

AMERICAN BEAVER FORAGING ECOLOGY:
PREDATION AVOIDANCE, DIET, AND FORAGE AVAILABILITY

By

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THESIS

Submitted to
Northern Michigan University
In partial fulfillment of the requirements
For the degree of

MASTER OF SCIENCE

Graduate Studies Office

2011

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ABSTRACT

AMERICAN BEAVER FORAGING ECOLOGY:

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I tested wolf urine as a potential tool to reduce human-beaver (*Castor canadensis*) conflicts, using infrared cameras to monitor use of terrestrial foraging trails by beavers in Seney National Wildlife Refuge, Michigan, September–November 2008. Numbers of beavers detected and time spent on urine-treated trails decreased 95%, and were unchanged on control trails. Beavers appear to use olfaction to assess predation risk, and wolf urine may be a suitable beaver deterrent. I used stable isotope analysis to estimate seasonal assimilated beaver diets in Voyageurs National Park, Minnesota, from April 2007–November 2008. Aquatic vegetation accounted for more assimilated winter diet than previously reported. Variation in total assimilated aquatic vegetation did not affect subadult and adult seasonal changes in body mass, tail thickness, or tail area, but kit body condition was negatively related to total assimilated aquatic vegetation. I investigated the influence of forage biomass on beaver diet, body condition, and reproduction, Voyageurs National Park, May–September 2008. Variation in floating leaf vegetation explained 31% of variation in assimilated floating leaf diets. I found no evidence that available aquatic vegetation affected beaver body condition or fitness. Beavers may forage on aquatic vegetation to reduce predation risk or minimize time spent foraging, rather than to maximize energy intake. Other factors such as water level fluctuations or climatic variables may also explain variation in beaver body condition.

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I dedicate this thesis to my grandfather William “Papa” Auger. Papa’s passion for nature inspired mine.

ACKNOWLEDGEMENTS

Thank you to my family, friends, and colleagues. Mom, Dad, Missy, and Pat have all put up with hearing about beavers for a long time now. And along the way we picked up Tim and Trisha. Also, many thanks go to the extended Severud and Auger clans.

Friends from all areas of my life have also been integral to the completion of this thesis: Plymouth/Maple Grove, Carleton, Japan, Montana, Voyageurs. The graduate student crew at NMU has always been there. Steve Schaar, Mike Peters, Grant Slusher, Jessie Simmon, Danny LeBert, Vanessa Thibado, Tiffany Opalka, Kim Hardenbrook, Trisha Sippel, Carla Serfas, Ericka McCarthy, Justin Segula, and Steve Davis, you all have made this experience unforgettable and wonderful.

Pat Brown, Jackie Bird, Jill Leonard, Tom Froiland, Erich Ottem, Alec Lindsay, Kate Teeter, Jennifer Myers-Jezylo, Jing-fang Niu, and Susie Piziali: you have all acted as mentors, teachers, and friends. Thank you.

Thank you to all the help I had in the field at Voyageurs and Seney: Brad Berhens, Laurent Gaillard, Bridget Henning, Jacob Moe, David Morris, Bryce Olson, Jake Randa, Katie Fryker, John Snyder, Cam Trembath, Dr. Tiffany Wolf, Dr. Brian McLaren, Doug Vincent, Steve Schaar, Katie Anderson, Danielle Ethier, and Josh Sayers.

Thank you to my committee: Drs. John Bruggink, Jerry Belant, Steve Windels, and Alan Rebertus. You have each contributed to the completion of this thesis in numerous and invaluable ways. I owe you all much gratitude.

Funding was provided by Northern Michigan University's Excellence in Education Grant, Biology Department Development Fund, Charles Spooner Grant, Graduate Studies Special Funding, Arts and Sciences Special Funding, National Park Service Great Lakes Research and Education Center Mini-grant, the Bruggink Wildlife Research Lab, Ruffed Grouse Society Scholarship, and Michigan Waterfowl Association Conservation Scholarship.

Equipment and/or logistical support was provided by Voyageurs National Park, Seney National Wildlife Refuge (D. Olson), Ohio Department of Natural Resources, Great Lakes Monitoring Network, Texas A&M-Kingsville, University of Georgia-Athens, Cornell University, and Northern Michigan University.

This thesis follows the format and style in the guidelines for submission to the Journal of Wildlife Management.

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CHAPTER ONE

PREDATOR CUES REDUCE AMERICAN BEAVER USE OF FORAGING TRAILS

INTRODUCTION

Optimal foraging theory suggests animals will maximize food intake while minimizing time spent foraging (MacArthur and Pianka 1966, Pyke et al. 1977). Animals must also balance foraging with avoiding risks, such as predation (Sih 1980). The recognition of risk-sensitivity can help in understanding behavior of foragers, which sometimes avoid areas with seemingly plentiful food if the threat of predation exists (Ripple and Beschta 2004). The risk allocation hypothesis accounts for temporal variation in predation risk, and how variation affects foraging (Lima and Bednekoff 1999). This hypothesis predicts that foragers exposed to chronic risk will show less pronounced antipredator behavior than foragers exposed to brief and infrequent pulses of risk. For example, a meta-analysis of terrestrial foraging and predation risk trade-offs revealed a large decrease in foraging effort with increased predation risk, with many rodents avoiding areas treated with predator scent (Verdolin 2006).

Predation risk may be perceived by observing the predator, indirect cues (e.g., odors), or habitat cues (Verdolin 2006). The presence of a predator may cause foragers to avoid foraging areas (Díaz et al. 2005), even after the predator has vacated the area (Sih 1992). Odor from predator urine or feces has been effective at inducing risk-sensitive behavior in mountain beavers (*Aplodontia rufa*), wood mice (*Apodemus sylvaticus*), and golden hamsters (Epple et al. 1993, Herman and Valone 2000, McPhee et al. 2010). In a cafeteria-style feeding experiment, Engelhart and Müller-Schwarze (1995) found that American beavers (*Castor canadensis*) avoided feeding on aspen treated with

solvent extracts of predator feces. Eurasian beavers (*C. fiber*) suppressed territorial scent marking in response to scent of sympatric Eurasian lynxes (*Lynx lynx*) and historically sympatric but now allopatric wolves (*Canis lupus*; Rosell and Sanda 2006).

American beavers eat a variety of terrestrial and aquatic plant species (Baker and Hill 2003). Beavers have been considered central place foragers that balance the costs of travel from water with the benefits of foraging in a particular area (Jenkins 1980a, Belovsky 1984, McGinley and Whitham 1985, Baker and Hill 2003). For example, beavers varied their selection of small and large aspen stems depending on distance from water, indicating beavers trade off maximization of energy gain against minimization of predation risk (Basey and Jenkins 1995). Beavers felled more large trees and were more selective as distance from shore increased in high quality habitat (Gallant et al. 2004, Raffel et al. 2009). However, in habitats of lower terrestrial forage quality, beavers may select more hazardous foraging sites and engage in riskier behavior (Sih 1980).

Predators of beavers include gray wolf, coyote (*Canis latrans*), cougar (*Puma concolor*), bears (*Ursus* spp.), wolverine (*Gulo gulo*), Canada lynx (*Lynx canadensis*), and bobcat (*L. rufus*), with the impact of wolf predation locally significant, varying with wolf density and available alternate prey (Baker and Hill 2003). In Ontario, when white-tailed deer (*Odocoileus virginianus*) populations declined over a 9-year period, beavers became the most important summer prey of wolves, with 55% of wolf scats containing beaver remains (Voigt et al. 1976). Smith and Peterson (1988) reported 47% of wolf scats in northern Minnesota during spring contained beaver remains. Black bears (*Ursus americanus*) suppressed beaver populations on Stockton Island in Lake Superior (Smith

et al. 1994). Beavers may perceive direct or indirect cues from large terrestrial predators like wolves and bears, and in response increase foraging on aquatic vegetation.

My objectives were to determine whether beavers use olfaction to assess predation risk, and whether wolf urine could be used as a potential tool to mitigate human-beaver conflicts. I hypothesized that beavers would alter their behavior in response to an indirect predator cue. Specifically, I predicted that foraging trails treated with predator urine would be used less than untreated control trails.

STUDY AREA

I conducted this study in Seney National Wildlife Refuge (SNWR), Schoolcraft County, Michigan (46° 14'N, 86° 00'W) from 18 September to 13 November 2008. The refuge is 38,678 ha, with 24,682 ha of marsh and 2,932 ha of open water (Herman et al. 1975). Most open water is contained in 21 constructed pools. Emergent vegetation covers 43% of the wetlands and includes cattail (*Typha latifolia*), sedges (*Carex* spp.), and bulrushes (*Scirpus* spp.). Forests cover 84% of the uplands and contain pines (*Pinus* spp.), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*; Baker et al. 1995). Beavers use wetlands throughout SNWR; potential predators include gray wolves, black bears, coyotes, northern river otters, and bobcats (D. Olson, U. S. Fish and Wildlife Service, personal communication). Monthly mean temperatures during the study ranged from 1.8° C to 15.1° C, and monthly mean liquid precipitation ranged from 1.27 mm to 1.52 mm. In November, 47.5 cm of snow fell (National Oceanic and Atmospheric Administration [NOAA] Midwestern Regional Climate Center).

METHODS

I conducted this study when beavers increased tree-cutting activities for constructing food caches (Busher 1996). I selected 16 beaver lodges based on recent tree

cutting activity and randomly assigned lodges equally to 1 of 4 groups based on accessibility. Each lodge was >200 m from its nearest neighbor (11 were >750 m), and if lodges were in the same body of water, active food caches were used to estimate if >1 colony was present. I sampled each group of 4 lodges for 2 weeks. At each lodge, I selected the 2 most active foraging trails and randomly selected 1 of those trails for urine treatment while the other trail was assigned as a sham or control. Responses to control and sham trails were not different, and were combined in all analyses as ‘controls’. One lodge was omitted due to lack of equipment, yielding 15 treatment trails and 15 control trails over the 8-week period. An infrared camera (Reconyx Silent Image Cameras RM30, Reconyx, Inc., Holmen, WI) was placed on each trail 10 cm above ground, 2 m from shore and aimed at shore. Cameras were set to take a picture every 0.5 sec once activated by heat and motion.

I monitored trails for 1 week before I applied 90 ml of wolf urine (Deerbusters, Frederick, MD) to treatment trails. Urine was placed 50 cm from shore on either side of the trail in a ‘PredatorPee Dispenser’ (Lexington Outdoors, Robinston, ME) about 10 cm above ground. I placed empty ‘PredatorPee Dispensers’ on sham trails, and placed nothing on control trails. I continued monitoring trails 1 week post treatment before moving cameras to another group of lodges. Methods followed procedures approved by Northern Michigan University’s Institutional Animal Care and Use Committee (Application # 105, Appendix A).

I counted number of beavers photographed, and mean amount of time beavers spent at the camera station per camera trap station. Amount of time spent was calculated using the time stamp difference between the first image and last image of the animal,

recorded in seconds. I used a generalized linear mixed model to test the Poisson loglinear full factorial model of treatment (urine or control), and week (week 1 or week 2) with time (18 September, 2 October, 16 October, or 30 October 2008) used as a random effect (SAS Institute Inc., Cary, NC). I decided a posteriori to conduct the same analyses for northern raccoons (*Procyon lotor*) and muskrats (*Ondatra zibethicus*) based on descriptive summaries of detections.

