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Original research article

# Diet and lake size are the main drivers of the territorial occupation dynamics of North American beaver

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A B S T R A C T

Beavers, as ecosystem engineers, create crucial wetlands and habitats for other species, altering the structure and function of the surrounding forests and affecting human infrastructure. However, despite these significant economic and ecological implications, the spatiotemporal patterns of beaver feeding strategies remain understudied. This study aimed to evaluate how forest stand type, lake size, and diet influence beaver territorial occupation in eastern Canada. We used a dendroecological approach to measure beaver occupation time and maximum browsing distance around 61 lakes. Around each beaver lodge, we established 1 $m^2$ plots along three transects in which we measured distance of browsing from shore and counted annual rings on coppices resulting from beaver presence. PERMANOVA revealed that both maximum browsing distance ( $p = 0.003$) and temporal occupation ( $p = 0.006$) differed significantly across lake size categories. The type of forest stand had no impact on beaver dynamics. Stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of beaver carcasses collected from local trappers showed that the beavers' diet included the consumption of conifer trees and a seasonal shift in food consumption. We found that lakes ranging from 4 to 20 ha were optimal for beavers, as this lake size mattered more than the availability of specific food sources. Beavers exhibited high adaptation skills by using different plant species depending on the season to maximize resource availability and energy cost trade-off. Understanding the factors involved in beaver territorial occupation dynamics is crucial for land managers and conservationists to effectively incorporate this species into forest management plans and mitigate beaver–human conflicts.

## 1. Introduction

The boreal forest is the world's largest terrestrial biome (Brandt et al., 2013; Gauthier et al., 2023). Natural disturbances have shaped its composition, succession, and landscape for millennia (Aakala et al., 2023; Lavoie et al., 2021; Martin et al., 2022). North

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American beavers (*Castor canadensis*) are a major disturbance within the boreal forest; they can transform a terrestrial landscape into a complex aquatic ecosystem (Grosbois et al., 2023; Milligan and Humphries, 2010; Rosell et al., 2005). By harvesting trees and damming rivers, beavers create most small lakes and wetland areas in the boreal forest (Hood and Bayley, 2008; Snodgrass, 1997) that are more diverse and productive aquatic ecosystems than larger lakes (Blackburn-Desbiens et al., 2023).

Beavers alter the structure and function of forest ecosystems. The lentic environment created by the impounded water of a beaver pond is essential to many wetland-dependent organisms and increases local biodiversity. These rodents also create gaps in the canopy that enhance the heterogeneity and resilience of forest stands (Cunningham et al., 2006; Westbrook et al., 2011). Despite this significant impact, there remains a knowledge gap regarding the ecological strategies used by beavers to occupy their territory in the boreal forest, specifically in conifer stands. Understanding this aspect is crucial to minimize beaver impacts on human infrastructure and activities, especially with the expected migration of temperate forests northward under climate change (Boisvert-Marsh et al., 2014; Jarema et al., 2009; McManus et al., 2012; Tape et al., 2018).

Habitat and diet are key drivers of the beaver's territorial occupation strategies. Beavers tend to prefer habitats with a low stream gradient, low Strahler order, stable and slow-running water levels, deciduous-covered banks, and loose soil substrate to build dams and ensure However, beavers are also seldom found living on steep, mountainous streams (Bylak and Kukuła, 2020; Bylak et al., 2014; Smith et al., 1991). Beavers are generalist herbivores; although they prefer species like poplar and willow, beavers can thrive on a wide array of plant species (Gallant et al., 2004; Müller-Schwarze et al., 1994; Vorel et al., 2015).

The territorial occupation dynamics of a species are conditioned by the area they use and the duration of their presence. Beaver territorial limits and browsing trips are usually limited to a 100 m radius from shore because they rely on the safety of their lodge to avoid predators such as bears and wolves (Collen and Gibson, 2001; Gallant et al., 2004). Although this article solely focuses on the North American beaver (*Castor canadensis*), the Eurasian beaver (*Castor fiber*) has been found to occupy their territory in a similar way

