03}	-0.004	-0.202	+	+	+	+	13	39.160	1.882	0.076
3.952	0.060	-4.05e^{-03}	-0.005	-0.056	+	+	+		11	39.181	1.903	0.075
											Total	*1.000*

Table A4. Model selection results from generalized mixed effect model sets linking availability of habitat types to reproductive probability and success for a given year in ten territories along the Gvarv and Straumen river in the period of 2010 – 2017. Model terms included in each model are displayed with estimates and the whole model with AICc, ΔAICc and Akaike weight. RPY symbolizes reproduction in the previous year (yes/no) and RSY reproductive success (litter size) in the previous year. Only models within ΔAICc < 2 of the top model are included.

Response	Intercept	Age	Density	RPY[1]/RSY[2]	Study site	Grassland	Agriculture	df	AICc	ΔAICc	Weight
	-5.220	0.035	0.902	-1.536[1]	+			7	2782.618	0.000	0.644
Reproduction probability	-5.221	0.035	0.901	-1.536[1]	+	6.38e-03		8	2784.612	1.994	0.237
	-5.218	0.035	0.901	-1.536[1]	+		-9.29e-03	8	2784.602	1.984	0.119
										Total	*1.000*
	-2.342	-0.035	0.408	-0.514[2]	+			7	4809.927	0.000	0.661
Reproduction success	-1.930	-0.036	0.405	-0.515[2]				6	4811.266	1.339	0.339
										Total	*1.000*

Table A5. Model selection results from generalized mixed effect model sets linking vegetation availability in the tree layer to reproductive probability and success for a given year in ten territories along the Gvarv and Straumen river in the period of 2010 – 2017. Model terms included in each model are displayed with estimates and the whole model with AICc, ΔAICc and Akaike weight. RPY symbolizes reproduction in the previous year (yes/no), RSY reproduction success (litter size) in the previous year and con dia diameter of coniferous trees. Only models within ΔAICc < 2 of the top model are included.

Response	Intercept	Age	Density	RPY[1]/RSY[2]	Study site	Con dia	df	AICc	ΔAICc	Weight
Reproduction probability	-5.220	0.035	0.902	-1.536[1]	+		7	2782.618	0.000	1.000
									Total	*1.000*
Reproduction success	-2.342	-0.035	0.408	-0.514[2]	+		7	4809.927	0.000	0.532
	-1.930	-0.036	0.405	-0.515[2]			6	4811.266	1.339	0.272
	-2.341	-0.035	0.408	-0.514[2]	+	$-3.86e^{-04}$	8	4811.924	1.998	0.196
									Total	*1.000*

Table A6. Model selection results from generalized mixed effect model sets linking vegetation availability in the field layer from the gradients NMDS 1(soil moisture), NMDS2 (human disturbance) and NMDS 3 (wetflushing) to reproductive probability and success for a given year in ten territories along the Gvarv and Straumen river in the period of 2010 – 2017. Model terms included in each model are displayed with estimates and the whole model with AICc, ΔAICc and Akaike weight. RPY symbolizes reproduction in the previous year (yes/no) and RSY reproduction success (litter size) in the previous year. Only models within ΔAICc < 2 of the top model are included.

Response	Intercept	Age	Density	RPY[1]/RSY[2]	Study site	df	AICc	ΔAICc	Weight
Reproduction probability	-3.752		0.711	-0.830[1]	+	6	718.693	0.000	0.525
	-3.068		0.707	-0.831[1]		5	720.058	1.365	0.265
	-3.916	0.014	0.717	-0.820[1]	+	7	720.533	1.841	0.209
								Total	*1.000*
Reproduction success	-1.548	-0.076	0.414	-0.593[2]		6	1331.445	0.000	0.542
	-1.947	-0.074	0.417	-0.592[2]	+	7	1331.785	0.340	0.458
								Total	*1.000*

Table A7. Model selection results for candidate models exploring beaver territory size in relation to diversity of habitat types (D0 and D1), availability of habitat types (H0 – H4), tree layer (T0 – T4), and field layer (F0 – F3) in ten territories along the Gvarv and Straumen river in the period of 2014 – 2018. SI is Shannon's index, Con dia diameter of coniferous trees, con abundance of coniferous trees per plot, dec dia diameter of deciduous trees, and dec abundance of coniferous trees per plot. Model terms included in each model are displayed with estimates, AICc, ΔAICc and Akaike weight.

Predictor	Model	Model term	Estimate	df	AICc	ΔAICc	Weight
Habitat type (diversity)	D0	Null model		2	20.178	0	0.890
	D1	SI	0.136	3	24.356	4.178	0.110
						Total	*1.000*
Habitat type (availability)	H1	Agriculture	-0.015	3	18.308	0.000	0.509
	H0	Null model		2	20.178	1.870	0.200
	H2	Forest	0.012	3	20.842	2.534	0.143
	H3	Grassland	0.020	3	21.142	2.834	0.123
	H4	Rural	-7.47e^{-03}	3	2.308	6.000	0.025
						Total	*1.000*
Tree layer	T3	Dec dia	0.277	3	12.478	0.000	0.968
	T3	Null model		2	20.178	7.700	0.021
	T4	Con dia	0.052	3	22.678	10.200	5.90e^{-03}
	T2	Con	0.044	3	24.210	11.732	2.74e^{-03}
	T1	Dec	0.095	3	24.284	11.806	2.64e^{-03}
						Total	*1.000*
Field layer	F0	Null model		2	20.178	0.000	0.619
	F2	NMDS 2	0.301	3	22.546	2.368	0.189
	F3	NMDS 3	-0.120	3	23.473	3.295	0.119
	F1	NMDS 1	-2.29e^{-03}	3	24.463	4.285	0.073
						Total	*1.000*