RESULTS

I obtained 60 beaver visits (Fig. 1.1), 14 on 15 control trails and 46 on 15 urine trails, representing 13% of all images ($n = 448$). Mean number of beavers detected on urine trails declined 95% from week 1 ($\bar{x} = 2.9$ images, $SE = 1.5$, $n = 15$) to week 2 ($\bar{x} = 0.1$, $SE = 0.1$, $n = 15$; Fig. 1.2, Table 1.1a). In contrast, mean number of beavers detected on control trails during week 1 ($\bar{x} = 0.5$ images, $SE = 0.3$, $n = 15$) and week 2 ($\bar{x} = 0.4$, $SE = 0.2$, $n = 15$) was similar. Mean number of beavers detected on urine trails was greater than on control trails during week 1 but not week 2.

There was an interaction between week and treatment for mean duration of beaver detections (Table 1.1a). Mean duration of beaver detections on urine trails declined 95% from week 1 ($\bar{x} = 6.4$ sec, $SE = 4.1$, $n = 15$) to week 2 ($\bar{x} = 0.3$, $SE = 0.3$, $n = 15$; Fig. 1.2), while mean duration of detections on control trails remained unchanged from week 1 ($\bar{x} = 11.2$ sec, $SE = 5.6$, $n = 15$) to week 2 ($\bar{x} = 9.3$, $SE = 6.1$, $n = 15$).

I obtained images from 16 taxa other than beaver (Fig. 1.1, Table 1.2). Unidentified small mammals were most abundant (27% of total images), followed by muskrats (18%), red squirrels (*Tamiasciurus hudsonicus*; 17%), and northern raccoons (6%). Mean total species richness decreased 40% from week 1 ($\bar{x} = 3.5$ species, $SE =$

0.6, $n = 15$) to week 2 ($\bar{x} = 2.1$, $SE = 0.4$, $n = 15$) on control trails, and increased 9% from week 1 ($\bar{x} = 2.1$, $SE = 0.4$, $n = 15$) to week 2 ($\bar{x} = 2.3$, $SE = 0.5$, $n = 15$) on urine trails (Fig. 1.3, Table 1.1b). Mean carnivore species richness decreased 33% from week 1 ($\bar{x} = 0.8$, $SE = 0.3$, $n = 15$) to week 2 ($\bar{x} = 0.53$, $SE = 0.2$, $n = 15$) on control trails, and increased 120% from week 1 ($\bar{x} = 0.3$, $SE = 0.1$, $n = 15$) to week 2 ($\bar{x} = 0.7$, $SE = 0.2$, $n = 15$) on urine trails.

Mean numbers of muskrats and raccoons detected were similar for treatment and control trails (Table 1.1c). There was no interaction between treatment and week for muskrats or raccoons. Mean number of muskrats detected on urine trails during week 1 ($\bar{x} = 0.7$, $SE = 0.3$, $n = 15$) was similar to week 2 ($\bar{x} = 0.9$, $SE = 0.7$, $n = 15$), and similar to control trails during week 1 ($\bar{x} = 2.2$, $SE = 0.9$, $n = 15$) and week 2 ($\bar{x} = 1.5$, $SE = 0.7$, $n = 15$). Mean number of raccoons detected on urine trails during week 1 ($\bar{x} = 0.4$, $SE = 0.3$, $n = 15$) was similar to week 2 ($\bar{x} = 0.4$, $SE = 0.2$, $n = 15$), and similar to control trails during week 1 ($\bar{x} = 0.4$, $SE = 0.2$, $n = 15$) and week 2 ($\bar{x} = 0.5$, $SE = 0.3$, $n = 15$). I did not achieve model convergence for comparisons of mean durations of detections for muskrats or raccoons.

DISCUSSION

I found a 95% reduction in beaver numbers at camera stations containing predator urine, indicating beavers altered their space use in response to an indirect cue of predation risk. Beavers also spent 95% less time at urine-treated camera stations, and exhibited no decrease in time spent at control camera stations. Decreased time spent at urine-treated camera stations suggests antipredator behavior in beavers in my study area is strong, consistent with the risk allocation hypothesis (Lima and Bednekoff 1999).

Decreased use and time spent at urine-treated camera stations suggests wolf urine is an effective deterrent to beaver activity, and that beavers use olfaction to assess predation risk. In my study area, wolves have large territories and range extensively (Mech 1974); hence, beavers may only experience occasional temporal pulses of risk from wolves. These pulses of risk may be perceived by beavers regardless of actual predation events, which may be affected by available alternate wolf prey (Voigt et al. 1976). Although my study was short in duration, it represented a brief pulse of elevated predation risk. That beavers avoided camera stations containing wolf urine supports the tenet of the risk allocation hypothesis that states brief infrequent pulses of high risk will elicit strong antipredator behaviors in prey species (Lima and Bednekoff 1999). My data suggest beavers either reduced total foraging activity or began using unmonitored or untreated trails. American and Eurasian beavers both have exhibited use of olfaction to assess risk, by repressing scent-marking behavior (Rosell and Sanda 2006) and foraging (Engelhart and Müller-Schwarze 1995, Rosell and Czech 2000) in response to predator odors. Beavers also foraged closer to shore on an island with bears than on an island without bears (Smith et al. 1994). My study supports Landré et al.'s (2010) conclusion that foragers can learn and respond to elevations in predation risk.

Carnivore species richness increased 120% following the application of urine. Carnivores increase activity around urine of other carnivore species (Roughton and Sweeny 1982, Gehrt and Prange 2007). Scent may provide information about conspecifics or other carnivore species, and this information may be used to avoid antagonistic encounters or to increase the likelihood of beneficial encounters (Howard et al. 2002). Semiochemicals in urine are produced during digestion, and digestion of high-

protein foods leads to higher levels of sulfur in urine (Mason et al. 1994). These sulfuric compounds attract carnivores and omnivores, yet repel herbivores (Mason et al. 1994, Nolte et al. 1994). Thus, the urine effect on beavers may have been enhanced by scent-marking of other carnivores attracted to the wolf urine.

Beavers can comprise a large portion of wolf diets (Mech 1974, Voigt et al. 1976, Paquet and Carbyn 2003, Urton and Hobson 2005), with beaver remains found in 7-75% of scats (Mech 1970, Voigt et al. 1976). Consequently, wolves can be an important source of mortality for beavers where they are sympatric (Baker and Hill 2003). Raccoons (Chavez and Gese 2005) and muskrats are rarely killed or consumed by wolves (Voigt et al. 1976, Urton and Hobson 2005), although muskrats comprised 16% of wolf diets when ungulates were at low densities in northwestern Minnesota (Chavez and Gese 2005). Beavers demonstrated aversion to wolf urine, while raccoons and muskrats showed no avoidance, suggesting prey species are more sensitive to predator scents than non-prey species. Apfelbach et al. (2005) suggested prey will not react to predator odors from predators with which they do not share evolutionary history. The risk allocation hypothesis states that prey animals subject to temporally uniform high or low risk should exhibit weak antipredator behaviors (Lima and Bednekoff 1999). Perhaps raccoons and muskrats are under a constant threat of predation from a variety of sources; thus, a perceived pulse of risk from wolf urine would not elicit an antipredator response.

Beavers can be viewed as nuisance animals where their range overlaps and activities conflict with human interests (Baker and Hill 2003). Annual timber losses to beaver impoundments were estimated to be \$22 million in the southeastern United States, not including trees felled or damaged by gnawing (Conover et al. 1995). Nonlethal

control measures for nuisance animals are more acceptable to the general public (Baker and Hill 2003). Bone tar oil, a deer repellent, has been equivocal in its effectiveness as a beaver deterrent (Owen et al. 1984, Hammerson 1994). Basey (1999) used extracts from a non-preferred forage species (Jeffrey pine [*Pinus jeffreyi*]) to inhibit feeding on a preferred species (quaking aspen). Engelhart and Müller-Schwarze (1995) claimed predator odors would be effective feeding repellents against beavers; my results demonstrate wolf urine can be effective in deterring beavers from foraging areas in the short term, and may attract carnivores. Extant predators, habituation to scent, and availability of resources may affect urine efficacy. Rosell and Sanda (2006) suggested Eurasian beaver responses to predator feces were innate, but response from sympatric predators was stronger and refined through learning. The risk allocation hypothesis states that if risk becomes chronic, antipredator behavior will be weak (Lima and Bednekoff 1999), and animals in low quality habitat may engage in riskier behavior (Sih 1980). Thus, application of wolf urine and other predator odors may have only short-term efficacy deterring beavers from selected foraging areas.

SUMMARY AND CONCLUSIONS

I tested the use of wolf urine as a potential tool to reduce human-beaver conflicts. I used infrared cameras to monitor use of terrestrial foraging trails by beavers. Mean number of beavers detected decreased 95% on urine-treated trails, and was unchanged on control trails. Beavers also spent 95% less time on urine-treated trails as estimated by photograph time stamps, but did not change time spent on control trails. Thus, American beavers appear to use olfaction to assess predation risk on land and wolf urine may be suitable as a deterrent against beaver herbivory. I detected 16 other taxa; however,

avoidance of urine-treated trails was not observed by species not generally preyed upon by wolves. Species richness increased with urine treatment, mostly due to an increase in visitation by carnivores, which may have enhanced beaver avoidance.

CHAPTER TWO

SEASONAL VARIATION IN ASSIMILATED DIETS OF AMERICAN BEAVERS

INTRODUCTION

American beavers are classified as choosy generalists (i.e., they select for certain species from among many species consumed; Baker and Hill 2003). For example, beavers in Massachusetts selected deciduous species over coniferous species (Busher 1996). Beaver diets vary seasonally, with terrestrial and aquatic herbaceous vegetation consumed when available and woody vegetation typically consumed during winter (Belovsky 1984, Roberts and Arner 1984, Baker and Hill 2003). For example, winter diets, mostly derived from food stored in a cache (Baker and Hill 2003), were 70-90% woody vegetation (Svendsen 1980, Roberts and Arner 1984), and summer diets were 30-50% aquatic vegetation (Svendsen 1980).

Terrestrial and aquatic vegetation contain similar calories (Gorham and Sanger 1967, Belovsky and Jordan 1978), but aquatic leaves, stems and tubers generally have 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). Thus, aquatic vegetation offers higher rates of nutrient assimilation than terrestrial forages, and may therefore be a crucial part of beaver diets. Beaver total body mass and tail size fluctuates seasonally as fat stores are depleted through winter, and beavers must gain mass over summer to offset winter losses (Aleksiuk 1970, Smith and Jenkins 1997). Higher relative assimilation of aquatic vegetation could facilitate this necessary increase in body mass and fat.

Beavers require less search time and incur lower risk of predation when foraging on aquatic vegetation than when foraging on terrestrial vegetation (Doucet and Fryxell 1993). For example, beavers obtained 2.5 times more food/unit effort when foraging on aquatic vegetation (Belovsky 1984), ostensibly safe from predation. Predators of beavers include the gray wolf, coyote, and bears (Voigt et al. 1976, Smith and Peterson 1988, Smith et al. 1994, Baker and Hill 2003). Beavers may perceive direct or indirect cues from large terrestrial predators (Chapter 1), and in response increase foraging on aquatic vegetation or terrestrial vegetation closer to shore (Smith et al. 1994). Time spent foraging on aquatic vegetation during summer was higher for kits and subadults than for adults (Svendsen 1980), and may in part reflect differential vulnerability to predation. Males and females of all age classes consume similar diets year round (Roberts and Arner 1984).