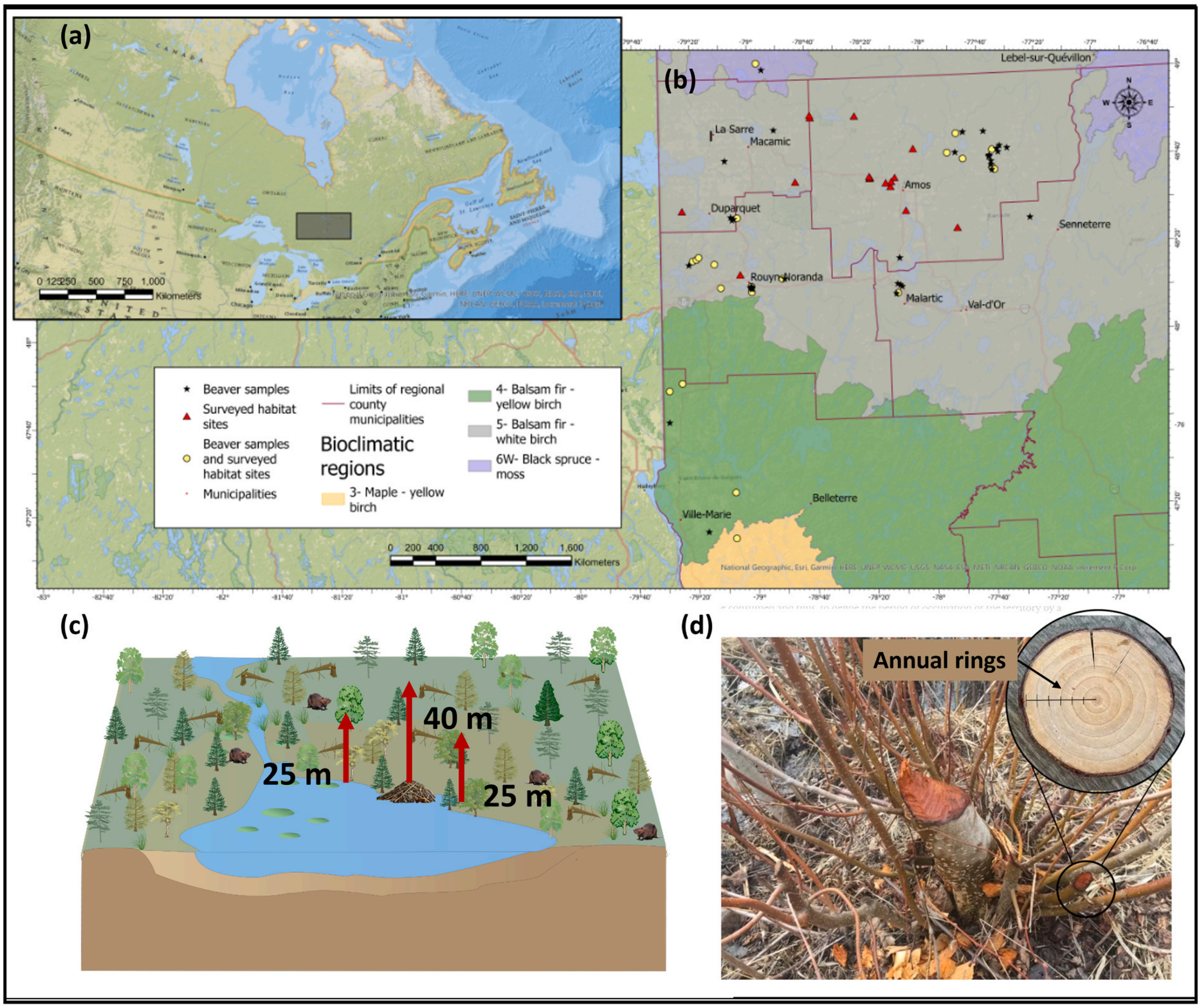


**Fig. 1.** Location of the collected beaver samples and associated beaver habitat sites (a, b); Sampling strategy around study lakes (c). Red arrows represent transects; Counting of annual rings on an alder coppice resulting from beaver browsing (d).

when living in comparable environments (Danilov and Fyodorov, 2015). Their territorial occupation averages 2.6 years to several decades (Hyvönen and Nummi, 2008; Johnston and Naiman, 1990; Nummi and Kuuluvainen, 2013), and this occupation time is highly dependent on regional climate and geomorphological characteristics, colony density, and available resources (Campbell et al., 2005; Jenkins, 1981; Touihri et al., 2018; Tremblay et al., 2017). The occupation time and territory size of beaver in the Canadian boreal forest, especially in conifer stands, remain unknown, as is the effect of lake size on beaver occupation dynamics.

Many factors influence the territorial occupation of beavers. Because North American beavers occupy a broad spectrum of ecoregions from Mexico to Alaska, territory size and occupation duration vary depending on geographic location (Rosell et al., 2005). Occupation can last less than three years in oligotrophic settings to several decades in more productive water bodies (Hyvönen and Nummi, 2008; Johnston and Naiman, 1990; Nummi and Kuuluvainen, 2013). The quantity of woody plants consumed per year is also influenced by latitude, as northern beaver colonies require a substantial food cache to survive through the cold season (Hartman and Axelsson, 2004). Driving factors that can increase occupation time include access to human-logged areas, as palatable species tend to grow in these areas, the use of multiple lodges on the same territory, the availability of palatable species, and the rate at which these plants regrow (Bluzma, 2003; Johnston and Naiman, 1990; Labrecque-Foy et al., 2020; McMaster and McMaster, 2001; Westbrook, 2021). Factors that can reduce occupation time include natural disturbances, such as insect outbreaks and forest fires (Naiman et al., 1988; Remillard et al., 1987), depletion of available palatable species, and drastic or frequent changes in water levels (Bloomquist et al., 2012; Pollock et al., 1995; Swinnen et al., 2017). Lastly, local colony density also affects the territory size and resource availability (Herr and Rosell, 2004). However, the effects of forest stand type and lake size on browsing distance and occupation duration have yet to be determined. The consequence is an absence of data regarding the territorial occupation dynamics of beaver in the boreal forest biome, a region where colony densities are high and deciduous trees are not dominant.

Our goal was to evaluate the influence of habitat characteristics (lake size and stand composition) and diet on the spatial and temporal occupation of beaver in eastern Canadian boreal forests. Specifically, we aimed to measure the maximum browsing distance from the lodge and occupation duration among different forest stands (deciduous, mixed, and coniferous) and lake sizes (small, medium, and large). We predicted that (1) maximum browsing distance would increase where the availability of deciduous species is reduced and decrease as lake size increases, as a larger perimeter favors greater resource accessibility; (2) occupation would be longer in deciduous stands and large lakes because of greater resource availability (Fryxell and Doucet, 1993; Westbrook, 2021); and (3) macrophyte consumption would increase with conifer abundance, as these aquatic plants provide an alternative source of food for beaver (Milligan and Humphries, 2010; Parker et al., 2007).

## 2. Materials and methods

### 2.1. Study area

Our study area was located in the Abitibi-Témiscamingue region of Québec, Canada (Fig. 1a). This region has two distinct bioclimatic domains: the balsam fir (*Abies balsamea* L. Mill.)–white birch (*Betula papyrifera* Marsh.) and the balsam fir–yellow birch (*Betula alleghaniensis* L.) domains (Blouin and Berger, 2002). Regional climate is humid continental (Natural Resources Canada, 2022) with a mean annual temperature of 1.5 °C and precipitation averaging 923 mm per year (1981–2010) (Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs, 2024). The growing season lasts 175–182 days per year. The topography is relatively flat with an elevation range of 240–450 m. The dominant tree species are black spruce (*Picea mariana* Mill. Britton, Sterns & Poggenburg), balsam fir, aspen (*Populus tremuloides* Michx.), and white birch (Blouin and Berger, 2002; Girona et al., 2023c; Gosselin, 2003). The region has over 20,000 lakes and the highest estimated density of beavers in the province at 5.5 colonies per 10 km$^2$ (Fortin et al., 2001; Hasan et al., 2023). Approximately 1000 licensed trappers practice beaver trapping to regulate populations (Ministère des Forêts, de la Faune et des Parcs, 2020).

### 2.2. Experimental design

We studied 61 lakes (Fig. 1b). Following the definition of "lakes" that refers to water bodies with a surface area > 5 ha compared to "ponds" (Richardson et al., 2022), we included both ponds and lakes in our study. As the majority of the selected water bodies were > 5 ha, we used the term 'lake' throughout the text to refer to both types of water bodies. Both types of water bodies may or may not have been created by the construction of a beaver dam. Both were analysed in the same manner. Lake selection was based on three criteria: trappers' activity, forest stand type, and lake size. Three types of forest stands were considered: deciduous ($n = 24$), mixed ($n = 22$), and coniferous ($n = 15$). The lakes were categorized by area to evaluate the effect of lake size on occupation dynamics: small (0–4 ha, $n = 16$), medium (>4–8 ha, $n = 16$), and large (>8 ha, $n = 29$).

### 2.3. Sampling and data compilation

Beaver carcasses were collected during the 2021–2022 trapping season (October 18, 2021, to March 21, 2022) by 11 trappers. Each trapper received a sampling kit containing the research protocol, the necessary measurements (see Supplementary material), and prefilled carcass identification tags. Beavers had to come from a lake having a lodge. Two freezers (storage at −22 °C) at the University of Québec in Abitibi-Témiscamingue (UQAT) were made available for the carcasses: one each at the Amos and Rouyn-Noranda campuses. Trappers donated either complete carcasses or a combination of organs and hair samples, frozen upon capture or within two hours of capture. Trappers recorded the geographic coordinates of the trapping location and the physical characteristics of the trapped beavers: individual weight (in kg), total body length (in cm), tail length and width (in cm), age categories (adult or juvenile), and sex (determined by palpation).

To characterize the habitats, we relied on the *Données ouvertes* and *Forêt ouverte* websites of Québec's ministère des Ressources Naturelles et des Forêts ([MRNF], 2023a; 2023b) to determine lake area (in ha), forest stand type (deciduous, mixed, or coniferous), slope (percentage categories), the distance to the closest road within 200 m (in m), and the distance to the closest harvested area (within 100 m and cut in the last 20 years, in m) of each surveyed site.

We applied a dendrochronological approach used by Paşca et al. (2016) and Labrecque-Foy et al. (2020) to determine the duration of beaver occupation at a site. At each site, we established three parallel transects perpendicular to the shoreline (Fig. 1c). The 40 m long middle transect, starting from the point on shore located closest to the lodge, served to determine the furthest distance with browsing signs. The two 25 m long outer transects were established 10 m away on either side of the central transect. Signs of chewing and annual rings on coppices, if present, were measured within sampling plots placed every 5 m along the transects. The first sampling plot was established at the lakeshore, closest to the beaver lodge, and subsequent plots extended along the transect into the forest, perpendicular to the shoreline. Each plot measured 1 $m^2$. A total of six sampling plots were set up along each 25 m transects, and nine plots along each 40 m transect. If present, we cut the largest coppice transversally at its base with pruning shears and counted the number of annual tree rings present from pith to bark (Fig. 1d). We considered the total number of rings as the number of growth years since browsing.

### 2.4. Laboratory analyses

We used tail and body measurements as an index to assess the health status of individual beaver (Parker et al., 2017). The width and length of the tail may vary depending on the season and available resources, as it serves as a fat storage organ in beavers, whereas the total body length remains constant throughout the year (Aleksiuk, 1970; Smith, 1997). To evaluate the beavers' ability to store extra energy, we calculated the ratio of tail area to overall body length (Parker et al. (2017).

In the GREMA laboratory, we dissected the beaver carcasses ($n = 97$) to retrieve three tissue samples: hair, muscle, and liver (referred to as tissues for brevity) (Parker et al., 2017). The samples were taken consistently from the same body location. These specific tissues were selected because their cell turnover rates are associated with different time windows of the beavers' diet (Carter et al., 2019). The liver provides insight into the diet from one to three weeks prior to sampling (winter diet in this case), the muscle reflects the diet from four to six weeks prior (late fall diet), and the hair, being an inert tissue, represents the diet since the beaver's last molt. Because beavers typically molt in late September, the hair tissue reflects the early fall diet. These timings are approximate.

After dissection, the samples were freeze-dried for 72 h and then ground. We weighed 1.0 mg (±10 %) of each sample using a microbalance (Sartorius Lab instruments CP2P, Göttingen, Germany) and encapsulated them in an 8 × 5 mm pressed tin combustion cup. The samples were sent to the Laboratoire d'analyse en écologie aquatique et en sédimentologie (LAEAS) at the University of Québec in Trois-Rivières (UQTR). Samples were analyzed using an elemental analyzer (Elementar Pyrocube, Langenselbold, Germany) interfaced with an IRMS mass spectrometer (Thermo-Fisher Scientific Delta V Plus, Waltham, MA, United States). Stable isotope values are presented in standard delta notation following the formula

$$\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 10^3$$

where $X$ is $^{13}C$ or $^{15}N$, and $R$ is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotopic ratio. The values were normalized to the international reference materials, USGS 40 ($\delta^{13}C = -26.39$ ‰; $\delta^{15}N = -4.52$ ‰) and USGS 41 ($\delta^{13}C = 37.63$ ‰; $\delta^{15}N = 47.57$ ‰), atmospheric $N_2$ ($\delta^{15}N$) and Vienna Pee Dee Belemnite ($\delta^{13}C$). Working standards were run every 10 samples to monitor instrument performance and verify data normalization. The laboratory standards had a precision of ±0.3 ‰ for C and N. No pre-analysis lipid treatment was applied to the samples.

We also collected leaf or needle samples of all dominant plant species observed at each site (coniferous, deciduous, herbaceous, and macrophytes). Samples were freeze-dried for 72 h and then ground. Between 3.0 and 3.2 mg of each sample was placed in a tin combustion cup and sent for $\delta^{13}C$ and $\delta^{15}N$ analysis at the Stable Isotopes in Nature Laboratory (SINLAB) at the University of New Brunswick. The samples were loaded into a PN150 autosampler and analyzed in a similar continuous-flow mode (Costech Analytical Technologies; Valencia, CA; USA) with an NC2500 elemental analyzer (Carlo-Elba; Milan; Italy) and a Delta V Plus isotope ratio mass spectrometer via a Conflo-IV interface (Thermo-Fisher Scientific; Waltham, MA; USA). The total analytical uncertainty was estimated to be less than 0.2 ‰ ($\delta^{13}C$: 0.16 ‰ and $\delta^{15}N$: 0.19 ‰).

### 2.5. Data analysis

We used Permutational Multivariate Analysis of Variance (PERMANOVA) using Euclidian distance to compare the mean maximum browsing distance and occupation duration among lake size categories and forest stand types. A pairwise comparison analysis was done when results were significant. A test for homogeneity of multivariate dispersion was also performed using betadisper for each PERMANOVA. Multiple linear regressions were conducted to assess correlations between occupation time, maximum browsing distance, $\delta^{13}C$ in tissues, and health index. The independent variables included lake size in hectares, type of forest stand, maximum browsing distance, distance to the closest road, and distance to the closest harvested area within 200 m. We used the simmr package in R version 4.3.2 to model the diet (Govan and Parnell, 2023; R Core Team, 2023). The model output of each tissue was kept separate because each corresponds to a different time window. We applied a specific trophic enrichment factor (TEF) for each tissue rather than a generic average value. The TEF for liver, hair, and muscle were each estimated using the SIDER package in R, as no existing TEF data were found for *Castor canadensis* (Healy et al., 2017; R Core Team, 2023).

## 3. Results

### 3.1. Spatial dynamics

The PERMANOVA revealed a statistically significant effect of the lake size on the maximum range ($F_{(2,\ 49)} = 8.66$, $R^2 = 0.261$, $p = 0.003$, permutations = 999), indicating that 26.1 % of the variation in range can be explained by the hydrological category (Fig. 2a). The test for homogeneity of multivariate dispersion showed no significant difference in dispersion across the hydrological categories ($F = 0.20$, $p = 0.823$), indicating that the assumption of equal group dispersion was met for the PERMANOVA analysis. Maximum browsing distance differed significantly across hydrological categories, indicating a strong effect in the small (F = 21.65, $R^2 = 0.454$, p = 0.001) and large lake classes (F = 7.54, $R^2 = 0.159$, p = 0.014), but not in the medium class (F = 2.91, $R^2 = 0.083$, p = 0.109). On average, browsing distance was significantly shorter in medium lakes (mean = 17 m) compared to small (33 m) and large lakes (26 m), corresponding to browsing distances that were 97 % longer in small and 57 % longer in large lakes than in medium ones. The type of forest stand did not influence maximum browsing distance (means of 21, 23, and 28 m respectively, Fig. 2b), despite the marked variability observed in deciduous stands ($F_{(2.49)} = 1.67$, $R^2 = 0.064$, $p = 0.195$, permutations = 999). Additionally, the test for homogeneity of multivariate dispersion showed no significant differences in dispersion among groups (F = 1.15, $p = 0.326$), confirming that the assumption of equal dispersion was met.

### 3.2. Temporal dynamics

Mean occupation time was influenced by the lake size category (Fig. 3a) ($F_{(2,\ 42)} = 6.55$, $R^2 = 0.238$, $p = 0.006$, permutations = 999), indicating that 23.8 % of the variation in temporal occupation is explained by differences among the hydrological categories (Fig. 3a).It was being significantly different in large lakes (7.5 years, SD = 3.26) when compared to small or medium lakes ($F = 8.72$, $R^2 = 0.244$, $p = 0.008$, $F = 6.51$, $R^2 = 0.153$, $p = 0.01$), while no significant difference were observed when comparing small to medium lakes ($F = 2.40$, $R^2 = 0.103$, $p = 0.141$). In comparison, the mean occupation time was 234 % shorter in small lakes (3.3 years, SD = 3.86) and 45 % shorter in medium lakes (5.2 years, SD = 2.2). The test for homogeneity of multivariate dispersion showed no significant difference in group dispersions ($F = 0.24$, $p = 0.784$), suggesting that the assumption of equal dispersion was met. The type of forest stand had no significant effect on mean occupation time (Fig. 3b) (F = 1.10, $R^2 = 0.050$, p = 0.33, permutations = 999).

