Mammalian Biology 78 (2013) 87–93

Contents lists available at SciVerse ScienceDirect

Mammalian Biology

journal homepage: www.elsevier.com/locate/mambio

Original Investigation

The role of forage availability on diet choice and body condition in American beavers (*Castor canadensis*)

William J. Severud[a,*], Steve K. Windels[b], Jerrold L. Belant[c], John G. Bruggink[a]

[a] *Northern Michigan University, Department of Biology, 1401 Presque Isle Avenue, Marquette, MI 49855, USA*
[b] *National Park Service, Voyageurs National Park, 360 Highway 11 East, International Falls, MN 56649, USA*
[c] *Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Box 9690, Mississippi State, MS 39762, USA*

ARTICLE INFO

Article history:
Received 15 September 2011
Accepted 11 December 2012
Available online 11 January 2013

Keywords:
American beaver
Available forage
Body condition
Castor canadensis
Diet
Minnesota
Stable isotope analysis

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.

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

* Corresponding author. Tel.: +1 906 227 2310; fax: +1 906 227 1063.
E-mail address: wseverud@nmu.edu (W.J. Severud).

1616-5047/$ – see front matter © 2013 Published by Elsevier GmbH on behalf of Deutsche Gesellschaft für Säugetierkunde.
http://dx.doi.org/10.1016/j.mambio.2012.12.001

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:

$$\text{biomass} = A \times (\text{dbh})^B$$

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