Stable isotope analysis of C and N can be used to reconstruct diets (Kelly 2000) with isotopic signatures of herbivores reflecting the stable isotope ratios of plants assimilated (Stewart et al. 2003). Plants can be separated into broad categories based on isotopic signatures (e.g., aquatic macrophytes from terrestrial plants; LaZerte and Szalados 1982, Cloern et al. 2002, Milligan et al. 2010). Keratin (in claws, hooves, or nails) has been used to estimate assimilated diet, providing less variable results than soft tissues (Kielland 2001, Struck et al. 2002, Belant et al. 2006). In addition, keratin can be sampled to represent a temporal record of assimilation, yielding insights such as timing of diet shifts (Mizukami et al. 2005). Stable isotope analysis also can be used to estimate trophic position (Kelly 2000). $\delta^{15}\text{N}$ typically increases with increasing trophic level

(Schoeninger and DeNiro 1984), although elevated $\delta^{15}\text{N}$ has not always been demonstrated in nursing neonates (Hobson and Sease 1998, Jenkins et al. 2001).

My objective was to assess seasonal diets of beavers by sex and age class using stable isotope analysis of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, emphasizing the relative contributions of aquatic and terrestrial vegetation. I hypothesized that kits would assimilate more aquatic vegetation, sexes would have similar assimilated diets and diets would reflect seasonal changes in forage availability (e.g., more aquatic vegetation during summer). I further hypothesized that kits would feed at a higher trophic level than adults due to nursing, and that percent assimilated aquatic vegetation would correlate positively with body mass and tail size changes. I also hypothesized that higher assimilated aquatic vegetation would correlate with improved body condition.

STUDY AREA

I conducted this study in Lake Kabetogama, Voyageurs National Park (VNP; 48° 36'N, 93° 25'W; 88,628 ha), Minnesota, 2007-2008. Lake Kabetogama (10,425 ha) is part of the larger Namakan Reservoir, whose water levels are regulated by 2 dams (Kallemeyn et al. 2003). The park is characterized as southern boreal forest, with some areas of northern hardwood forest (Kurmis et al. 1986). July temperatures average 18.6° C and January temperatures average -16.1° C. Generally ice-in occurs in mid-November and ice-out in late April or early May (Kallemeyn et al. 2003). A combination of logging and fire throughout the 1930s-1960s created ideal beaver habitat with abundant aspen (*Populus* spp.), and beaver densities exceeded 1 colony/km² from the 1980s to early 2000s (Smith and Peterson 1988; S. Windels, National Park Service, unpublished data).

Beaver predators in the park include wolves and black bears (*U. americanus*; Baker and Hill 2003).

METHODS

Livetrapping

I livetrapped beavers in Hancock traps (Hancock Traps Co., Buffalo Gap, SD) set on trails or baited with aspen and ground castoreum during spring (May 2008) and fall (September-October 2007-2008) on Lake Kabetogama. I manually restrained beavers, attached ear tags (No. 3 monel, National Band and Tag Co., Newport, KY) 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). I determined sex by external palpation (Osborn 1955), genetic analysis (Williams et al. 2004), or necropsy of recovered carcasses of beavers that emigrated from the study site and were subsequently trapped during the state regulated harvest season. I collected claw samples from the third toe of the right hind foot using a razor to obtain a thin layer along the dorsal surface from the cuticle to the distal tip. I aged carcasses using dentition (van Nostrand and Stephenson 1964, Larson and van Nostrand 1968) and used carcass measurements to create a mass and zygomatic arch discriminant function to classify beavers as adult (>3 y), subadult (1.5-3 y) or kit (0-1.5 y; S. Windels, National Park Service, unpublished data).

Stable Isotope Analysis

I used stable isotope analysis of C and N to assess resource use. I opportunistically collected 1 sample each of 26 food species (Appendix B) from 6 sites within the study area to characterize isotopic signatures of potential beaver food items. I

collected leaves and twigs of terrestrial woody vegetation, all aboveground biomass of terrestrial herbaceous vegetation and entire plants of aquatic macrophytes. I placed samples in plastic bags and froze them until analysis. I collected vegetation samples in summer only, as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ have exhibited temporal consistency (Kielland 2001, Milligan et al. 2010). I estimated average seasonal growth rates for claws by examining beavers marked and recaptured in consecutive trapping periods (e.g., beavers captured in fall and the following spring were used to calculate winter growth rate) using data from a larger study at VNP from 2006-2010 (S. Windels, National Park Service, unpublished data). I measured the mark from the previous cut to the cuticle (± 0.1 mm) and calculated a 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). I estimated ice-in dates (date when the entire lake is covered with ice) for Lake Kabetogama by examining weather forecast office (WFO) daily climate data (NOAA, <http://www.crh.noaa.gov> for International Falls, MN), with ice-in estimated as the fourth consecutive day of -1°C average temperature. Using mean seasonal claw growth rates and season lengths, I divided claw samples into summer (ice-free; 30 April 2007-17 November 2007; 9 May 2008-11 November 2008) and winter (iced-over; 18 November 2007-8 May 2008). I assumed entire kit claws represented summer diets.

Stable isotope analyses of vegetation and beaver claws were conducted by University of Georgia-Athens and Cornell University's Stable Isotope Laboratory, respectively, using Finnigan isotope ratio mass spectrometers with elemental analyzer interfaces. Ratios were reported in parts per thousand (‰) using:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

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

I used isotopic signatures of claws to calculate mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ levels of each age class, sex and season to estimate assimilated diets. I grouped vegetation samples by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using hierarchical cluster analysis (Phillips et al. 2005) from squared Euclidean distance and Ward's Distance cluster method. I estimated dietary contributions of the 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 10 Oct 2009). IsoError partitions 3 sources using 2 isotopic signatures. Required inputs are means, standard deviations and number of samples of each source and mixture. IsoError calculates estimates and confidence intervals of source contributions (e.g., vegetation types) to a mixture (e.g., beaver claw). Trophic shift values have not been calculated for captive beavers, so I used other mammalian herbivores as proxies to account for trophic shift correction of food sources ($\Delta \delta^{13}\text{C} = 3.0\text{‰}$, $\Delta \delta^{15}\text{N} = 2.7\text{‰}$; Sponheimer et al. 2003a, b).

Statistical Analyses

I compared seasonal claw growth rates (winter 2007-2008, summer 2008, winter 2008-2009) using 1-way analysis of variance (ANOVA). I used paired-samples t -tests on beaver claws that had summer and winter sections from the same individual to compare seasonal $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios and the percentage of each diet source. All tests were 1-tailed and considered significant at $\alpha = 0.05$.

I calculated percent change in body mass, tail thickness and tail area (tail length \times tail width) as body condition indices of beavers recaptured in consecutive trapping sessions (Aleksiuk 1970, Smith and Jenkins 1997). To estimate body condition of beavers from single captures from fall 2008, I calculated scaled mass index values (Peig and Green 2009), using the equation:

$$\hat{M}_i = M_i [L_0 / L_i]^b$$

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 .

I used multivariate ANOVA (MANOVA) to estimate the effect of total aquatic vegetation (i.e., emergent and floating leaf) in assimilated subadult and adult diets on seasonal percentage changes in body mass, tail thickness and tail area. Because I did not have morphometric measurements at birth for kits, I used MANOVA to estimate the effect of total aquatic vegetation in assimilated kit diets on body mass, tail thickness and tail area measured during fall trapping. I assumed kits to have been born with similar body mass, tail area and tail thickness (Bradt 1939; S. Windels, National Park Service, unpublished data), so I used absolute morphometric measurements of kits in fall as an index of body condition change over summer. Total aquatic vegetation was categorized as $<50\%$ or $\geq 50\%$ of assimilated diets. Total aquatics and season were fixed factors. I used Type III sum of squares, and included the intercept, both main effects and their interaction. I used Pillai's trace as the test statistic for hypothesis testing (Zar 1999).

I used an independent samples 1-tailed *t*-test to compare scaled mass index values between beavers having <50% and ≥50% total aquatic vegetation in assimilated diets. The test was 1-tailed because my a priori hypothesis was that increased amounts of assimilated aquatic vegetation would lead to greater body condition.

I reported means as $\bar{x} \pm \text{SD}$, unless otherwise noted. I performed statistical tests using SPSS v.19 (SPSS, Inc., Chicago, IL). Methods followed procedures approved by Northern Michigan University's Institutional Animal Care and Use Committee (Application #0087, Appendix C).

RESULTS

Mean daily claw growth rates were similar ($F_{2,27} = 45.67$, $P < 0.001$, Tukey HSD, $P = 0.07$) during winters 2007-2008 (0.04 ± 0.01 mm/d, $n = 6$) and 2008-2009 (0.06 ± 0.01 , $n = 18$), and were combined to calculate an overall winter claw growth rate. Combined mean daily claw growth rate during winter (0.06 ± 0.01 mm/d, $n = 24$) was less ($t_{28} = -8.60$, $P < 0.001$) than summer 2008 (0.12 ± 0.02 mm, $n = 7$).

From cluster analysis, I categorized vegetation as emergent aquatic macrophytes, floating leaf aquatic macrophytes and terrestrial herbaceous and woody vegetation clusters (Fig. 2.1, Appendix B) based on squared Euclidean distance = 6. Ward's Distance indicated emergent and floating leaf vegetation $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were more similar to each other than to terrestrial vegetation. If all food sources beavers consumed were analyzed, beaver isotopic signatures would occur within the triangle created by the 3 points of the food source clusters (Fig. 2.2).

Claws from 74 beavers were analyzed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$: 43 from spring 2008 (11 male, 30 female, 2 unknown; 27 subadult, 16 adult) and 31 from fall 2008 (12 male, 19

female; 13 kit, 6 subadult, 12 adult). Claws from spring 2008 were divided into summer 2007 and winter 2007-2008; claws from fall 2008 were divided into summer 2008 and winter 2007-2008. Overall mean (\pm 95% confidence interval [CI]) assimilated diet was $44.5 \pm 11.4\%$ terrestrial vegetation, $33.5 \pm 7.9\%$ floating leaf vegetation and $22.0 \pm 14.5\%$ emergent aquatic vegetation (Table 2.1).

Paired samples from 53 beavers were compared by season, sex, and age class (17 male, 34 female, 2 unknown; 31 subadult, 22 adult). For individual beavers of all age classes, $\delta^{13}\text{C}$ did not differ seasonally (Table 1, $t_{52} = -1.65$, $P > 0.05$), but $\delta^{15}\text{N}$ was 7.4% higher in summer ($3.2\text{‰} \pm 1.4$, $n = 53$) than in winter (3.0 ± 1.5 , $n = 53$; $t_{52} = 2.08$, $P = 0.02$). There was 19.6% more floating leaf vegetation in winter diets ($\bar{x} \pm \text{SD}$; $39.1 \pm 32.4\%$, $n = 53$) than summer diets ($32.7 \pm 30.1\%$, $n = 53$; $t_{52} = 1.71$, $P < 0.05$), and 45% more assimilated emergent aquatic vegetation in summer diets ($23.4 \pm 34.6\%$, $n = 53$) than winter diets ($16.1 \pm 36.0\%$, $n = 53$; $t_{52} = -2.41$, $P = 0.01$). There were no seasonal differences in assimilated terrestrial vegetation (Table 2.1).

Season affected subadult and adult gains in all morphometric measurements ($F_{3,14} = 9.92$, $P < 0.01$; Table 2.2). Over-summer mass gain ($28.9 \pm 20.5\%$, $n = 9$) was higher than over-winter ($-6.8 \pm 9.5\%$, $n = 11$), over-summer tail thickness gain ($4.5 \pm 20.1\%$, $n = 9$) was higher than over-winter ($-20.2 \pm 17.0\%$, $n = 11$), and over-summer tail area gain ($8.6 \pm 10.4\%$, $n = 9$) was higher than over-winter ($-1.9 \pm 7.2\%$, $n = 11$). Variation in proportion of total assimilated aquatic plants in diets did not affect any subadult or adult gains in morphometric measurement ($F_{3,14} = 0.49$, $P = 0.35$). There was no interaction of total aquatic vegetation and season for percent change in subadult or adult body mass, tail area, or thickness ($F_{3,14} = 1.02$, $P = 0.21$).

Zygomatic breadth was similar between kits with <50% and \geq 50% total aquatic assimilated diets ($t_{13} = 0.70$, $P = 0.49$). Total assimilated aquatics in diets had a multivariate effect on kit morphometric measurements ($F_{3,9} = 4.84$, $P = 0.01$; Fig. 2.3), with mass 15.8% ($F_{1,11} = 2.70$, $P = 0.06$), tail area 19.2% ($F_{1,11} = 6.67$, $P = 0.01$), and tail thickness 25.7% ($F_{1,11} = 14.09$, $P < 0.01$) higher in kits with <50% total aquatic assimilated diets.

Scaled mass index values were similar between beavers with <50% (13.64 ± 5.99 kg, $n = 10$) and \geq 50% (12.39 ± 6.14 , $n = 18$) total aquatic vegetation in assimilated diets ($t_{26} = 0.52$, $P = 0.30$) for all age classes.

DISCUSSION

I hypothesized beaver diets would include more assimilated aquatic vegetation in summer; however, aquatic vegetation was assimilated at similar levels throughout the year and represented 55% of assimilated diets overall. Previous studies have found aquatic vegetation comprised up to 50% of food consumed by beavers in summer (Jenkins and Busher 1979, Svendsen 1980), but little quantitative information is available for winter (Dennington and Johnson 1974, Jenkins 1980*b*, Ray et al. 2001). The high use of aquatic vegetation in winter I observed has not been reported previously. Winter diets have largely been assumed to include the food cache (Baker and Hill 2003) and aquatic vegetation when available (Northcott 1972), although caches are not calorically sufficient to sustain body mass of all colony members through winter (Novakowski 1967). Beavers endure this apparent winter food shortage through such mechanisms as fat storage (Aleksiuk 1970), activity suppression (Lancia et al. 1982) and core body temperature depression (Smith et al. 1991); reliance on aquatic vegetation is another.

Emergent aquatics were less common in winter diets, likely due to lack of above-substrate vegetation or lack of access to tubers when emergent aquatic plants were frozen into shoreline ice. Water lilies grow in deeper water than cattails (Northcott 1972), and their tubers may be more accessible under ice. Under stable water level conditions, beavers should have winter access to tubers of water lilies (cached or rooted), which store abundant starch and can retain leaves in milder winters (Heslop-Harrison 1955). Seasonal diets were comparable between sexes in my study, similar to previous work (Svendsen 1980, Roberts and Arner 1984). Svendsen (1980) found kit and subadult beavers used more aquatic forage than adults during summer, and I hypothesized younger beavers would assimilate more aquatic vegetation to avoid predation. In my study, all age classes assimilated similar percentages of aquatic and terrestrial vegetation. Kits and adult beavers have been proposed to differentially use food caches (Novakowski 1967, Smith and Jenkins 1997). If I assume all age classes assimilate each food source similarly, then the relative amount of time consuming food sources should also be similar.

Nursing young of some species have $\delta^{15}\text{N}$ signatures at a higher trophic level than adults (Hobson and Sease 1998, Hobson et al. 2000), but I found no enrichment of $\delta^{15}\text{N}$ in beaver kits. This lack of enrichment supports previous work (Jenkins et al. 2001), who found milk is depleted in $\delta^{15}\text{N}$ compared to maternal body tissue. Alternatively, the lack of elevated $\delta^{15}\text{N}$ signatures in kits may be a sampling artifact. Beaver parturition occurs May-June, with parturition occurring later in more northerly populations (Wigley et al. 1983). Kits switch to mostly solid food by 1 month of age and are weaned at 45-50 days (Baker and Hill 2003). I trapped kits 23 September-13 October 2008. Assuming kits

were born 1 June, began taking solid foods at 30 days and were weaned at 50 days, 23-26% of their summer diets would be mostly milk, 15-18% mixed milk and solid foods and 56-63% solid food only. Any $\delta^{15}\text{N}$ enrichment that may have occurred may have been masked by the solid diet, lost when samples from mothers and offspring were decoupled, or too slight to show a trophic level increase (Jenkins et al. 2001).

Aquatic vegetation is higher in many measures of nutrition (Fraser et al. 1984), and is safer and less energetically expensive to procure (Belovsky 1984, Doucet and Fryxell 1993). However, higher use of aquatics did not lead to improved body condition. Individual adult and subadult beavers' seasonal percent changes in body mass, tail thickness or tail area were not affected by the amount of aquatic vegetation assimilated, but kits were heavier and had larger tails in fall if <50% of their assimilated summer diet was derived from aquatic sources. Zygomatic breadth was similar between kits with <50% and \geq 50% assimilated total aquatic diet, so I can infer that absolute measurements are reflective of the effect of aquatic forage on condition. Scaled mass index values were similar between beavers of all age classes with <50% and \geq 50% assimilated total aquatic diet. Greater use of aquatic vegetation can reduce predation risk and energy expenditure (Belovsky 1984, Doucet and Fryxell 1993). However, Belovsky (1984) developed a linear model of herbivore optimal foraging on Isle Royale, Michigan, and found beavers cannot meet dietary needs by consuming aquatic vegetation alone based on energy maximization. Beaver preference trials found white water lily (*Nymphaea odorata*) ranked lowest in digestible energy but second in preference compared with quaking aspen (*Populus tremuloides*), raspberry (*Rubus idaeus*), speckled alder (*Alnus rugosa*) and red maple (*Acer rubrum*). A linear model based on digestible energy predicted water lily

leaves to be ranked lowest (Doucet and Fryxell 1993). However, both studies failed to include aquatic tubers in their analyses, which are higher in starches and protein than water lily leaves and stems (Belovsky 1984, Doucet and Fryxell 1993).

My results indicate beavers use aquatic vegetation extensively throughout the year, but higher use of aquatic vegetation did not confer better body condition. Milligan and Humphries (2010) found beaver diets in the subarctic were comprised of 60-80% aquatic vegetation, but over shorter time frames (using sections of hair 8-10 mm from skin) and using fewer forage items in their analyses. High observed levels of aquatic vegetation in assimilated diets may be due to relative availability. However, aquatic vegetation may yield secondary benefits including lower energetic cost to procure and reduced predation risk (Belovsky 1984, Doucet and Fryxell 1993).

SUMMARY AND CONCLUSIONS

I estimated mean annual beaver diets as 45% terrestrial and 55% aquatic vegetation (22% emergent and 33% floating leaf) using stable isotope analysis of C and N. Until now, the aquatic component of beaver diets had been assumed to be restricted to summer months. Percentages of floating leaf and terrestrial vegetation were similar between winter and summer, but emergent vegetation increased 45% in summer, possibly due to accessibility. I found high assimilation of aquatic vegetation throughout the year. I found no differences by age class or sex, nor in percentage of emergent, floating leaf or terrestrial vegetation by age class or sex. Kits did not exhibit increased $\delta^{15}\text{N}$ relative to adults and subadults, contrary to studies of other taxa. Although aquatic vegetation is higher in many nutritional aspects than terrestrial vegetation, total assimilated aquatic vegetation did not affect subadult and adult seasonal changes in body mass, tail thickness

or tail area. However, kit body condition was negatively related to total assimilated aquatic vegetation.

CHAPTER THREE

THE ROLE OF FORAGE AVAILABILITY ON DIET CHOICE AND BODY CONDITION IN AMERICAN BEAVERS

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 growth rates depend on available forage, as well as latitude, 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 1996), 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 VNP, MN, 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). However, kits can increase body mass and tail size over winter (Smith and Jenkins 1997, chapter 2).

Stable isotope analysis of C and N can be used to reconstruct diets (Kelly 2000), with isotopic signatures of herbivores reflecting the stable isotope ratios of plants assimilated (Stewart et al. 2003). Isotopic signatures can be used to separate plants into broad categories (e.g., aquatic macrophytes from terrestrial plants; LaZerte and Szalados 1982, 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).

My objective was to elucidate the role of available forage on beaver diet choice and fitness. I 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. I predicted higher use of aquatic vegetation than expected by availability of aquatic biomass. I predicted that greater available biomass of aquatic vegetation would lead to improved body condition, which would result in higher kit production. I 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), I predicted a positive relationship between density of quaking aspen stems and kit production.

STUDY AREA

I conducted this study in Lake Kabetogama, VNP, Minnesota, 2007–2008. Lake Kabetogama (10,425 ha) is part of Namakan Reservoir, which is regulated by 2 dams (Kallemeyn et al. 2003). The park lies at the southern limit of boreal forest, with areas of northern hardwood forest (Kurmis et al. 1986). July temperatures average 18.6° C and January temperatures average –16.1° C. Generally ice-in occurs in mid-November and ice-out in late April or early May (Kallemeyn et al. 2003). Timber harvest and fire during the 1930s–1960s created ideal beaver habitat with abundant aspen (*Populus* spp.), and beaver densities exceeded 1 colony/km² from the 1980s to early 2000s (Smith and Peterson 1988; S. K. Windels, U.S. National Park Service, unpublished data). Beaver predators in the park include wolves (*Canis lupus*) and black bears (*Ursus americanus*; Baker and Hill 2003).

METHODS

Livetrapping

I livetrapped beavers in Hancock traps (Hancock Traps Co., Buffalo Gap, SD) set on trails or baited with aspen and ground castoreum during spring (May 2008) and fall (September–October 2007–2008). I manually restrained beavers, attached ear tags (No. 3 monel, National Band and Tag Co., Newport, KY) 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). I determined sex by external palpation (Osborn 1955), genetic analysis (Williams et al. 2004), or necropsy. I 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. I 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 beavers as adult (>3 y), subadult (1.5–3 y) or kit (0–1.5 y; S. K. Windels, U.S. National Park Service, unpublished data). I 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).

Vegetation Sampling

I estimated available forage in 22 beaver territories from Lake Kabetogama, using a 400-m radius around each lodge (Smith and Peterson 1988). To survey terrestrial vegetation, I arranged 12 equally spaced transects perpendicular to shoreline. Smith and

Peterson (1988) found cut stems ≤ 40 m from shore; my transects were 60 m long to account for beavers potentially foraging farther inland as preferred species were depleted closer to shore. I divided transects into 12 5-m-long by 3-m-wide plots. Within each plot, I recorded species and diameter at breast height (dbh) of all trees and shrubs with ≥ 2 cm dbh.

I 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, I 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 shrubs, viburnum (*Viburnum* spp.), and hawthorn (*Crataegus* spp.). I 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. I used Ter-Mikaelian and Korzukhin's (1997) balsam fir (*Abies balsamea*) equation for all conifers. I summed edible biomass for each of the 12 transects for each territory.

I surveyed aquatic vegetation from late-July to August to coincide with maximum leaf-out. I delineated the perimeter of each patch using GPS units and estimated patch area in ArcGIS (Environmental Services Research Institute, Inc., Redlands, CA). I estimated density of each aquatic species in each patch by counting individual plants

within 1-m² quadrats, at a sampling intensity of about 1 quadrat/10 m². Because cattail (*Typha* spp.) grows at high densities, I used a 0.25-m² quadrat for cattail stems at the same sampling intensity. I 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. I collected 10 entire individuals of each aquatic species. I oven dried aquatic plants at 65 °C to a constant mass and weighed samples. I assumed entire plants were edible and estimated total above- and belowground biomass by multiplying plant density by mean biomass per species.

Stable Isotope Analysis

I used stable isotope analysis of C and N to assess resource use. To characterize isotopic signatures of potential beaver food items, I opportunistically collected 1 sample each of 26 food species (chapter 2) from 6 sites within the study area. I collected leaves and twigs of terrestrial woody vegetation, all aboveground biomass of terrestrial herbaceous vegetation, and entire plants of aquatic vegetation. I placed samples in plastic bags and froze them until analysis. I collected vegetation samples in summer only, as $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ exhibit temporal consistency (Kielland 2001, Milligan et al. 2010). To estimate average seasonal growth rates for claws, I 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. K. Windels, U.S. National Park Service, unpublished data). I 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). I estimated ice-in dates (date when the entire lake is covered with ice) for Lake Kabetogama by examining climate data (NOAA, <http://www.crh.noaa.gov> for International Falls, Minnesota), with ice-in estimated as the fourth consecutive day of -1°C average temperature. Using mean seasonal claw growth rates and season lengths, I divided claw samples into summer (ice-free; 30 April 2007–17 November 2007; 9 May 2008–11 November 2008) and winter (iced-over; 18 November 2007–8 May 2008). I 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:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

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

I used isotopic signatures of claws to calculate mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ levels of each age class, sex and season to estimate assimilated diets. I grouped vegetation samples by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using hierarchical cluster analysis (Phillips et al. 2005) from squared Euclidean distance and Ward's Distance cluster method. I 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 10 Oct 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). I used other mammalian herbivores as proxies to account for trophic shift correction of food sources because trophic shift values have not been calculated for captive beavers ($\Delta \delta^{13}\text{C} = 3.0\text{‰}$, $\Delta \delta^{15}\text{N} = 2.7\text{‰}$; Sponheimer et al. 2003a, b).

Statistical Analyses

I 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. I used territory as a blocking variable.

To estimate body condition of beavers from single captures from fall 2008, I calculated scaled mass index (SMI) values (Peig and Green 2009) using the equation:

$$\tilde{M}_i = M_i [L_0 / L_i]^b$$

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 \tilde{M}_i is the predicted body mass for individual i when zygomatic breadth is standardized to L_0 .

I used linear regression with backward selection to test the relationship between body condition (SMI) and available forage (edible terrestrial biomass and total aquatic

biomass) per territory, using territory as a blocking variable. I ran a correlation matrix on independent variables. If 2 variables were correlated ($r > 0.70$), I removed the variable with the least assimilated dietary contribution (Chapter 2) from the regression.

I used linear regression to test the relationship between female adult SMI and kit CPUE in fall 2008. I used 1-tailed independent samples t-tests to compare spring 2009 body condition of adults that overwintered with kits. I 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). I used Cook's distance (D_i) for outlier analysis, and eliminated observations if $D_i > 4/n$ (Cook 1979).

I performed statistical tests using SPSS v.19 (SPSS, Inc., Chicago, IL), and considered all tests significant at $\alpha = 0.05$. Methods followed procedures approved by Northern Michigan University's Institutional Animal Care and Use Committee (Application #0087, Appendix C).

RESULTS

From cluster analysis, I categorized vegetation as emergent aquatic macrophytes, floating leaf aquatic macrophytes, and terrestrial herbaceous and woody vegetation (chapter 2) based on squared Euclidean distance = 6. Ward's Distance indicated emergent and floating leaf vegetation $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were more similar to each other than to terrestrial vegetation. If all food sources beavers consumed were analyzed, beaver isotopic signatures would occur within the triangle created by the 3 points of the food source clusters (Fig. 3.1). Seven territory means fell outside the triangle, but within 1 SE of the triangle.

Proportions of available edible biomass of emergent and terrestrial vegetation varied by an order of magnitude among territories (Table 3.1). 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 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. 3.2).

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 ($t = 0.28$, $P = 0.78$), emergent ($t = -0.31$, $P = 0.76$), or floating leaf ($t = 0.36$, $P = 0.72$) vegetation explained variation in 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. 3.3). 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

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. I 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.

My 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 I detected little available aquatic forage, there was still assimilation of aquatic vegetation (Fig. 3.2). Either my vegetation survey failed to detect aquatic vegetation, or beavers were foraging beyond my 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., *Potamogeton* spp.) has similar isotopic signatures to floating leaf vegetation (Milligan et al. 2010), and percentages of assimilated aquatic vegetation may include submersed species. I 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). These possible diet sources may account for some mean assimilated diets of beavers in some territories falling outside my mixing model (Fig. 3.1). Also, I pooled all species of terrestrial woody vegetation to calculate total terrestrial biomass. Although beavers consume a diverse array of tree

species, some species I included in the terrestrial calculations may not often be consumed (e.g., conifers, but see Jenkins 1979).

My results did not support the hypothesis that forage availability affects beaver body condition. There may be a threshold of available vegetation that beavers require before establishing territories (Allen 1983, Barnes and Mallik 1997). My focal beavers may be occupying territories with non-limiting resources during the period studied. Food availability was associated with mean colony size and probability of year-to-year occupancy in Ontario, 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 1997*b*). Physically suitable territory sites were abandoned due to resource depletion in California (Beier and Barrett 1987). Many territories in my study have been occupied for several years, and beavers in this system often move between winter and summer lodges (S. K. Windels, National Park Service, unpublished data). Comparing available forage between occupied and recently abandoned territories may reveal limiting levels of forage availability.

I 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). My 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 overwinter 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 overwinter while subadults and adults lose mass and tail size (Smith and Jenkins 1997). However, recent evidence suggests all colony members use the cache similarly (Chapter 2). Similar SMI values of adults and subadults in territories with and without kits overwinter also refute the idea that kits preferentially use the food cache to the detriment of other colony members.

I detected considerable variation in body conditions 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 (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 used to assess fitness, forage

availability is an intermediate measure of resource use (between cover type and assimilated diet). Availability is difficult to quantify and may not be a good predictor of use and therefore condition and fitness.

Similarly, untested abiotic variables such as climate or water level changes may influence beaver body condition and fitness in my 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 my study except for a brief high water event in summer 2008 (www.lwcb.ca/historicalgraphs.html). Predation avoidance may influence aquatic vegetation use. Aquatic vegetation accounted for >50% of assimilated beaver diets in VNP (Chapter 2) and in the subarctic (Milligan and Humphries 2010), but I 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).

SUMMARY AND CONCLUSIONS

Forage availability was not a reliable indicator of beaver diets or body condition. Available terrestrial and emergent aquatic forage varied by an order of magnitude, yet floating leaf aquatic forage was scarce in all territories. Emergent and terrestrial

vegetation were assimilated at levels irrespective of availabilities, but variation in available floating leaf vegetation explained 31% of the variation in assimilated floating leaf diets. Body condition of adult females did not affect kit production, and overwinter body condition of adults was similar between territories with and without kits.

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Table 1.1. Results from generalized linear mixed model analyses ($df = 1,57$) testing the effect of treatment (urine or control), and week (week 1 or week 2) with time used as a random factor, on (a) mean number of beavers detected and mean duration of detection of beavers, (b) mean species richness and mean carnivore species richness, and (c) mean number of muskrats detected and mean number of raccoons detected on beaver foraging trails, Seney National Wildlife Refuge, Michigan, September-November 2008.

a.	Number of beavers		Duration of detection	
	Source	<i>F</i>	<i>P</i>	<i>F</i>
Treatment	15.67	<0.001	17.56	<0.001
Week	0.28	0.596	2.51	0.119
Treatment × week	9.49	0.003	34.43	<0.001

b.	Species richness		Carnivore species richness	
	Source	<i>F</i>	<i>P</i>	<i>F</i>
Treatment	5.64	0.021	4.06	0.049
Week	5.08	0.028	0.79	0.378
Treatment × week	4.26	0.044	3.82	0.056

c.	Number of muskrats		Number of raccoons	
	Source	<i>F</i>	<i>P</i>	<i>F</i>
Treatment	2.55	0.116	<0.01	0.999
Week	1.77	0.189	0.28	0.596
Treatment × week	0.98	0.326	0.03	0.864

Table 1.2. Total number of detections by cameras on beaver foraging trails pre and post treatment by taxon, Seney National Wildlife Refuge, Michigan, September-November 2008.

Taxon	Number of detections			
	Control trails ($n = 15$)		Urine trails ($n = 15$)	
	Week 1	Week 2	Week 1	Week 2
Small mammal	43	28	22	27
Muskrat (<i>Ondatra zibethicus</i>)	34	23	10	14
Red squirrel (<i>Tamiasciurus hudsonicus</i>)	20	10	31	14
American mink (<i>Neovison vison</i>)	8	5	1	3
American beaver (<i>Castor canadensis</i>)	8	6	44	2
Northern raccoon (<i>Procyon lotor</i>)	6	9	6	6
White-tailed deer (<i>Odocoileus virginianus</i>)	5	0	1	0
Long-tailed weasel (<i>Mustela frenata</i>)	4	0	2	0
Eastern chipmunk (<i>Tamias striatus</i>)	3	0	0	0
Common snipe (<i>Gallinago gallinago</i>)	1	0	0	1
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	1	0	0	0

Northern river otter (<i>Lontra canadensis</i>)	1	0	0	0
American black bear (<i>Ursus americanus</i>)	1	0	0	0
Unknown passerines	1	7	2	6
Fisher (<i>Martes pennanti</i>)	0	4	3	7
Wood duck (<i>Aix sponsa</i>)	0	0	1	1
Snowshoe hare (<i>Lepus canadensis</i>)	0	0	0	1

Table 2.1. Mean isotopic signatures (‰) and diet estimates (%) for summer and winter in beavers ($n = 53$), Voyageurs National Park, Minnesota, May and September-October 2008.

	Summer		Winter	
	Mean	SD	Mean	SD
Isotopic signature (‰)				
$\delta^{13}\text{C}$	-23.96	0.96	-23.75	1.04
$\delta^{15}\text{N}$	3.23 *	1.39	2.99 *	1.48
% diet				
Floating leaf	32.69 *	30.07	39.10 *	32.44
Emergent	23.43 *	34.56	16.07 *	36.04
Terrestrial	43.88	21.72	44.82	24.22

*Different within rows ($P < 0.05$)

Table 2.2. Mean beaver body mass, tail area (length \times width) and tail thickness by age class, Voyageurs National Park, Minnesota, May and September-October 2008.

Morphometric	Spring			Fall		
	Mean	SD	<i>n</i>	Mean	SD	<i>n</i>
Body mass (kg)						
Adult	16.26	1.63	16	18.73	1.97	12
Subadult	10.02	2.99	28	14.78	1.87	6
Kit	-	-	-	5.38	0.92	13
Tail area (cm ²)						
Adult	359.75	23.84	15	371.62	28.15	12
Subadult	255.00	60.07	28	335.01	36.58	6
Kit	-	-	-	143.42	21.38	13
Tail thickness (mm)						
Adult	10.32	2.08	16	11.33	1.59	12
Subadult	8.07	1.64	28	10.43	0.60	6
Kit	-	-	-	6.48	1.04	13

Table 3.1. Available edible biomass [kg] of floating leaf aquatics, emergent aquatics, and terrestrial plants within 400 m of American beaver lodges, Voyageurs National Park, Minnesota, June–August 2008.

Lodge	Available edible biomass in kg (% of total)							
	Floating leaf		Emergent		Terrestrial		Total	
Across from WP	94	(<1)	19	(<1)	18,560	(99)	18,672	
Lost Lake 2	242	(3)	461	(5)	8,255	(92)	8,957	
Wolf Island	<1	(<1)	4	(<1)	8,469	(99)	8,472	
Blind Ash Bay	172	(1)	4,297	(26)	11,960	(73)	16,430	
Daley S Fork	68	(1)	2,400	(52)	2,122	(46)	4,590	
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)	5,330	(36)	9,333	(63)	14,731	
Daley E of Bridge	4	(<1)	2,701	(40)	4,024	(60)	6,729	
Bay W of Indian Cr	<1	(<1)	8	(<1)	7,438	(99)	7,446	
Daley E Fork	7	(<1)	3,539	(52)	3,297	(48)	6,843	
Long Slu Central	108	(1)	902	(8)	9,754	(91)	10,764	
Long Slu Pond	42	(<1)	3,731	(17)	18,307	(83)	22,080	
Lost Bay NE	234	(4)	1,424	(21)	4,974	(75)	8,252	
\bar{x}	89	(1)	1,554	(16)	10,279	(83)	11,922	



Figure 1.1. American beaver, northern raccoon, northern river otter, and American black bear detected on beaver foraging trails, Seney National Wildlife Refuge, Michigan, September-November 2008.

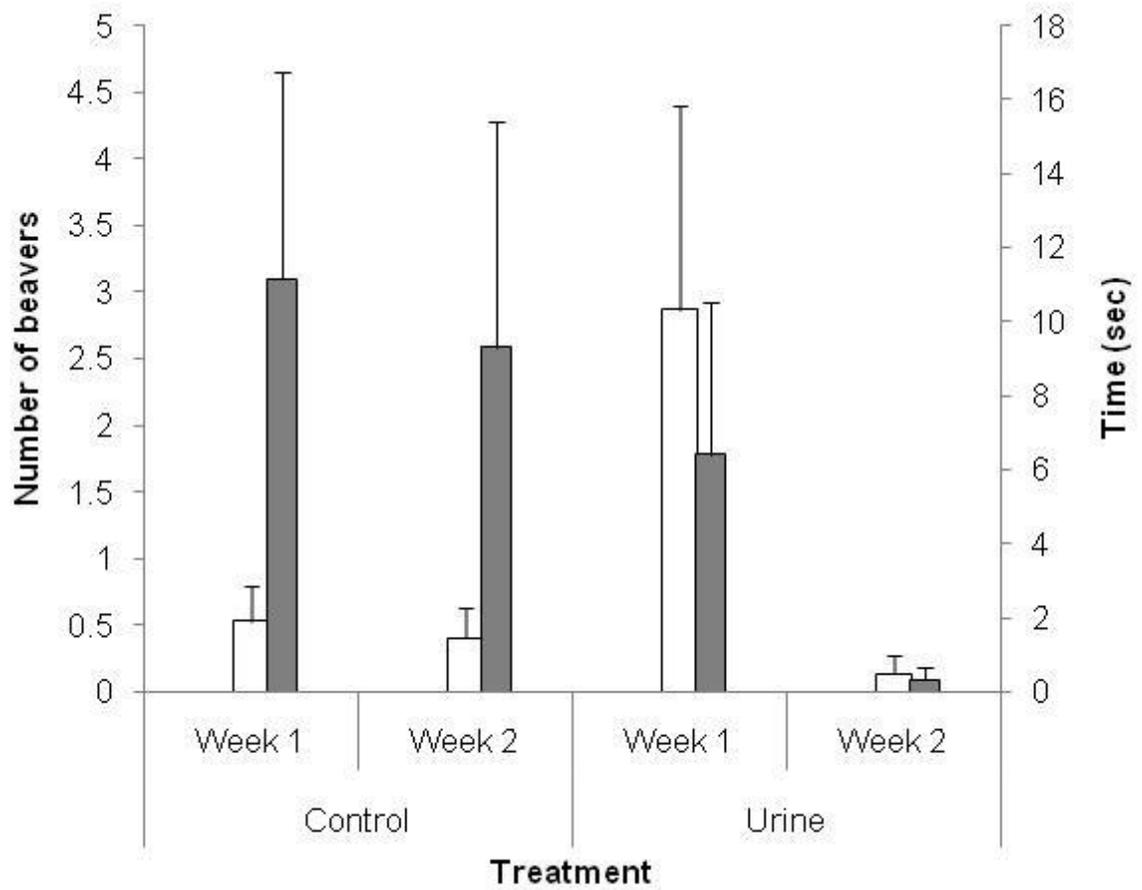


Figure 1.2. Mean (+ SE) number of American beavers photographed (open bars), and mean (+SE) duration of detection (sec) (shaded bars) on urine-treated and control trails from week 1 to week 2 on 15 beaver foraging trails, Seney National Wildlife Refuge, Michigan, September-November 2008.

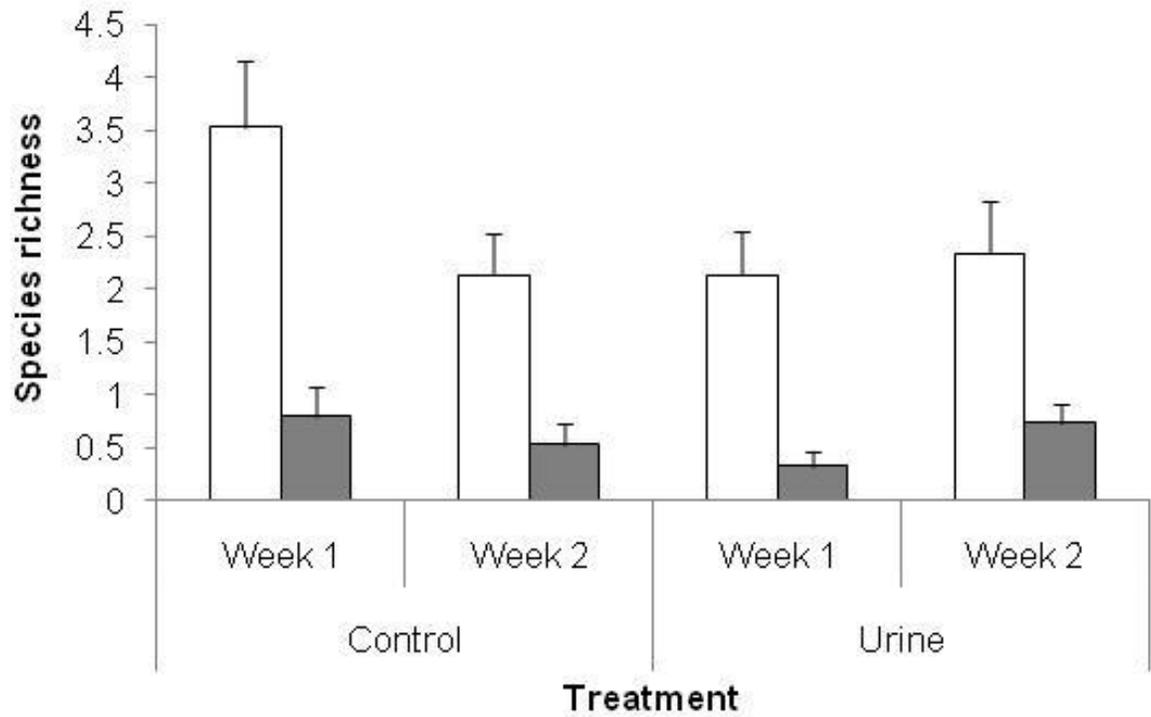


Figure 1.3. Mean (+SE) total species richness (open bars) and carnivore species richness (shaded bars) on urine-treated and control trails from week 1 to week 2 on 15 beaver foraging trails, Seney National Wildlife Refuge, Michigan, September-November 2008.

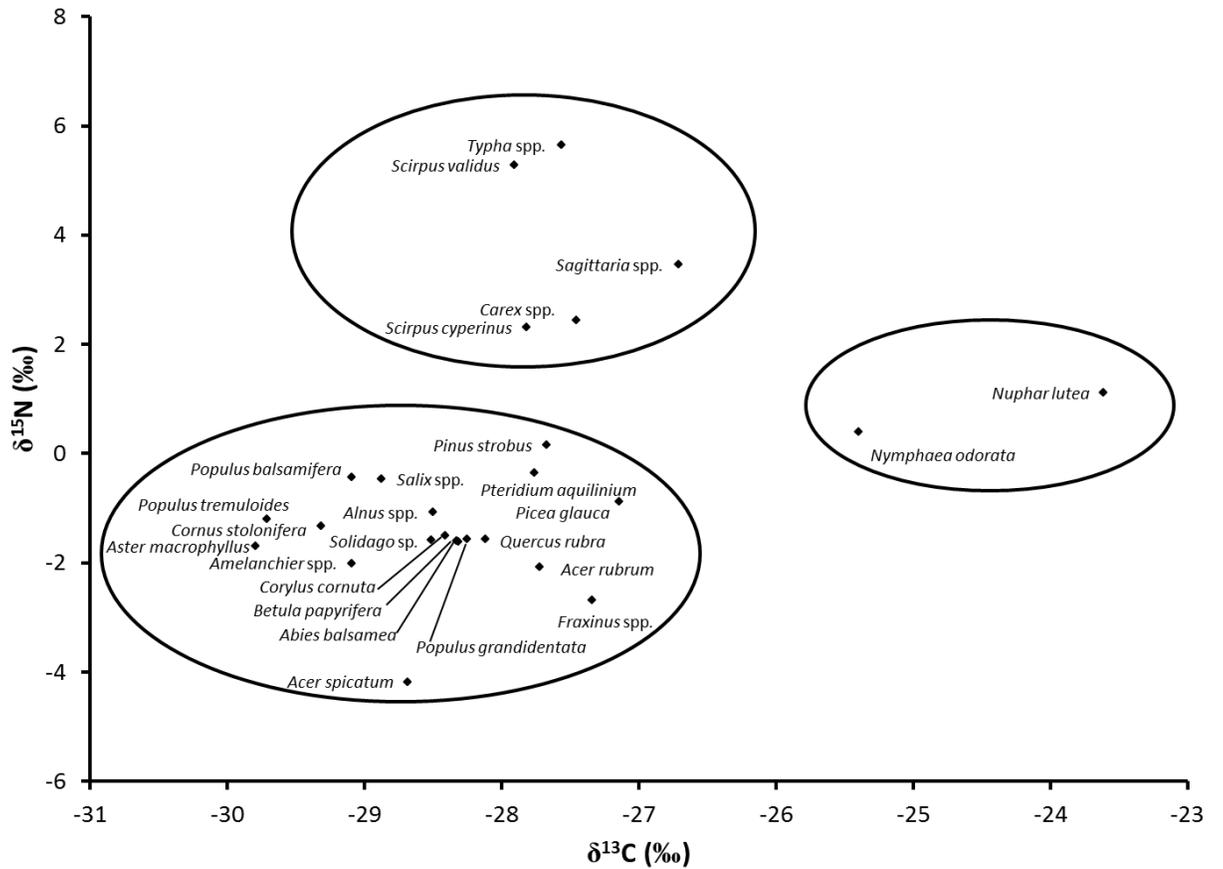


Figure 2.1. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot of beaver forage species ($n = 6$ for each species), Voyageurs National Park, Minnesota, July-August 2007. Symbols are mean isotopic signature values (‰), with circles around source groups determined using cluster analysis.

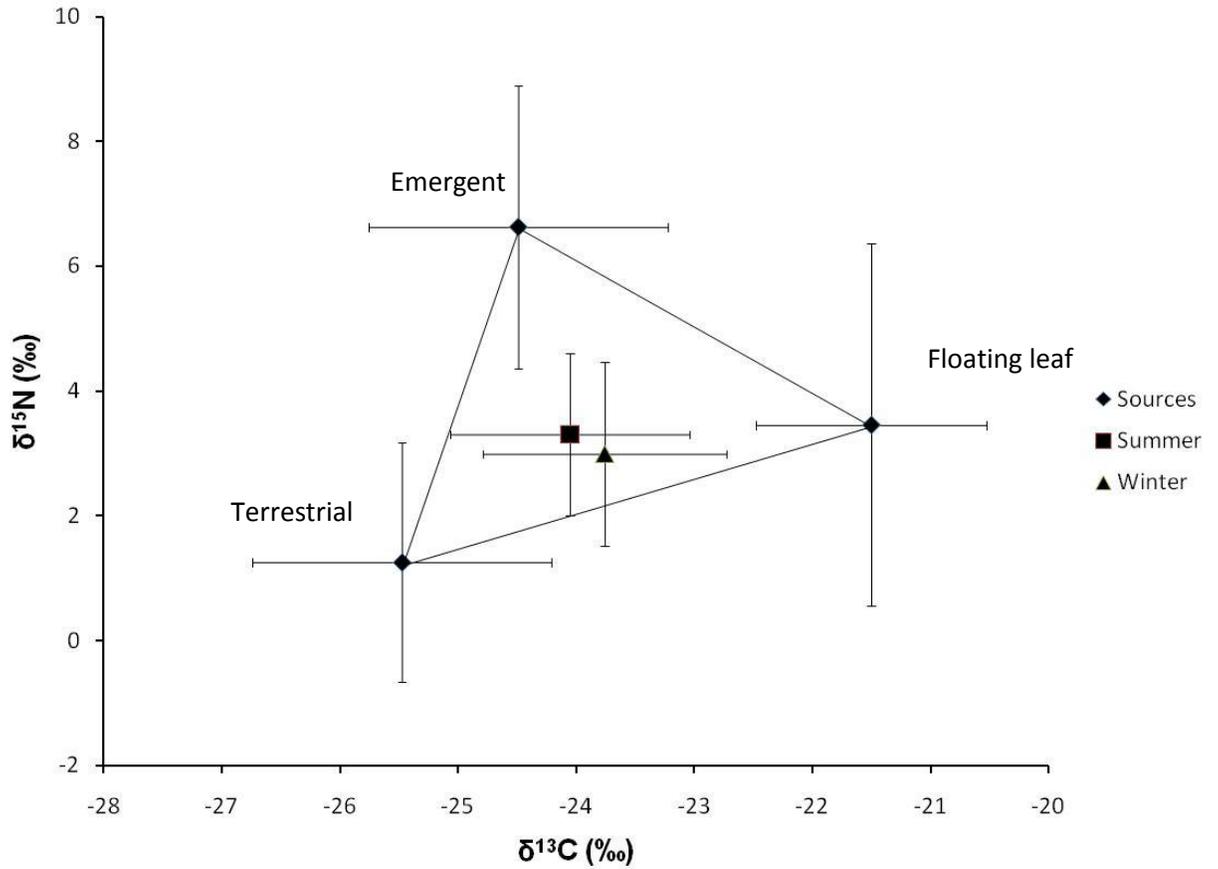


Figure 2.2. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot showing mixing triangle with seasonal beaver diet means (summer 2007 and 2008, winter 2007-2008) by vegetation category (July-August 2007), Voyageurs National Park, Minnesota. Symbols are mean (\pm SD) isotopic values (‰), corrected for trophic shifts.

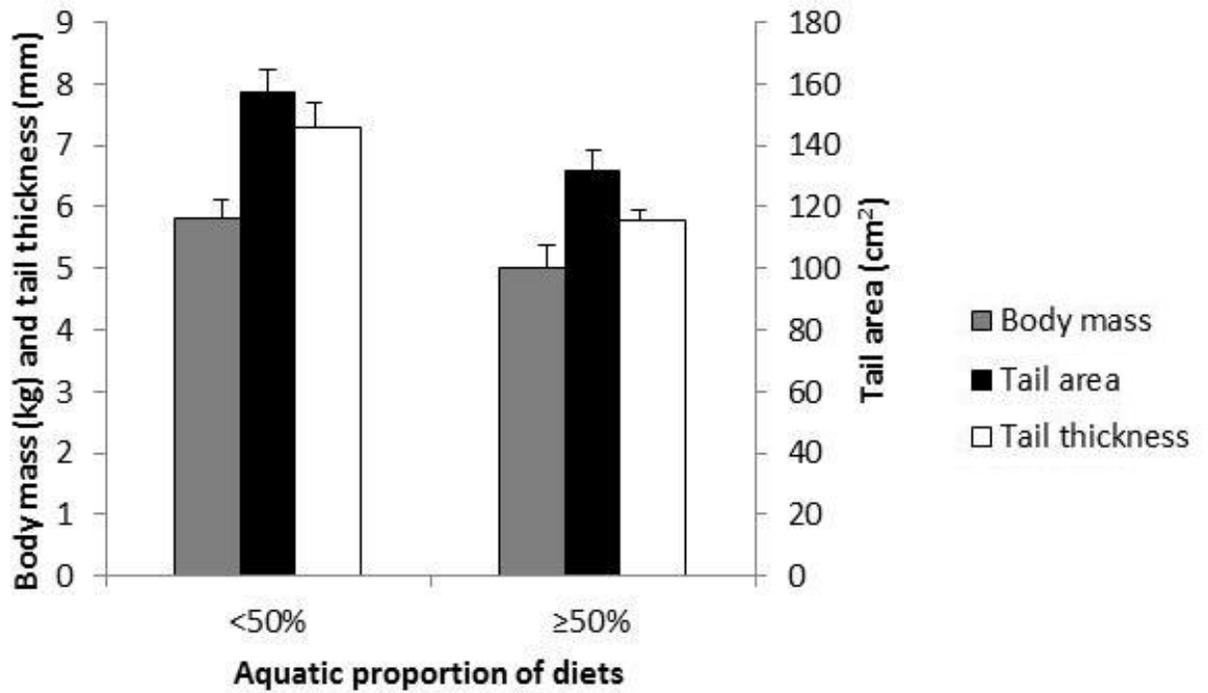


Figure 2.3. Mean (+SE) beaver kit (<1 y) body mass, tail area and tail thickness by percentage of total assimilated aquatic diets, Voyageurs National Park, Minnesota, September-October 2008.

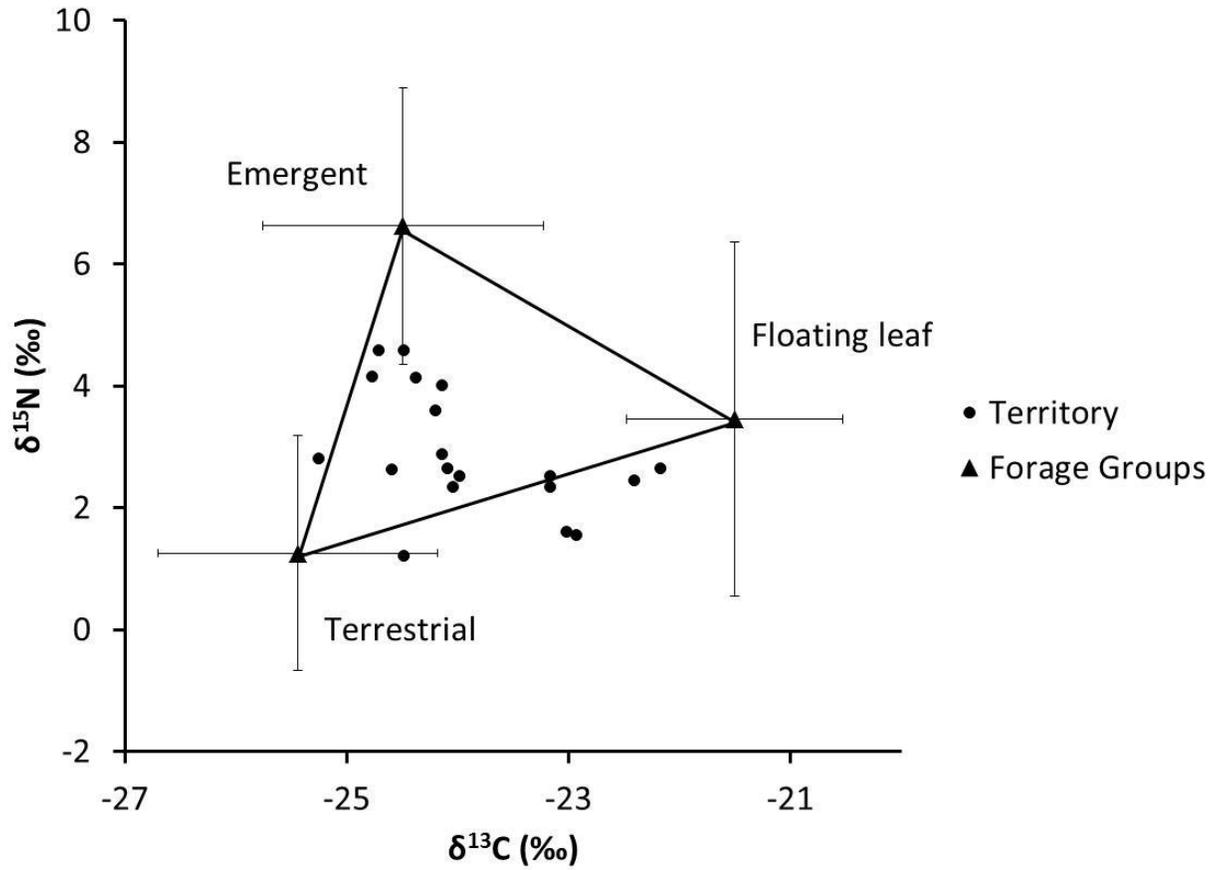


Figure 3.1. $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ biplot of beaver plant forage groups and mean assimilated diets of beavers by territory, Voyageurs National Park, Minnesota, winter 2007–2008 and summer 2008. Symbols are mean isotopic signature values (‰) for forage groups ($\pm\text{SE}$) and territories.

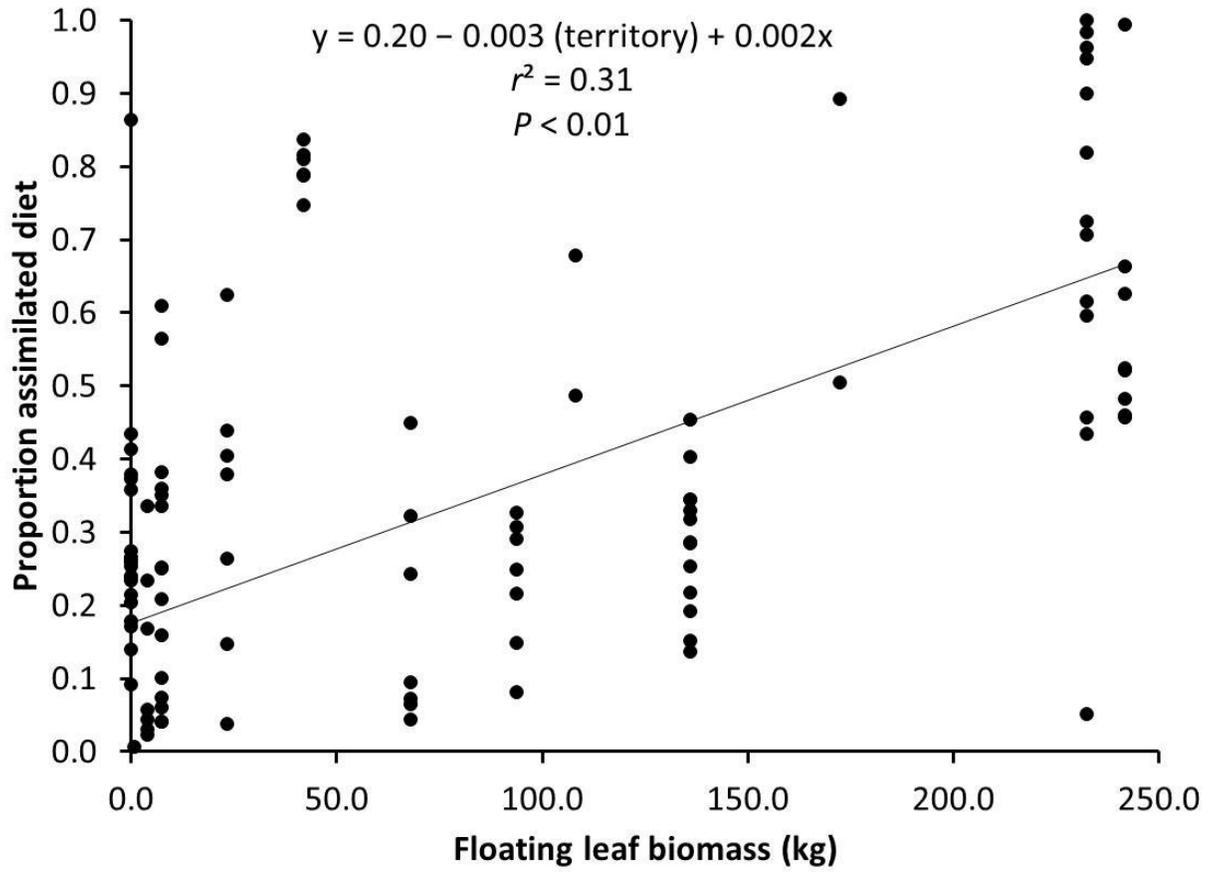


Figure 3.2. Proportion of assimilated beaver diets and total floating leaf biomass available by territory, Voyageurs National Park, Minnesota, summer 2008.

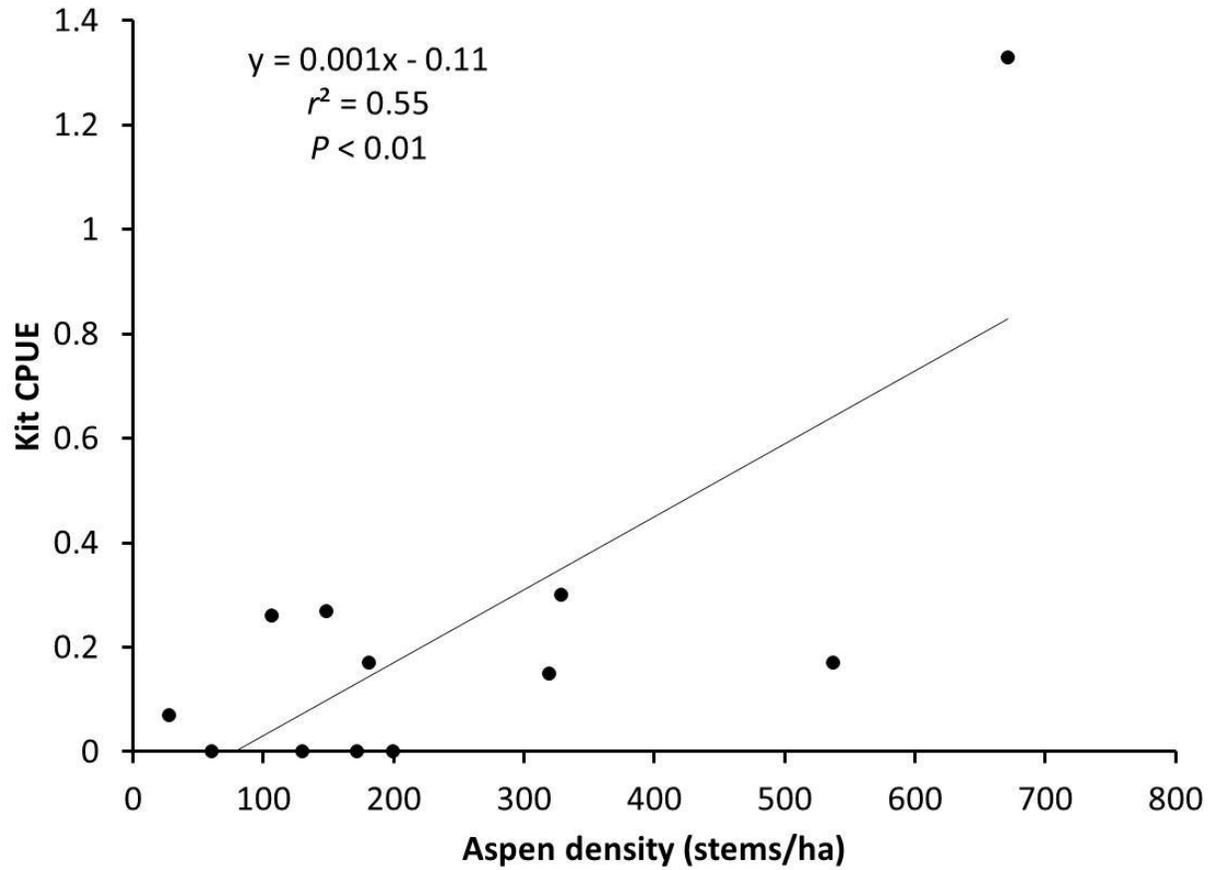


Figure 3.3. Quaking aspen (*Populus tremuloides*) density (stems/ha) and beaver kit catch per unit effort by territory, Voyageurs National Park, Minnesota, May–October 2008.

When 2 outliers are removed, the relationship was not significant ($r^2 = 0.20$, $F_{1,9} = 2.28$, $P = 0.17$).

APPENDIX A

Northern Michigan University's Institutional Animal Care and Use Committee (IACUC) approval.



Continuing Education
1401 Presque Isle Avenue
Marquette, MI 49855-5301

MEMORANDUM

October 7, 2008

TO: Dr. John Bruggink
William J. Severud
Department of Biology

FROM: Cynthia A. Prosen, Ph.D. 
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**
Application # IACUC 105
Approval Period: 10/06/2008-11/30/2008

The Institutional Animal Care and Use Committee have approved your application to use vertebrate animals in research, "Foraging Ecology of Beavers".

If you have any questions, please contact me.

kjm

APPENDIX B

Source clusters based on hierarchical cluster analysis for beaver forage species,
Voyageurs National Park, Minnesota, July-August 2007, with $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

Source	Species	$\delta^{15}\text{N}$				$\delta^{13}\text{C}$			
		Mean	SD	Min	Max	Mean	SD	Min	Max
Emergent aquatic macrophyte									
Sedge	<i>Carex</i> spp.	2.44	1.95	0.38	5.04	-27.45	1.29	-28.16	-25.53
Arrowhead	<i>Sagittaria</i> spp.	3.47	1.46	2.22	6.06	-26.71	2.23	-29.56	-23.09
Softstem bulrush	<i>Scirpus validus</i>	5.28	2.22	1.90	7.87	-27.91	0.67	-28.83	-27.16
Wool grass	<i>Scirpus cyperinus</i>	2.32	1.68	-0.43	4.26	-27.82	0.89	-29.06	-26.45
Cattail	<i>Typha</i> spp.	5.65	2.17	3.31	9.62	-27.56	0.62	-28.39	-26.72
Floating leaf aquatic macrophyte									
Yellow pond-lily	<i>Nuphar lutea</i>	1.11	3.15	-2.13	7.05	-23.61	0.34	-24.04	-23.22
White water lily	<i>Nymphaea</i> spp.	0.40	2.88	-2.82	4.96	-25.40	0.27	-25.76	-24.99
Terrestrial woody/herbaceous									
Balsam fir	<i>Abies balsamea</i>	-1.61	1.03	-2.85	0.11	-28.32	1.19	-29.52	-26.09
White spruce	<i>Picea glauca</i>	-0.88	1.50	-3.17	1.05	-27.14	1.54	-28.30	-24.95
White pine	<i>Pinus strobus</i>	0.16	1.98	-2.87	2.61	-27.67	1.30	-29.70	-26.23
Red maple	<i>Acer rubrum</i>	-2.08	3.64	-4.81	4.77	-27.72	1.48	-28.98	-24.95
Mountain maple	<i>Acer spicatum</i>	-4.18	1.43	-5.93	-1.70	-28.68	0.87	-30.17	-27.58
Speckled alder	<i>Alnus incana</i>	-1.08	0.95	-2.42	0.37	-28.50	1.13	-29.65	-26.39
Serviceberry	<i>Amelanchier</i> spp.	-2.01	2.33	-4.50	0.73	-29.09	1.17	-30.48	-27.27
White birch	<i>Betula papyrifera</i>	-1.60	1.82	-3.90	1.49	-28.33	1.14	-29.75	-26.80
Red-osier dogwood	<i>Cornus stolonifera</i>	-1.33	2.44	-4.72	1.62	-29.32	1.21	-31.06	-27.73
Beaked hazel	<i>Corylus cornuta</i>	-1.49	1.22	-2.51	0.63	-28.41	0.63	-29.24	-27.43
Green ash	<i>Fraxinus pennsylvanica</i>	-2.68	1.64	-4.54	-0.12	-27.34	1.73	-29.58	-24.69
Balsam poplar	<i>Populus balsamifera</i>	-0.44	0.69	-1.13	0.72	-29.09	0.81	-30.32	-28.22

Bigtooth aspen	<i>Populus grandidentata</i>	-1.57	1.12	-3.33	0.07	-28.12	1.01	-29.60	-27.14
Quaking aspen	<i>Populus tremuloides</i>	-1.20	2.85	-3.81	3.74	-29.71	0.66	-30.73	-28.64
Red oak	<i>Quercus rubra</i>	-1.57	1.21	-2.84	0.02	-28.25	1.27	-30.10	-26.21
Willow	<i>Salix</i> spp.	-0.47	2.76	-4.24	3.46	-28.87	1.15	-30.33	-26.86
Large-leaved aster	<i>Aster macrophyllus</i>	-1.50	0.83	-2.41	-0.54	-29.61	1.09	-31.39	-28.49
Bracken fern	<i>Pteridium aquilinum</i>	-0.33	0.82	-1.43	0.94	-27.60	0.62	-28.51	-26.71
Goldenrod	<i>Solidago</i> spp.	-1.57	1.16	-3.55	-0.32	-28.51	0.63	-29.33	-27.75

APPENDIX C

Northern Michigan University's IACUC approval.



Continuing Education & Sponsored Programs
1401 Presque Isle Avenue
Marquette, MI 49855-5325

MEMORANDUM

November 5, 2007

TO: Dr. John Bruggink
Biology Department

William J. Severud
Co-Principal Investigator

FROM: Cynthia A. Prosen, Ph.D. 
Dean of Graduate Studies & Research

RE: **Application to use Vertebrate Animals**

Application # IACUC 0087
Approval Period: May 2007-May 2009

The Institutional Animal Care and Use Committee have approved your application to use vertebrate animals in research, "Summer Ecology of Beavers in Voyageurs National Park".

If you have any questions, please contact me.

kjm