### 3.3. Diet and food sources

The $\delta^{13}C$ ratios differed significantly among all three tissues ($F_{(2,\ 199)} = 378.6$, p = 0.001, with tissue type explaining 79.2 % of the variation in $\delta^{1\ 3}C$ ($R^2 = 0.7919$)) (Fig. 4). Hair samples had the highest enrichment (mean ± SD = −25.0 ‰ ± 0.5 ‰), whereas the liver had the lowest (mean ± SD = −27.1 ‰ ± 0.5 ‰). Muscle tissue fell in between (mean ± SD = −26.1 ‰ ± 0.6 ‰). However, there was no significant difference in $\delta^{13}C$ levels (across all tissues) in relation to lake size, forest stand type, slope, or geographic subregion. When each tissue was analyzed separately, $\delta^{13}C$ in hair and muscle showed significant differences between deciduous and coniferous stands ($F_{(2,81)} = 4.62$, p = 0.014.and $F_{(2,\ 18)} = 4.20$, $p = 0.025$ respectively) (Figs. 4a and b). Liver $\delta^{13}C$ did not differ significantly among all forest stand types ($F_{(2,\ 94)} = 0.26$, $p = 0.7762$) (Fig. 4c).

Macrophytes were present in 10 of the 23 sampled lakes. Macrophytes were similarly distributed across the lake size categories (small = 3, medium = 3, large = 4), but they were three times more common in deciduous forest stands ($n = 6$) than in mixed ($n = 2$) and coniferous stands ($n = 2$). Their presence affected maximum browsing distance ($F_{(1,\ 342)} = [10.59]$, $p = 0.001$). Maximum browsing distance was longer (mean = 25 m) when macrophytes were present ($F_{(1,\ 342)} = [10.59]$, $p = 0.00125$). Macrophyte presence

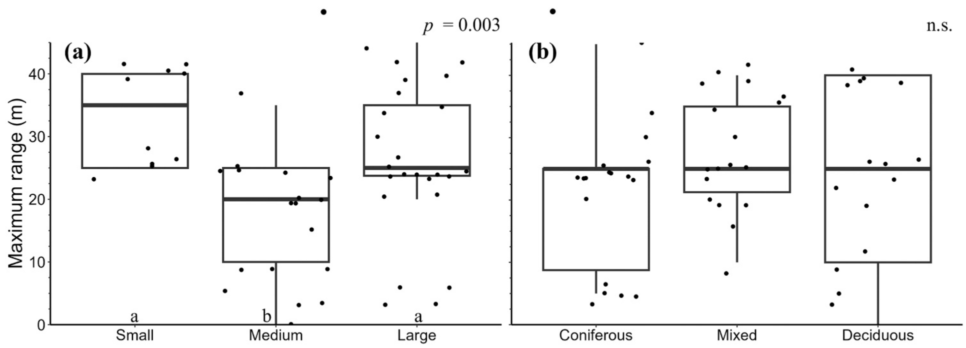


**Fig. 2.** Maximum browsing distance according to (a) lake size category and (b) forest stand type. Same letters are not significantly different at α = 0.05; nonsignificant, n.s.

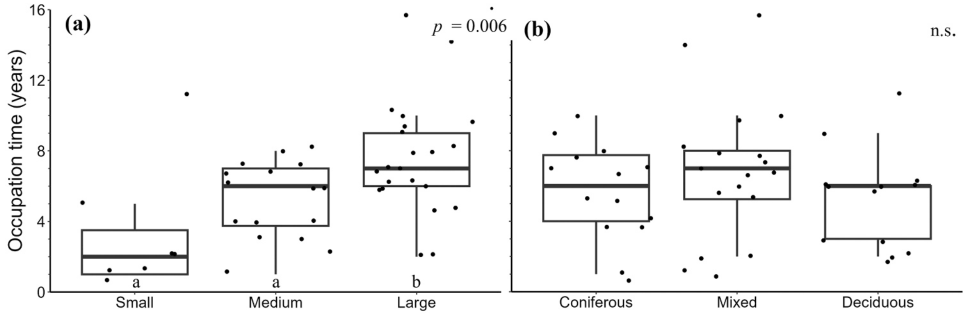


**Fig. 3.** Mean occupation time per colony according to (a) lake size category and (b) forest stand type. Same letters are not significantly different at α = 0.05; nonsignificant, n.s.

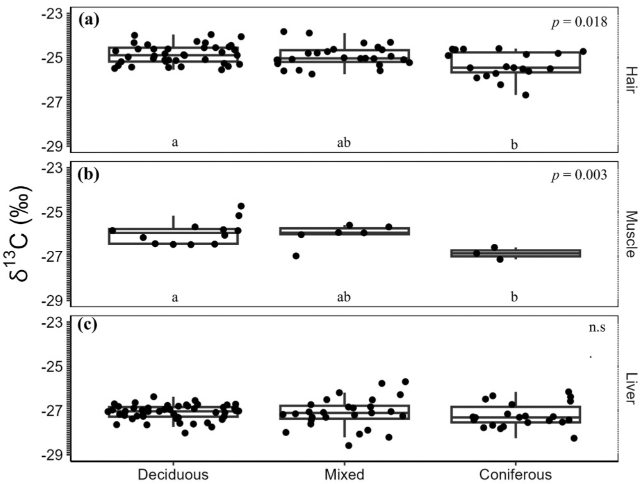


**Fig. 4.** Values of $\delta^{13}C$ in beaver tissues according to forest stand type from which the tissues originated. The $\delta^{13}C$ in deciduous and coniferous stands differed significantly from each other but were similar among all stand types for the liver samples. Same letters are not significantly different at α = 0.05; nonsignificant, n.s.

did not affect mean occupation duration ($F_{(2,\ 342)} = [2.507]$, $p = 0.114$), and the presence/absence of macrophytes in the lake did not affect diet (all tissues combined and separated) ($F_{(1,\ 152)} = [0.065]$, $p = 0.798$ for all tissues, $F_{(1,\ 72)} = [0.343]$, $p = 0.56$ for liver, $F_{(1,\ 59)} = [0.188]$, $p = 0.667$ for hair, and $F_{(1,\ 17)} = [4.156]$, $p = 0.0573$ for muscle).

The diet model showed a different composition in each tissue. Hair samples averaged the least negative $\delta^{13}C$ values and highest $\delta^{15}N$ values of all tissue types (Fig. 5a), whereas liver samples demonstrated the highest proportion of conifer in the diet (Fig. 5c).

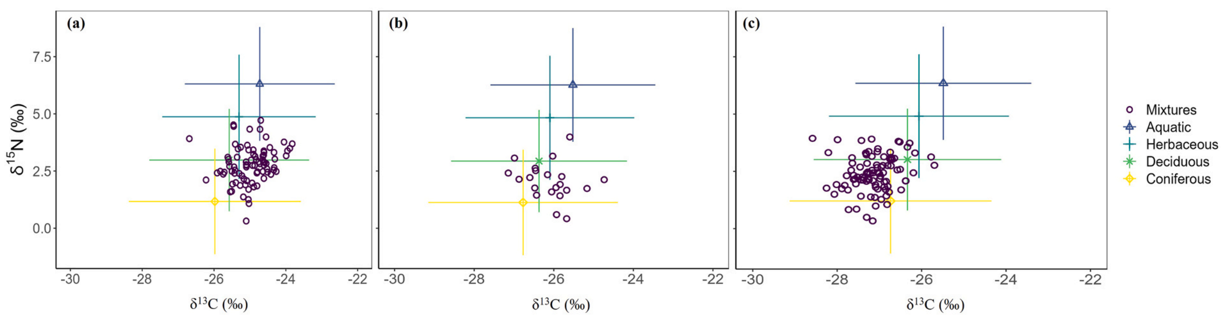


**Fig. 5.** Stable isotopes in beaver (a) hair, (b) muscle, and (c) liver according to surveyed habitats. Crosses represent the mean and standard deviation of the $\delta^{13}C$ and $\delta^{15}N$ for each group of plants.

### 3.4. Health index

The health index was similar across all lake size categories and types of forest stands ($F_{(2,\ 86)} = [0.443]$, $p = 0.643$ and $F_{(2,\ 86)} = [0.358]$, $p = 0.7$ respectively). We found no significant correlations between the health index and lake area, proximity to a road, maximum browsing distance, or occupation time, when taken individually. Nor did we find a correlation between the health index and the $\delta^{13}C$ ratio in the liver tissue ($F_{(1,\ 87)} = [1.4773]$, $p = 0.228$).

Multiple linear regressions revealed that the health index was significantly influenced by forest stand type and distance to the nearest road, explaining 52 % of the variation ($R^2 = 0.52$; Table 1). Health index was significantly lower in deciduous and mixed stands compared to coniferous stands and increased with greater distance from roads.Occupation time was best predicted by a combination of forest stand type, lake area, and distance to the nearest road, accounting for 58 % of the variance ($R^2 = 0.58$). Occupation time was significantly longer in mixed stands but decreased with increasing lake area and shorter distances to roads. The model for maximum browsing distance explained 62 % of the variance ($R^2 = 0.62$), with forest stand type as the only significant predictor. Browsing distances were significantly higher in deciduous and mixed stands compared to coniferous ones, while lake area and road proximity had no significant effect. Finally, $\delta^{1\ 3}C$ values increased with both lake area and maximum browsing distance, with the model explaining 59 % of the variance ($R^2 = 0.59$; Table 1, Fig. 6).

## 4. Discussion

As a keystone species, beavers preserve wetlands, stabilize water levels, and increase forest resilience (Cunningham et al., 2006; Gallant et al., 2016; Hering et al., 2001; Puttock et al., 2021; Stringer and Gaywood, 2016; Westbrook et al., 2011). Despite this ecological importance, there is still limited research on the territorial occupation dynamics of beavers. In this study, we examined 61 lakes and 97 beaver carcasses, finding that lake size is the main driver of territorial occupation dynamics for beavers, with resource availability having a limited effect.

### 4.1. Spatial dynamics

Spatial and temporal dynamics are highly correlated for many species, as territory size determines occupation time (Graf et al., 2016). However, our study is the first to demonstrate the importance of lake size on beavers' territorial occupation dynamics in the boreal biome. Therefore, the maximum observed browsing distance that beavers will forage from the lake is a good indicator of territory size. We found that the shortest maximum browsing distance was associated with medium-sized lakes (4–8 ha), which is likely the optimal territory size that a beaver colony can defend and occupy (Campbell et al., 2005). Optimal territory size varies depending on the region, ecotone, local population density, habitat quality, and the number of members per colony; therefore, no consensus exists on optimal territory size for beavers (Campbell et al., 2005). Occupying a large territory consumes a high amount of energy and requires much time to defend and patrol, even when more resources are available (Mayer et al., 2017). In our study area, we found that the optimal territory size for a colony ranged from 4 to 20 ha. We also observed that the maximum browsing distance increased rapidly in lakes 20 ha and larger but was not correlated with occupation time, likely because of the presence of other nearby beaver colonies. Beaver families are territorial and defend exclusive areas around their lodge or dam, typically ranging from 0.5 to 3 km of shoreline (Novak, 1987). However, when multiple families inhabit the same lake, especially a large one, territories may overlap, increasing intraspecific competition for resources. The maximum browsing distance was not influenced by the type of forest stand, slope, presence of a harvested area, or presence of a road. Thus, beavers have a generalist strategy and a high adaptability (Baker

**Table 1**
Stepwise multiple linear regressions of health index, occupation time, maximum browsing distance, and diet ($\delta^{13}C$ values). Significance: ***, 0.001; **, 0.01; *, 0.05; nonsignificant, n.s.

| Response variable | $R^2$ | Model *p*-value | Independent variable | Slope | Standard error | *t*-ratio | VIF | *P*-value |
|---|---|---|---|---|---|---|---|---|
| Health index | 0.5188 | 0.000965 | Forest stand (intercept) | 3.157756 | 0.198745 | 15.888 | 1.592432 | **< 0.0001** |
| | | | Forest stand (deciduous) | −1.306911 | 0.287242 | −4.550 | | **0.0002** |
| | | | Forest stand (mixed) | −0.940772 | 0.352946 | −2.665 | | **0.016** |
| | | | Distance to nearest road | 0.007377 | 0.002263 | 3.260 | 1.592432 | **0.004** |
| Occupation time (years) | 0.5787 | 0.0111 | Forest stand (intercept) | 10.22388 | 1.86883 | 5.471 | 2.802673 | **0.0002** |
| | | | Forest stand (deciduous) | −1.63081 | 1.95219 | −0.835 | | 0.423 |
| | | | Forest stand (mixed) | 7.66093 | 2.40737 | 3.182 | | **0.01** |
| | | | Area | −0.48160 | 0.14822 | −3.249 | 1.965239 | **0.009** |
| | | | Distance to nearest road | −0.04007 | 0.01249 | −3.207 | 1.559070 | **0.009** |
| Maximum browsing distance | 0.6178 | 0.007032 | Forest stand (intercept) | 0.52389 | 6.26558 | 0.084 | 2.802673 | 0.935 |
| | | | Forest stand (deciduous) | 30.93980 | 6.54507 | 4.727 | | **0.001** |
| | | | Forest stand (mixed) | 30.41749 | 8.07112 | 3.769 | | **0.004** |
| | | | Area | 0.67306 | 0.49693 | 1.354 | 1.965239 | 0.205 |
| | | | Distance to nearest road | −0.06632 | 0.04189 | −1.583 | 1.559070 | 0.144 |
| $\delta^{13}C$ | 0.5869 | 0.001972 | (Intercept) | −27.96085 | 0.266473 | −104.92 | | **< 0.0001** |
| | | | Area | 0.073299 | 0.018691 | 3.922 | 1.035993 | **0.002** |
| | | | Max. browsing distance | 0.015468 | 0.008713 | 1.775 | 1.035993 | 0.101 |

and Hill, 2003; Jenkins, 1975).

### 4.2. Temporal dynamics

Most disturbances caused by beavers are related to the colonization of new habitats (Johnston and Naiman, 1990). Thus, understanding the factors influencing occupation time is essential for anticipating potential changes in the ecosystem. In our study, beavers stayed longer in the larger lake category (mean 7.5 years), implying that lake size influenced occupation time. A larger lake provides a longer perimeter and therefore more access to resources, which can delay resource depletion on the territory. Graf et al. (2016) also found a territory size–dependent trade-off between resource benefits and defense that was more advantageous to Eurasian beavers in larger lakes. Colonies in larger lakes spend more time patrolling but stay closer to the shore to browse, whereas colonies in smaller lakes must forage further inland to browse because of resource depletion and therefore face a higher risk of predation (Graf et al., 2016). In our study, occupation time tended to increase with lake size but was significantly longer only in lakes larger than 8 ha, probably because of a higher availability of food resources associated with a longer perimeter. Other variables, such as frequent fluctuations in beaver pond water levels, may also influence occupation time, as entrances must remain constantly submerged and deep enough (minimum 0.7 m) to prevent freezing in winter (Bloomquist et al., 2012; Hartman and Törnlöv, 2006).

### 4.3. Diet and health

Diet composition affects territory use and helps predict beaver damage in forest stands (Gallant et al., 2004). Therefore, it is essential to examine beavers' feeding strategies in landscapes with fewer palatable species (Fryxell and Doucet, 1993). The $\delta^{13}C$ values were similar across all categories of lake size and forest stand types but differed significantly among tissues (Fig. 4). In our study, hair samples had the highest $\delta^{13}C$ values, whereas liver samples had the lowest. Muscle samples had intermediate $\delta^{13}C$ ratios. Depleted $\delta^{13}C$ ratios (approx. −27 ‰) are associated with terrestrial woody plants like coniferous and deciduous trees (Grosbois et al., 2020), whereas enriched $\delta^{13}C$ values (between approx. −22 ‰ and −20 ‰) are associated with herbaceous plants and macrophytes (Grosbois et al., 2017a,b; Kumar et al., 2016; Meyers, 1994). The observed $\delta^{13}C$ ratios can also reflect different seasons (Carter et al., 2019).

The enriched $\delta^{13}C$ ratios in hair samples suggest a diet high in herbaceous plants and macrophytes in the early fall, whereas the depleted $\delta^{13}C$ ratios in the liver samples reflect a winter diet mainly composed of coniferous and deciduous woody plants, consistent with the use of a food cache (Carter et al., 2019). Beavers experience unique conditions during winter when fresh foliage is unavailable and terrestrial access is limited. They rely on the stored underwater food cache accumulated outside their lodge in the fall, supplemented with occasional macrophyte rhizomes from the lake floor (Jenkins and Busher, 1979). Previous studies mentioned beaver browsing on conifers, but it was assumed to be for construction and repairs rather than consumption (Flynn, 2006). Our stable isotope data suggests that beavers do consume conifers in boreal forest settings, primarily during winter when deciduous resources are scarce.

The abundance, diameter, and density of palatable deciduous trees can positively affect beavers' spatial dynamics (Fryxell and Doucet, 1993). However, in coniferous forest stands with fewer palatable species, beavers may use alternative strategies to avoid increasing browsing distance or delaying migration. To conserve energy and reduce predation risk, beavers may consume other sources such as macrophytes and conifers rather than embarking on longer browsing trips (>50 m) (Gallant et al., 2016; Westbrook, 2021). We also examined the influence of macrophytes on diet composition. Milligan and Humphries (2010) found that macrophytes could account for up to 80 % of a beaver's diet in autumn and winter. In our study, macrophytes were most prevalent in hair and muscle samples (early and late fall) and least prevalent in the liver (winter). Although there were no differences in $\delta^{13}C$ between lakes with and without macrophytes, the results indicated a tendency toward a greater consumption of herbaceous plants and macrophytes in deciduous stands than in coniferous stands, contrary to our hypothesis. This observation could be explained by beavers' opportunistic feeding strategy and the greater abundance of macrophytes in deciduous stands than in mixed or coniferous stands. Although we were unable to quantify the use of herbaceous plants and macrophytes in the beavers' diet, our study revealed a seasonal shift suggesting increased consumption of these resources in the fall (Phillips and Gregg, 2003). This likely indicates an accumulation strategy of essential molecules, such as healthy fats, for winter survival and early spring reproduction similar to other aquatic organisms (Grosbois et al., 2017a,b; Grosbois and Rautio, 2018; Schneider et al., 2017). Further research using stable isotope and fatty acid analyses across different biomes and habitat characteristics would greatly enhance our understanding of macrophyte and conifer consumption in beavers.

The health index from the tail serves as a valuable tool for assessing the well-being of beaver colonies in the surrounding forest stand and the quantity/quality of available resources. In our study, the health index remained consistent regardless of stand type or lake size. We specifically relied on liver samples for this assessment because the beavers were captured in late fall and winter, which best corresponds to the diet time window recorded by the liver samples. The lack of correlation with the health index suggests that beavers possess a high level of adaptability, enabling them to thrive independently of the available resources in their habitat (Gallant et al., 2016; Touihri et al., 2018).

### 4.4. Implications for ecosystem-based forest management

In recent decades, ecosystem-based forest management has aimed to simulate natural disturbance effects on forest landscapes to reduce differences between natural and managed stands and increase forest resilience (Gauthier, 2009; Girona et al., 2023a,b,c; Hasan et al., 2020; Johnstone et al., 2016). Understanding the natural disturbance regime of a region is crucial for achieving these goals (Girona et al., 2023a,b,c). This management approach primarily focuses on major, intense disturbances, e.g., fire and insect outbreaks

(Molina et al., 2022; Subedi et al., 2023), rather than smaller-scale, secondary disturbances such as beavers . However, incorporating beavers as a common natural disturbance into boreal forest ecosystem-based management plans could provide a valuable framework, especially given their expected increase due to climate change (Boisvert-Marsh et al., 2014; Jarema et al., 2009; McManus et al., 2012; Tape et al., 2018). Beavers also create important habitats and offer resources for both aquatic and terrestrial fauna and flora, while helping to protect aquatic ecosystems during intense natural disturbances such as wildfires and droughts (Fairfax and Whittle, 2020; Hood and Bayley, 2008). Furthermore, they help buffer landscapes from ecological degradation caused by logging and nutrient runoff (Guimond et al., 2024; Westbrook et al., 2006), thereby reducing the conditions that favor cyanobacterial blooms (Grosbois et al., 2024).

Our study is one of the first to demonstrate that lake size significantly influences a beaver's territory occupation time and maximum browsing distance in the boreal forest. Thus, beavers inhabiting large lakes are less likely to relocate in the near future. Forest managers can use this information, along with other factors identified in our study, to choose suitable sites for harvesting or infrastructure installation that are less susceptible to beaver damage. This can help prevent and minimize the costs and conflicts associated with human–beaver interactions (Tremblay et al., 2017).

## 5. Conclusion

The territorial occupation by beavers is a complex, poorly understood, and quite understudied phenomenon (Curtis and Jensen, 2004; Feldman et al., 2020; Labrecque-Foy et al., 2020). In this study, we found that the spatiotemporal use of the territory was primarily influenced by lake size and that resource quality and availability had limited effects. Over time, however, an established beaver colony can adapt the size of its aquatic habitat by building or expanding dams to reach additional resources farther inland. To extend their occupation time, beavers also adapt by shifting their browsing to alternate food choices, e.g., macrophytes and conifers, rather than migrating to a new territory (Swinnen et al., 2017). Our study demonstrated that beavers are very adaptable, from the way they occupy their territory to how they use available food resources. Our results will be helpful for predicting and minimizing the impact of beavers on forest ecosystems, and we recommend further research focused on the adaptability and resilience of this species, as climate change will cause a northward shift in the distribution range the deciduous trees preferred by beavers (Boisvert-Marsh et al., 2014; Hof et al., 2021; Jarema et al., 2009; McManus et al., 2012).

## Ethics statement

Not applicable: This manuscript does not include human or animal research.

## CRediT authorship contribution statement

**Mélanie Arsenault:** Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Guillaume Grosbois:** Writing – review & editing, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Conceptualization. **Julie-Pascale Labrecque-Foy:** Writing – review & editing, Methodology, Data curation. **Miguel Montoro Girona:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

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## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Miguel Montoro Girona reports was provided by UQAT (Canada). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03723.

## Data availability

Data will be made available on request.

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