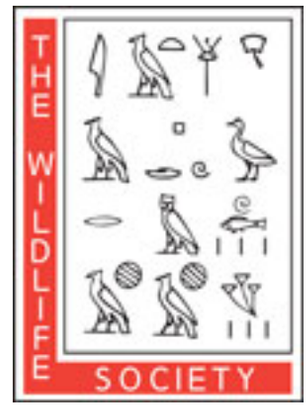

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Should diet be based on biomass? Importance of larger prey to the American marten

Roderick E. Cumberland, Jeff A. Dempsey, and Graham J. Forbes

Abstract Most research on diet of the American marten (*Martes americana*) has concluded that based on percentage frequency of occurrence, small mammals such as voles (Arvicolinae) are primary prey items. We investigated the diet of marten in New Brunswick by percentage occurrence and also by percentage caloric intake, which we feel better represents the importance of prey items in the diet. Our results of percentage occurrence reflected those from previous research; small mammals comprised 45% (26.4% Murinae and 15.8% *Sorex* spp.), with ruffed grouse (*Bonasa umbellus*), spruce grouse (*Canachites canadensis*), red squirrel (*Tamiasciurus hudsonicus*), flying squirrel (*Glaucomys_sabrinus*), and snowshoe hare (*Lepus americanus*) comprising 31% of the diet. However, when considering each prey item using minimum caloric estimates, snowshoe hare, grouse, and squirrel comprised approximately 95% of total calories consumed. On our study area, where large and small prey items are available, 10 years of track indices for marten, hare, grouse, and squirrel and 5 years of trap data for small mammals over a 10-year period indicated a correlation of larger prey with increasing marten abundance the following year, but was related inversely with small-mammal abundance in the same or following year. Our data suggest that we should change our understanding of marten foraging strategy, habitat quality, and population modeling that has centered previously on small mammals as the primary prey species.

Key words American marten, energetics, food habits, foraging, *Martes americana,* New Brunswick

The species that a predator consumes and the areas where they forage for that prey are major predictors of that predator's habitat needs. Wildlife managers rely on such information to identify and maintain critical habitat for species and to model population growth based on prey abundance. In mammals, identifying species-specific hair patterns from scats or stomach contents has long been a means to establish prey preference and niche breadth in predator–prey communities. Typically, any preference is inferred from the relative abundance of a species among all the species in the hair or stomach (gastrointestinal) sample. A major limitation in using percentage frequency of occurrence to interpret diet is that it equates hairs equally, regardless of prey size (Day 1966). This bias is important because larger prey would constitute more biomass and calories to a predator, particularly to species that will return to a carcass for repeated feedings.

We present recent work on a widespread American mesocarnivore, the American marten (*Martes americana*), to exemplify the need to consider

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caloric value instead of percentage frequency of occurrence to establish diet of a species.

The diet of the American marten has been described in detail across its range (reviews by Buskirk and Ruggiero 1994, Martin 1994). Generally, they reported that marten consumed mostly small mammals (i.e., voles, mice, shrews). Larger prey (i.e., hare, grouse) dominated marten diets in several northern-region studies (Bateman 1986, Raine 1987), although in most studies, large prey occurred in lower proportions in the diet and were not considered important in the feeding requirements or foraging behavior of marten. Almost all (21 of 22) studies reviewed by Martin (1994) used percentage frequency to determine the value of certain species to marten energetics and habitat use.

The belief that small mammals dictate marten food ecology is evident in management of marten populations and habitat. Furbearer management models often use prey abundance as an influence on home range size and fecundity (e.g., Thompson 1986). Habitat suitability index models and indicator forecasting emphasize habitat with mature softwood, coarse woody debris, and voles (Allen 1982, Naylor et al. 1994), rather than younger forest habitat associated with hares and grouse. In New Brunswick, Canada, marten habitat requirements are used as the surrogate to maintain 32 vertebrate species associated with old-growth forest (New Brunswick Department Natural Resources and Energy [NBDNRE] 1994).

Methods

We removed gastrointestinal (GI) tracts from 746 marten (525 male:217 female) carcasses collected from trappers following a 2-week commercial trapping season (22 Nov–7 Dec 1992). Marten were trapped using leghold and instant-kill traps. Marten in leghold traps may defecate but retain stomach contents, leading to a potential bias in stomach analysis between trap types. However, bias should be minimal because 76% of marten were harvested with Conibear instant-kill traps; both trap types were used throughout the study area, and trappers baited with beaver (*Castor canadensis*) and muskrat (*Ondatra zibethica*), species that were not considered prey items for marten (DNRE, unpublished data). Carcasses originated from the northern two-thirds of the province, approximately a 38,000-km^2 area. We washed and separated material found in the 594 (413 male:181 female) GI tracts with food (79.6% of GI tracts) in a 20-grade sieve. Marten with empty stomachs were not used in the analysis. We identified prey remains using reference collections of prey types and keys on skulls and hair (Day 1966, Adorjan and Kolenosky 1969). We identified mammalian prey to species except voles and shrews, which we identified to genus. We did not attempt to identify invertebrates or woody material. We restricted our analysis to categories that comprised >3% frequency of the total: voles (*Clethrionomys gapperi, Microtus* sp.), shrews (*Blarina brevicauda*, *Sorex* sp.), mice (*Peromyscus maniculatus,* Zapodidae), squirrels (*Tamiasciurus hudsonicus, Glaucomys sabrinus*), hares (*Lepus americanus*), grouse (*Bonasa umbellus*, *Canachites canadensis*), passerine birds, other fauna, and berries–fruit.

Studies of food consumption in captive marten are lacking, so we used estimates of prey consumption established by Thompson (1986) for marten and Powell (1981) from captive fishers (*Martes pennanti*) as estimated conservative (minimum) and maximum values to calculate total metabolizable energy (Kcal) of major prey items. Larger prey, such as snowshoe hares (<500 g of meat) and grouse (<300 g), may not be totally consumed in one meal. It is possible for a marten to have the edible parts from an entire snowshoe hare in its stomach at one time (Thompson 1986); therefore, we used one as a maximum. However, it is more likely that 3 meals are obtained from a snowshoe hare and we used a conservative estimate of 0.33 hares. Similarly, we used a maximum of one and a minimum of 0.7 for grouse. Vole and mouse distribution can be clumped (Bowman et al. 2000); therefore, we used one as a minimum and 1.5 as a maximum for each occurrence. Minimum and maximum values for shrews, mice, squirrels, and passerines was one occurrence. Metabolizable energy (Kcal) provided by major prey items was as follows: voles (30 Kcal), shrews (5 Kcal), mice (25 Kcal), snowshoe hares (1,350 Kcal), squirrels (470 Kcal), grouse (600 Kcal), and passerines (5 Kcal) (Powell 1981, Thompson 1986). All caloric values represent those calculated from prey items in winter. Weights of prey items were determined from average weights of New Brunswick mammals (Dilworth 1984).

We determined marten and prey-species abundance using small-mammal trapping (1987–1991) and winter track surveys (1987–1996) within the core of marten range in northern New Brunswick (47°24′N, 66°30′W). We trapped small mammals in fall, every 12 m, with Victor and Museum Special

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mouse traps along 32 300-m-long transects, each a minimum 1 km apart. We situated transects in 9 forest cover types. We recorded tracks of marten and prey species within 24 hours of snowfall along transects, 3 times between December and March. We derived fecundity of the marten population from average number of blastocysts produced/pregnant female, multiplied by percentage of successful breeders in the population (Strickland and Douglas 1987). We processed, on average, 520 female marten annually for the past 14 years and are confident that this large sample of female reproductive tracts was a reliable indicator of breeding success. All carcasses were submitted to government within 2 weeks of the 2- to 3-week trapping season. We developed a regression model to relate prey abundance to marten abundance in the same year and following year. We used the delay to test for possibility of a temporal lag between marten fecundity and prey abundance, as shown by Thompson and Colgan (1987) and Weckwerth and Hawley (1962).

Results

Marten diet during early winter in New Brunswick is dominated by a few prey species. Percentage occurrence of prey types indicated that small mammals composed 45% of the diet: 26.4% voles and 15.8% shrews (Table 1). Larger prey items such as ruffed and spruce grouse, squirrels, and snowshoe hares composed 31% of the total diet. Numerous species were consumed, but in many cases they were single records that likely represented opportunistic feeding. A small proportion of the diet consisted of white-tailed deer (*Odocoileus virginianus,* 2.4%), bobcat (*Lynx rufus*, 0.1%), and porcupine (*Erethizon dorsatum*, 0.3%). Marten comprised 0.8% of the diet, but we do not know whether this was from self-grooming, scavenging, or cannibalism. Amphibians consisted of wood frogs (*Rana sylvatica*) and spotted salamander (*Ambystoma maculatum*). Undigested pieces of flesh in stomachs (10.6%) were considered to be bait. Interviews with trappers indicated that beaver and muskrat were used as bait; these species comprised 1.8% of the items. All berries found in stomachs were American mountain ash (*Sorbus americana*) and comprised 2.3% of the diet. We assumed the egg was cached previously.

A few large species contributed to most of the caloric intake of New Brunswick marten; snowshoe hares, grouse, and squirrels comprised 93.4% of total calories provided by prey items using maximum estimates and 95% of total calories using conservative estimates (Figure 1). Snowshoe hares contributed the greatest proportion (43.6%) of total calories in the diet using maximum estimates, whereas grouse and squirrels contributed the greatest proportion (34.2% and 35.3% respectively) of total calories in the diet using conservative estimates. Small mammals comprised 5.4% and 6.3% of total calories in the diet from maximum and conservative estimates, respectively. Passerines contributed less than 0.05% of the total calories from maximum and conservative estimates.

Contrary to expected results, marten abundance did not correlate with small-mammal abundance ($P = 0.250$, $R^2 = -0.64$). Marten fecundity was associated negatively with small-mammal abundance ($P = 0.02$, $R^2 = -0.98$). Marten abundance in the following year was predicted positively by abundance of hares, squirrels,

Table 1. Diet from 594 marten stomachs and gastrointestinal tracts from New Brunswick in early winter 1992, expressed as percentage frequency occurrence (n = 739 items).

Mammals		Birds		Other	
Species	% Occurrence	Species	% Occurrence	Species	% Occurrence
vole spp.	26.4	grouse	12.2	flesh	10.6
shrew spp.	15.8	gray jay (*Perisoreus canadensis*)	1.2	berries	2.3
red squirrel	10.8			amphibians	0.7
snowshoe hare	8.0	unidentified sp.	1.4	invertebrates	0.7
white-tailed deer	2.4			fish	0.3
deer mouse	3.2			fruit	0.1
beaver	1.4			egg	0.1
jumping mouse	0.8				
American marten	0.8				
flying squirrel	0.4				
muskrat	0.4				
porcupine	0.3				
woodchuck (*Marimota monax*)	0.1				
bobcat	0.1				
weasel spp.	0.1				

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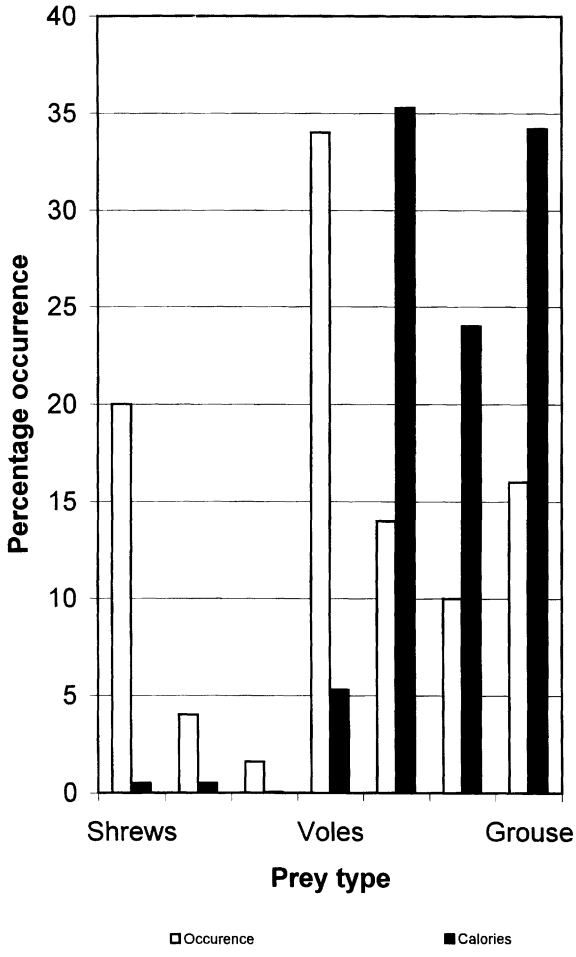

Figure 1. Comparison of important food items in stomach and gastrointestinal tracts of marten from New Brunswick, indicating emphasis on small prey when using percentage frequency occurrence and larger prey when using conservative estimates of caloric value. Only items >3.0% of total are shown.

and grouse, relatively large prey (marten = 0.250–0.0462 [hare] + 0.0874 [squirrel] + 2.04 [grouse]; $P=0.039$, $R^2=0.79$).

Discussion

Diets of New Brunswick marten appear to be similar to those found elsewhere; small mammals were the most frequent food items during early winter. However, larger prey (snowshoe hares, grouse, squirrels) comprised much of the energy intake in the marten diet. This result suggests that marten may feed on a range of prey items but gain considerable value from consuming large prey species, though they occur in the diet less frequently (31.4% frequency occurrence) than smaller prey species (voles, mice, shrews, passerines, 48.8%). Marten may be encountering smaller prey, which provide energy at a minimal cost, while foraging primarily for larger prey (Thompson and Colgan 1990). Conversely, marten may be foraging for small prey in areas of abundant prey and simultaneously gaining access to large prey species. These foraging strategies would be complicated by a changing availability of prey between years and seasons. Thompson (1986) found that small mammals comprised 50% of caloric value in snow-free seasons but large prey comprised 85% of calories during winter.

Snowshoe hare abundance in 1992 was considered to be at a low to moderate level of the population cycle. We cannot determine whether marten were selecting prey proportional to their abundance because the large size of the study area limited intensive surveys. Our measures of marten productivity were collected over a larger area than indices for small-mammal abundance, and even though habitat is similar throughout the study area, we note the possibility that scale effects could limit extrapolation. However, the strength of association between indices of annual marten numbers to annual indices of grouse, hare, and red squirrel abundance from the previous year is noteworthy. We did not find a significant relationship between indices of marten numbers and indices of small-mammal abundance. The negative correlation of small-mammal abundance and marten fecundity and abundance may relate to the small caloric contribution made by small mammals (5–6% mice, voles and shrews).

Marten change diet according to the seasonal availability of a range of fruits, insects, vegetation, and mammals. Diets in winter are believed to be most important because of the thermal limitations of marten (Taylor and Buskirk 1994). Our data were based on the early winter season and likely cannot be extrapolated to late winter. Several studies have shown that fewer small mammals are consumed in late winter, possibly due to increasing snow depth and decreasing access (Zielinski et al. 1983, Buskirk and MacDonald 1984, Thompson and Colgan 1990). However, if marten foraging strategy is based on pursuing larger prey such as hare, the decline in small-mammal consumption may instead be due to a need for larger prey as physiological stress accumulates by late winter.

Management implications

Most furbearer models adjust home range size and rates of fecundity and mortality based on prey

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abundance. However, our findings suggest that using prey abundance based on prey occurrence may be erroneous. Our work suggests that percentage caloric intake is more reflective of marten welfare and thus models should consider alternate inputs to better reflect marten energetics. Other furbearer species (i.e., bobcat, fisher) that feed on a range of prey sizes may be similarly biased.

In conclusion, we do not negate the importance of small mammals in the diet of marten, particularly when large prey items are not present or when fluctuations in the availability of rodents and hares appear to influence prey selection by marten (Cowan and Mackay 1950, Thompson and Colgan 1990). Marten may be foraging at several spatial and temporal scales, and importance of large prey and small prey likely varies. Marten consume a large proportion of calories from prey larger than voles, when such prey is available. Our point is to state not that marten cannot persist on small prey but that in areas where larger prey is consumed, the practice of not converting percentage frequency values to caloric values suggests that the importance of larger prey may have been overlooked in many studies throughout North America. In 10 of 16 studies available to us in the review in Martin (1994), hares, squirrels, and grouse constitute percentage frequencies similar to or greater than those found in our study; conversion of their results would yield a similar importance of larger prey items to marten food ecology and, by extension, to the need to consider additional habitat types.

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Literature cited

Adorjan, A. S., and G. B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Research Report (Wildlife) No. 90, Department of Lands and Forests, Toronto, Ontario, Canada.

Allen, A. W. 1982. Habitat suitability index models: marten. United States Fish and Wildlife Service, FWS/OBS-82/10.45, Fort Collins, Colorado, USA.

Bateman, M. C. 1986. Winter habitat use, food habits and home range size of the marten, *Martes americanus*, in western Newfoundland. Canadian Field-Naturalist 100: 58–62.

Bowman, J. C., G. Forbes, and T. Dilworth. 2000. The spatial scale of variability in small-mammal populations. Ecography 23: 328–334.

Buskirk, S. W., and S. W. MacDonald. 1984. Seasonal food habits of marten in south-central Alaska. Canadian Journal of Zoology 62: 944–950.

Buskirk, S. W., and S. W. MacDonald. 1989. Analysis of variability in home-range size of the American marten. Journal of Wildlife Management 53: 997–1004.

Buskirk, S. W., and Ruggiero. 1994. American marten. Pages 17–37 *in* Ruggiero, L., K. Aubry., S. Buskirk, J. Lyon, and W. Zielinski, editors. Scientific basis for conserving large carnivores: American marten, fisher, lynx and wolverine in the western United States. United States Department of Agriculture General Technical Report RM-254, Washington, D. C., USA.

Cowan, I. M., and R. H. MacKay. 1950. Food habits of the marten (*Martes americanus*) in the Rocky Mountain region of Canada. Canadian Field-Naturalist 64: 100–104.

Day, M. G. 1966. Identification of hair and feather remains in the gut and faeces of stoats and weasels. Journal of Zoology 148: 201–217.

Dilworth, T. 1984. Land Mammals of New Brunswick. Unipress, Fredericton, New Brunswick, Canada.

Martin, S. K. 1994. Feeding ecology of American martens and fishers. Pages 297–315 in S. Buskirk, A. Harestad, M. Raphael, and R. Powell, editors. Martens, sables, and fishers: biology and conservation. Cornell University, Ithaca, New York, USA.

Naylor, B., T. Bellhouse, S. Christilaw, and P. Wellandt. 1994. Development and validation of a habitat suitability index for the American marten in central Ontario. Technical Report 28, Ontario Ministry of Natural Resources, Toronto, Canada.

New Brunswick Department of Natural Resources and Energy. 1994. A vision for New Brunswick forests. Fredericton, New Brunswick, Canada.

Powell, R. 1981. Hunting behavior and food requirements of the fisher (*Martes pennanti*). Pages 883–917 *in* J. A. Chapman and D. Pursley, editors. Proceedings first worldwide furbearer conference. University of Maryland, 3–11 August 1980, Frostburg, USA.

Raine, R. M. 1987. Winter food habits and foraging behaviour of fishers (*Martes pennanti*) and martens (*Martes americana*) in southeastern Manitoba. Canadian Journal of Zoology 65: 745–747.

Strickland, M. A., and C. W. Douglas. 1987. Marten. Pages 530–547 *in* M. Novak, J. A. Baker, M. E. Obbard and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Toronto, Canada.

Taylor, S., and S. