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Original Investigation

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ABSTRACT

Forage availability can affect body condition and reproduction in wildlife. We used terrestrial and aquatic vegetation sampling, stable isotope analysis, and livetrapping to investigate the influence of estimated forage biomass on diet, body condition, and reproduction in American beavers (*Castor canadensis*) in the Namakan Reservoir, Voyageurs National Park, Minnesota, USA, May 2008–September 2009. Available terrestrial and emergent aquatic forage varied greatly among territories, but floating leaf aquatic forage was low in abundance in all territories. Variation in estimated biomass of available emergent and terrestrial vegetation did not explain variation in respective assimilated diets, but variation in floating leaf vegetation explained 31% of variation in assimilated floating leaf diets. No models using available vegetation explained variation in body condition. Body condition of individual females in spring did not affect kit catch per unit effort, and overwinter body condition of subadults and adults was similar between territories with and without kits. We found no evidence that available aquatic vegetation affected beaver body condition or fitness. Available forage may be above minimum thresholds to detect differences in diet choice or body condition. Other factors such as water level fluctuations or climatic variables may also explain variation in beaver body condition.

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Introduction

Forage availability can limit herbivore populations, and affect foraging behavior and growth rates (Shelton, 1966; Therrien et al., 2008). Reduced foraging time can limit energy gained by an animal, adversely affecting body condition and subsequent reproductive success (McNamara and Houston, 1992; Belant et al., 2006). For example, American beaver (*Castor canadensis*) growth rates depend on available forage, as well as climate, and degree of population exploitation (Baker and Hill, 2003). Body mass and tail size are common indices of body condition in beavers (Aleksiuk, 1970; Smith and Jenkins, 1997) and have been directly associated with forage availability (Shelton, 1966; Breck et al., 2001).

Habitat quality and maternal mass were positively associated with beaver productivity (Rutherford, 1964; Wigley et al., 1983). Aquatic and terrestrial forage availability has been used to infer habitat quality, with beaver litter size increasing with overall forage availability (Fryxell, 2001; Baker, 2003; Baker et al., 2005). Further, beavers select certain plant species among many species consumed (e.g., deciduous species over coniferous species; Busher,

1995), and are more selective in high-quality habitat (Gallant et al., 2004), presumably to improve fitness. For example, beavers feeding on quaking aspen (*Populus tremuloides*), considered a high-quality food, produced more kits than beavers feeding on cottonwoods (*P. deltoides*), willows (*Salix* spp.), or birch (*Betula papyrifera*; Huey, 1956; Longley and Moyle, 1963; Shelton, 1966). In Voyageurs National Park, MN, USA, quaking aspen density was positively correlated with kit production (Smith, 1997). Aquatic vegetation has also been considered high-quality food, with aquatic vegetation generally having higher digestibility (Belovsky, 1984; Doucet and Fryxell, 1993); higher mineral and protein content (Fraser et al., 1984); and lower amounts of cellulose, lignin and secondary metabolites (Doucet and Fryxell, 1993) than terrestrial vegetation.

During winter, northern populations of beavers are restricted from accessing most forage. Novakowski (1967) hypothesized that beaver caches in northern latitudes are not calorically sufficient to meet colony energy requirements, and that methods of energy conservation such as lipolysis (Aleksiuk, 1970), decrease in activity (Lancia et al., 1982), and core body temperature depression (Smith et al., 1991) are necessary for winter survival. Smith et al. (1991) found decreases in overwinter body temperature of yearling and adult beavers, but not in kits. Limited forage during winter results in adult and subadult mass loss (Smith and Jenkins, 1997). The presence of kits in the lodge over winter increases mass loss in

adults and subadults sharing the lodge, presumably because of increased forage limitations (Smith and Jenkins, 1997). Winter diets are generally assumed to include the food cache (Baker and Hill, 2003) and aquatic vegetation may constitute a significant portion of winter diets when present (Northcott, 1972; Dennington and Johnson, 1974; Jenkins, 1980; Ray et al., 2001; Severud et al., 2013). Availability of aquatic forage items in winter may therefore have important consequences for diet choice and fitness in beavers.

Our objective was to elucidate the role of available forage on beaver diet choice and fitness. We hypothesized that if beavers are limited by high quality forage (e.g., quaking aspen, aquatic vegetation), then availability of that forage would affect body condition. We predicted higher use of aquatic vegetation than expected by availability of aquatic biomass. We predicted that greater available biomass of aquatic vegetation would lead to improved body condition, which would result in higher kit production. We also predicted that adults that overwintered with kits would be in poorer condition in spring than adults that did not overwinter with kits. From Smith (1997), we predicted a positive relationship between density of quaking aspen stems and kit production.

Material and methods

Study area

We conducted this study in the Namakan Reservoir, Voyageurs National Park (VNP; 48° 36′N, 93° 25′W; 88,628 ha), Minnesota, USA, 2007–2008, which is regulated by two dams at its outlet (Kallemeyn et al., 2003). The park lies at the southern limit of the boreal forest and includes areas of northern hardwood forest (Kurmis et al., 1986). July temperatures average 18.6 °C and Jan. temperatures average −16.1 °C. Generally ice-in occurs in mid-Nov. and ice-out in late Apr. or early May (Kallemeyn et al., 2003). Timber harvest and fire from the 1930s to the 1960s created ideal beaver habitat with abundant aspen (*Populus* spp.), and beaver densities exceeded 1 colony/km^2 from the 1980s to the early 2000s (Smith and Peterson, 1988; Windels, 2008). Uplands are dominated by quaking aspen (*P. tremuloides*), paper birch (*Betula papyrifera*), pines (*Pinus* spp.), balsam fir (*Abies balsamea*), and spruce (*Picea* spp.); wetlands are dominated by white water lily (*Nymphaea odorata*), cattail (*Typha* spp.), and bulrushes (*Scirpus* spp.; Hop et al., 2001). Beaver predators in the park include wolves (*Canis lupus*) and black bears (*Ursus americanus*; Baker and Hill, 2003).

Livetrapping

We livetrapped beavers near active lodges using Hancock traps (Hancock Traps Co., Buffalo Gap, South Dakota, USA) set on trails or baited with aspen and ground castoreum gland during spring (May 2008–2009) and fall (Sep.–Oct. 2007–2008). We manually restrained beavers without using anesthesia, attached ear tags (No. 3 monel, National Band and Tag Co., Newport, Kentucky, USA) and measured body mass (±0.01 kg); maximum tail length (±0.1 cm) and width (±0.1 cm); tail thickness at length midpoint, halfway between center and edge of tail (±0.1 mm); and zygomatic arch breadth (±0.1 mm). We determined sex by external palpation (Osborn, 1955), genetic analysis (Williams et al., 2004), or necropsy. We used a razor to collect claw samples from the third toe of the right hind foot, obtaining a thin layer along the dorsal surface from the cuticle to the distal tip. Tagged beavers that died of natural causes or were legally trapped were occasionally recovered. We aged carcasses using dentition (van Nostrand and Stephenson, 1964; Larson and van Nostrand, 1968) and used measurements taken at capture from aged beavers to create a mass and zygomatic arch discriminant function to classify all livetrapped beavers as adult (>3 y), subadult (1.5–3 y) or kit (0–1.5 y). We divided

number of kits livetrapped by number of adjusted trap nights (Beauvais and Buskirk, 1999) at each lodge to calculate catch per unit effort (CPUE). Lodges were generally trapped using 5 traps over 3 consecutive nights. Methods confirmed to guidelines of the American Society of Mammalogists (Sikes et al., 2011) and were approved by Northern Michigan University's Institutional Animal Use and Care Committee.

Vegetation sampling

We estimated available forage in 22 beaver territories from the Namakan Reservoir, using a 400-m radius around each lodge (Smith and Peterson, 1988). To survey terrestrial vegetation, we arranged 12 equally spaced transects perpendicular to shoreline. Smith and Peterson (1988) found cut stems ≤40 m from shore; our transects were 60 m long to account for beavers potentially foraging farther inland as preferred species were depleted closer to shore. We divided transects into 12 5-m-long by 3-m-wide plots. Within each plot, we recorded species and diameter at breast height (dbh) of all trees and shrubs with ≥2 cm dbh.

We calculated total edible terrestrial woody biomass (leaves, twigs, bark) for each territory using species-specific allometric equations of the form:

$$biomass = A \times (dbh)^B$$

where biomass is in dry kg, and A and B are species-specific coefficients (Connolly and Grigal, 1983; Buech and Rugg, 1995; Ter-Mikaelian and Korzukhin, 1997). As equations were not available for all species (Appendix 1), we used Buech and Rugg's (1995) combined species (mountain maple [*Acer spicatum*], alder [*Alnus rugosa* and *A. crispa*], serviceberry [*Amelanchier* spp.], and beaked hazelnut [*Corylus cornuta*]) equation for unknown shrubs, viburnum (*Viburnum* spp.), and hawthorn (*Crataegus* spp.). We used Ter-Mikaelian and Korzukhin's (1997) red maple equation for boxelder (*Acer negundo*), mountain maple, and red maple; and their paper birch (*Betula papyrifera*) equation for hophornbeam (*Ostrya virginiana*), as they are both Betulaceae. We used Ter-Mikaelian and Korzukhin's (1997) balsam fir (*Abies balsamea*) equation for all conifers. We summed edible biomass for each of the 12 transects for each territory, and did not include cut stems in biomass estimations.

We surveyed aquatic vegetation (Appendix 1) from late-July to August to coincide with maximum leaf-out. We delineated the perimeter of each patch using GPS units and estimated patch area in ArcGIS (Environmental Services Research Institute, Inc., Redlands, California, USA). We estimated density of each aquatic species in each patch by counting individual plants within 1-m^2 quadrats, at a sampling intensity of about 1 quadrat/10 m^2. Because cattail (*Typha* spp.) grows at high densities, we used a 0.25-m^2 quadrat for cattail stems at the same sampling intensity. We counted wool grass (*Scirpus cyperinus*) by number of flowering stems, softstem bulrush (*Scirpus validus*) by number of all stems, and arrowhead (*Sagittaria* spp.), yellow pond-lily (*Nuphar lutea*), and white water lily (*Nymphaea odorata*) by number of leaves. We collected 10 entire individuals of each aquatic species. We oven dried aquatic plants at 65 °C to a constant mass and weighed samples. We assumed entire plants were edible and estimated total above and below ground biomass by multiplying plant density by mean dry biomass per species.

Stable isotope analysis

Stable isotope analysis of carbon (C) and nitrogen (N) can be used to reconstruct diets (Kelly, 2000), with isotopic signatures of herbivore tissues reflecting the stable isotope ratios of plants

assimilated (Stewart et al., 2003). Isotopic signatures can be used to separate plants into broad categories based on such qualities as photosynthetic pathway or carbon source (e.g., aquatic macrophytes from terrestrial plants; LaZerte and Szalados, 1982; Keeley, 1998; Cloern et al., 2002; Milligan et al., 2010). Keratin (in claws, hooves, or nails) provides less variable results than soft tissue when used to estimate assimilated diet (Kielland, 2001; Struck et al., 2002; Belant et al., 2006), and can be sampled to represent a temporal record of assimilation (Mizukami et al., 2005).

We used stable isotope analysis of C and N to assess resource use. To characterize isotopic signatures of potential beaver food items, we opportunistically collected 1 sample each of 26 food species (Severud et al., 2013) from 6 sites within the study area. We collected leaves and twigs of terrestrial woody vegetation, all above-ground biomass of terrestrial herbaceous vegetation, and entire plants of aquatic vegetation. We placed samples in plastic bags and froze them until analysis. We collected vegetation samples in summer only, as $\delta^{15}N$ and $\delta^{13}C$ exhibit temporal consistency (Kielland, 2001; Milligan et al., 2010). To estimate average seasonal growth rates for claws, we examined marks on claws from beavers captured in consecutive trapping periods (i.e., beavers captured in fall and the following spring were used to calculate winter growth rate) using data from a larger study at VNP from 2006 to 2010 (S. Windels, unpublished data). We measured the mark from the previous cut to the cuticle (± 0.1 mm) and calculated mean daily growth rate by dividing the amount of growth by the number of days between captures.

Voyageurs National Park staff and the International Falls Daily Journal recorded ice-out dates (date when boat traffic is deemed safe). We estimated ice-in dates (date when the entire lake is covered with ice) for the Namakan Reservoir by examining climate data (National Oceanic and Atmospheric Administration, http://www.crh.noaa.gov for International Falls, Minnesota, USA), with ice-in estimated as the fourth consecutive day of $-1\,°C$ average temperature. Using mean seasonal claw growth rates and season lengths, we divided claw samples into summer (ice-free, 9 May 2008–11 Nov. 2008) and winter (iced-over, 18 Nov. 2007–8 May 2008). We assumed entire kit claws represented summer diets.

University of Georgia-Athens and Cornell University performed stable isotope analyses using Finnigan isotope ratio mass spectrometers with elemental analyzer interfaces. Ratios were reported in parts per thousand (‰) using:

$$\delta X = \left[\left(\frac{R_{sample}}{R_{standard}} \right) - 1 \right] \times 1000$$

where δX is $\delta^{13}C$ or $\delta^{15}N$ and R is the fraction of the heavy (or rare) to light (or abundant) isotope. PeeDee Belemnite limestone ($\delta^{13}C$; Craig, 1957) and atmospheric nitrogen ($\delta^{15}N$; Mariotti, 1984) were used as standards.

We used isotopic signatures of claws to calculate mean $\delta^{15}N$ and $\delta^{13}C$ levels of each age class, sex and season to estimate assimilated diets. We grouped vegetation samples by $\delta^{13}C$ and $\delta^{15}N$ using hierarchical cluster analysis (Phillips et al., 2005) from squared Euclidean distance and Ward's Distance cluster method. Ward's method minimizes sum of squares between hypothetical clusters (Ward, 1963). We estimated dietary contributions of forage groups (sources) using a linear multiple source mixing model (IsoError; Phillips et al., 2005; http://www.epa.gov/wed/pages/models/stableIsotopes/isotopes/isoerror1_04.htm, accessed 9/2009). IsoError partitions 3 sources using 2 isotopic signatures. Required inputs are means, standard deviations, and n for each source and mixture. IsoError calculates estimates and 95% confidence intervals of source contributions (e.g., vegetation types) to a mixture (e.g., beaver claw). We used other mammalian herbivores (hair of alpaca, llama, cattle, goat, horse) as proxies to account for trophic shift

correction of food sources because trophic shift values have not been calculated for captive beavers ($\Delta\delta^{13}C = 3.0‰$, $\Delta\delta^{15}N = 2.7‰$; Sponheimer et al., 2003a,b).

Statistical analyses

We considered all tests significant at $\alpha = 0.05$. We used linear regressions to explore relationships between available and assimilated forage. Dependent variables were percentages of each forage group (floating leaf, emergent, and terrestrial) in assimilated diets, and independent variables were available edible biomass of each forage group. We used territory as a blocking variable.

To estimate body condition of beavers from single captures, we calculated scaled mass index (SMI) values (Peig and Green, 2009) using the equation:

$$\hat{M}_i = M_i \left[\frac{L_0}{L_i} \right]^b$$

where M_i is body mass (kg) and L_i is zygomatic breadth (mm) of individual i; b is the scaling exponent estimated by a regression of M against L; L_0 is the mean zygomatic breadth for all fall 2008 captures; and $\hat{M}_i$ is the predicted body mass for individual i when zygomatic breadth is standardized to L_0.

We used linear regression with backward selection (MacNally, 2000) to test the relationship between body condition (SMI) in fall 2008 and available forage (edible terrestrial biomass and total aquatic biomass) per territory, using territory as a blocking variable. We ran a correlation matrix on independent variables. If 2 variables were correlated (Pearson $r > 0.70$), we removed the variable with the least assimilated dietary contribution (Severud et al., 2013) from the regression.

We used linear regression to test the relationship between female adult SMI in spring 2008 and kit CPUE in fall 2008. We used 1-tailed independent samples t-tests to compare spring 2009 body condition of adults that overwintered with kits to adults that overwintered without kits. We calculated density of quaking aspen (stems/ha) in each territory, and used linear regression to test the effect of aspen density on kit CPUE (Smith, 1997). We used Cook's distance (D_i) for outlier analysis, and eliminated observations if $D_i > 4/n$ (Cook, 1979).

Results

We captured and measured 117 beavers (40 males:77 females; 49 adults:41 subadults:27 kits) from 22 lodges during the period May 2008–2009. Assimilated diets were estimated from 74 beavers: 43 from spring 2008 (11 males:30 females:2 unknowns; 27 subadults:16 adults) and 31 from fall 2008 (12 males:19 females; 13 kits:6 subadults:12 adults) (Severud et al., 2013).

From cluster analysis, we categorized vegetation as emergent aquatic macrophytes, floating leaf aquatic macrophytes, and terrestrial herbaceous and woody vegetation (Severud et al., 2013) based on squared Euclidean distance = 6. Ward's Distance indicated emergent and floating leaf vegetation $\delta^{15}N$ and $\delta^{13}C$ were more similar to each other than to terrestrial vegetation. Coniferous and deciduous tree species were not different based on $\delta^{15}N$ and $\delta^{13}C$. Seven territory means fell outside the triangle created by mean $\delta^{15}N$ and $\delta^{13}C$ values of forage groups, but within 1 SE of the triangle (Fig. 1).

Proportions of available edible biomass of emergent and terrestrial vegetation varied by 1 of magnitude among territories (Table 1). Availability of floating leaf aquatic vegetation was low in all territories (0.01–234.10 kg, <1–4% of total edible biomass). Available terrestrial ($r^2 = 0.02$, $F_{2,125} = 1.50$, $P = 0.23$) and emergent aquatic vegetation ($r^2 = 0.02$, $F_{2,125} = 1.22$, $P = 0.30$) did not explain variation in assimilated diets. However, available floating leaf

Table 1
Available edible biomass [kg] of floating leaf aquatics, emergent aquatics, and terrestrial plants within 400 m of American beaver lodges, Voyageurs National Park, Minnesota, USA, June–August 2008.

Lodge	Available edible biomass in kg (% of total)						Total
	Floating leaf		Emergent		Terrestrial		
Across from WP	94	(<1)	19	(<1)	18,560	(99)	18,672
Lost Lake 2	242	(3)	461	(5)	8255	(92)	8957
Wolf Island	<1	(<1)	4	(<1)	8469	(99)	8472
Blind Ash Bay	172	(1)	4297	(26)	11,960	(73)	16,430
Daley S Fork	68	(1)	2400	(52)	2122	(46)	4590
Deer Creek	23	(<1)	385	(4)	10,440	(96)	10,848
Kohler NW	232	(1)	807	(5)	16,286	(94)	17,325
North Daley	68	(<1)	5330	(36)	9333	(63)	14,731
Daley E of Bridge	4	(<1)	2701	(40)	4024	(60)	6729
Bay W of Indian Cr	<1	(<1)	8	(<1)	7438	(99)	7446
Daley E Fork	7	(<1)	3539	(52)	3297	(48)	6843
Long Slu Central	108	(1)	902	(8)	9754	(91)	10,764
Long Slu Pond	42	(<1)	3731	(17)	18,307	(83)	22,080
Lost Bay NE	234	(4)	1424	(21)	4974	(75)	8252
$\bar{x}$	89	(1)	1554	(16)	10,279	(83)	11,922

vegetation explained 31% of the variation in assimilated floating leaf percentage of diets ($r^2 = 0.31$, $F_{1,125} = 27.57$, $P < 0.01$; Fig. 2).
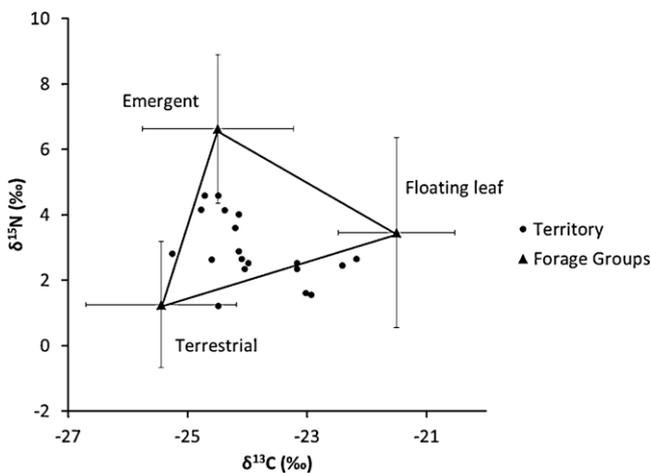
When comparing SMI values and available forage, no variables were eliminated from model runs based on correlation. No models using estimated available biomass of terrestrial ($t_3 = 0.28$, $P = 0.78$), emergent ($t_3 = -0.31$, $P = 0.76$), or floating leaf ($t_3 = 0.36$, $P = 0.72$) vegetation explained variation in fall 2008 SMI values.

Spring 2008 SMI values of adult female beavers did not explain variation in kit CPUE for fall 2008 ($r^2 = 0.11$, $F_{2,7} = 0.44$, $P = 0.33$). Also, spring 2009 SMI values were similar ($t_{26} = 0.41$, $P = 0.35$) between territories with kits (10.8 ± 2.5 kg) and territories without kits (11.3 ± 2.2) in fall 2008.
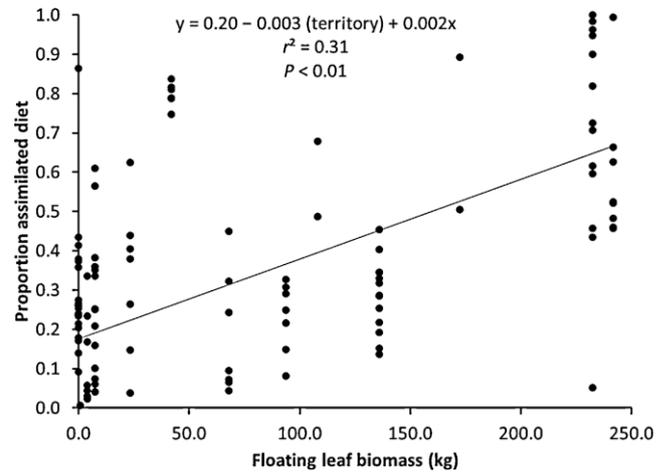
Quaking aspen density explained 56% of the variation in kit CPUE ($r^2 = 0.56$, $F_{1,11} = 14.24$, $P < 0.01$; kit CPUE = aspen density $\times 0.001 - 0.11$; Fig. 3). Two territories (North Daley Bay and North Sullivan Bay) were outliers, and when removed, the relationship was not significant ($r^2 = 0.20$, $F_{1,9} = 2.28$, $P = 0.17$).

Discussion

We failed to support our hypothesis that forage availability affects beaver body condition. There may be a threshold of available vegetation that beavers require before establishing territories

Fig. 2. Proportion of floating leaf assimilated beaver diets and total floating leaf biomass available by territory for individual beavers, Voyageurs National Park, Minnesota, USA, summer 2008.

Fig. 1. δ^{13}C–δ^{15}N biplot of beaver plant forage groups and mean assimilated diets of beavers by territory, Voyageurs National Park, Minnesota, USA, winter 2007–2008 and summer 2008. Symbols are mean isotopic signature values (‰) for forage groups ($\pm$SE) and territories.
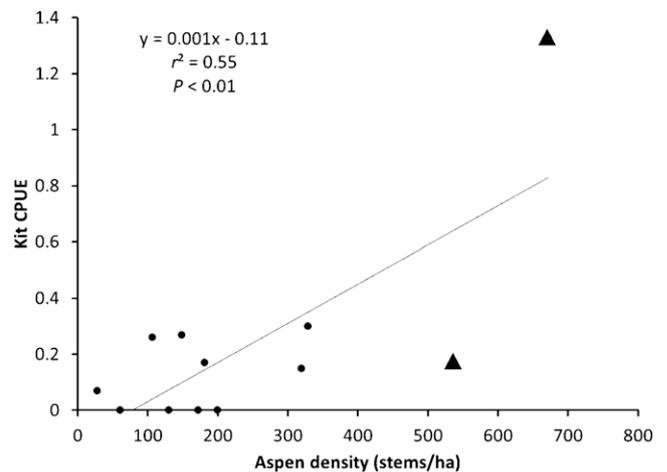
Fig. 3. Quaking aspen (*Populus tremuloides*) density (stems/ha) and beaver kit catch per unit effort by territory, Voyageurs National Park, Minnesota, USA, May–Oct. 2008. When 2 outliers (triangles) are removed, the relationship was not significant ($r^2 = 0.20$, $F_{1,9} = 2.28$, $P = 0.17$).

(Allen, 1983; Barnes and Mallik, 1997). Our focal beavers may be occupying territories with non-limiting resources during the period studied. Smith (1997) found 50–200 aspen and birch stems/ha at inland pond lodges in VNP; our observed aspen densities were within or exceeded this range (Fig. 3). Food availability was associated with mean colony size and probability of year-to-year occupancy in Ontario, Canada, with territories having high amounts of aquatic vegetation sustaining high levels of occupancy and kit production (Fryxell, 2001). Beavers may have multiple active and inactive lodges within their territories (Baker and Hill, 2003), and may move between lodges seasonally (Wheatley, 1997b). Physically suitable territory sites were abandoned due to resource depletion in California, USA (Beier and Barrett, 1987). Many territories in our study have been occupied for several years, and beavers in this system often move between winter and summer lodges. Comparing available forage between occupied and recently abandoned territories may reveal limiting levels of forage availability.

Available floating leaf aquatic vegetation explained 31% of the variation in assimilated floating leaf percentages of beaver diets. Beavers from all territories assimilated emergent and terrestrial vegetation irrespective of availability. Although floating leaf vegetation occurred in low abundance in all territories, beavers assimilated more floating leaf vegetation in territories where more was available. We found no relationship between body condition and availability of broad forage classes. However, aspen density explained 56% of the variation in kit CPUE with 2 outliers included. Smith (1997) found aspen positively correlated with kit production during 1984–1993, although his study population was from small inland ponds. Smith (1997) also reported beavers reproduced every other year in habitat without abundant aspen and aquatic plants.

Our broad vegetation classes or biomass estimations may have been too coarse to detect if changes in availability affected assimilated diet or body condition. In territories where we detected little available aquatic forage, there was still assimilation of aquatic vegetation (Fig. 2). Milligan and Humphries (2010) reconstructed beaver diets using stable isotope analysis with similar results, and the method has been employed using claws (Belant et al., 2006) and IsoError (Phillips, 2012). Either our vegetation survey failed to detect aquatic vegetation, or beavers were foraging beyond our defined 400-m radius foraging area. Lake beavers generally have relatively small home ranges (Wheatley, 1997a) but have been reported to swim up to 1 km to foraging sites (Hiner, 1938; Shelton, 1966; Raffel et al., 2009). Also, submersed aquatic vegetation (e.g., *Potomogeton* spp.) has similar isotopic signatures to floating leaf vegetation (Milligan et al., 2010), and percentages of assimilated aquatic vegetation may include submersed species. We did not estimate biomass of some possible diet sources, such as submersed aquatic vegetation, nor some species of emergent aquatic vegetation (e.g., *Sparganium* spp.; Parker et al., 2007). We also did not control for aquatic vegetation browsed by beavers before sampling occurred. These possible diets sources may account for some mean assimilated diets of beavers in some territories falling outside our mixing model, although all territory means fell within the variability of the 3 food sources (Fig. 1). Also, we pooled all species of terrestrial woody vegetation to calculate total terrestrial biomass and did not include stems <2 cm dbh. Although beavers consume a diverse array of tree species, some species we included in the terrestrial calculations may not often be consumed (e.g., conifers, but see Jenkins, 1979). Similarly, stems <2 cm dbh may be an important component of beaver diets.

We found no relationship between adult female body condition and reproduction, which suggests beavers were occupying territories above threshold vegetation levels or were equally nutritionally stressed, such that recruitment was similar over the range of observed maternal conditions. Noyce and Garshelis (1994) found recruitment in black bears was unrelated to maternal condition below a threshold; bear litters declined with declining nutrition and then stabilized across a range of maternal masses. American martens (*Martes americana*) failed to reproduce when food was scarce, therefore females did not show low masses in times of resource scarcity (Thompson and Colgan, 1987). In territories lacking adequate aspen or aquatic vegetation, beavers may only breed in alternate years (Smith, 1997). Lactation is energetically expensive, and may cause mothers to catabolize body tissues (Rogowitz, 1996). Our methods would not reveal if females were in poor condition due to lack of available forage and did not reproduce, or if females did reproduce and were in poor condition due to lactation.

Kit presence over winter did not affect adult spring body condition. Because the food cache may not be calorically sufficient to sustain an entire colony (Novakowski, 1967), kits have been hypothesized to preferentially use the cache, as they gain mass over winter while subadults and adults lose mass and tail size (Smith and Jenkins, 1997). However, recent evidence suggests all colony members use the cache similarly (Severud et al., 2013). Similar SMI values of adults and subadults in territories with and without kits over winter also refute the idea that kits preferentially use the food cache to the detriment of other colony members.

We detected considerable variation in body condition of individuals from the same territory. Smith (1997) reported available forage was heterogeneous within territories in VNP. Although a colony shares a foraging territory, individuals may forage in different locations within a territory (Urton and Hobson, 2005). Beavers avoid contact with colony members outside the lodge to minimize predation risk (Baker and Hill, 2003), and these interactions may affect functional availability of forage to individual beavers (Buskirk and Millspaugh, 2006). Beaver forage availability may need to be addressed at within-territory spatial scales as available forage at the territory scale was not a good predictor of body condition and fitness. Along a gradient of resource metrics that could be measured, forage availability is the least directly linked to fitness and other biological outcomes (Ayers et al., 2012). Availability is difficult to quantify and may not be a good predictor of use and therefore condition and fitness.

Untested abiotic variables such as climate or water level changes may influence beaver body condition and fitness in our reservoir study site (Smith and Jenkins, 1997; Baker and Hill, 2003). During extreme reservoir drawdown, beaver lodge interiors may be exposed to lower air temperatures, requiring greater energy expenditures to regulate body temperature (Smith and Peterson, 1991; Smith et al., 1991; Smith and Jenkins, 1997). Water levels were within normal range allowed during our study except for a brief high water event in summer 2008 (www.lwcb.ca/historicalgraphs.html), however individual lodges differ in their vulnerability to low water based on site-specific characteristics such as local bathymetry. A moderately severe winter in 2007–2008 (ice-out on Lake Kabetogama was 10 days later than the median) may have also confounded our results as beaver body condition may have been below average entering the ice-free period in 2008.

Predation avoidance may influence aquatic vegetation use. Aquatic vegetation accounted for >50% of assimilated beaver diets in VNP (Severud et al., 2013) and in the subarctic (Milligan and Humphries, 2010), but we found no evidence that access to or use of aquatic vegetation improved beaver body condition or fitness. Smith and Peterson (1988) found 47% of wolf scats in VNP contained beaver remains, and Gogan et al. (2004) found beaver remains in 7% of winter wolf scats, and 35% of summer scats. Aquatic vegetation appears to be a supplemental food source for beavers, and may allow colonies to persist in 'poor' habitat (Howard and Larson,

1985), or where predators are relatively abundant (e.g., in VNP; Gogan et al., 2004).

Acknowledgements

Appendix 1.

Forage species surveyed as available beaver forage among 3 forage groups, Voyageurs National Park, Minnesota, USA, Jul.–Aug. 2007. Forage groups also corresponded with results from hierarchical cluster analysis of $\delta^{15}N$ and $\delta^{13}C$ from representative plants from each forage group (Severud 2011)

Forage group	Species
Aquatic emergent macrophyte	
Arrowhead	*Sagittaria* spp.
Softstem bulrush	*Scirpus validus*
Wool grass	*Scirpus cyperinus*
Cattail	*Typha* spp.
Aquatic floating leaf macrophyte	
Yellow pond-lily	*Nuphar lutea*
White water lily	*Nymphaea* spp.
Terrestrial woody plant	
Quaking aspen	*Populus tremuloides*
White birch	*Betula papyrifera*
Maple	*Acer rubrum*, *A. spicatum*
Willow	*Salix* spp.
Shrub (Speckled alder, serviceberry, red-osier dogwood, beaked hazel, hawthorn, cherry, viburnum, unknown shrub)	*Alnus incana*, *Amelanchier* spp., *Cornus stolonifera*, *Corylus cornuta*, *Crataegus* spp., *Prunus* spp., *Viburnum* spp.
Other deciduous tree (Boxelder, ash, hophornbeam, balsam poplar, bigtooth aspen, oak, American basswood, elm, unknown)	*Acer negundo*, *Fraxinus pennsylvanica*, *F. nigra*, *Ostrya virginiana*, *Populus balsamifera*, *P. grandidentata*, *Quercus* spp., *Tilia americana*, *Ulmus* spp.
Conifer (Balsam fir, white spruce, black spruce, white pine, red pine, jack pine, tamarack, northern white cedar)	*Abies balsamea*, *Picea glauca*, *Picea mariana*, *Pinus strobus*, *Pinus resinosa*, *Pinus banksiana*, *Larix laricina*, *Thuja occidentalis*

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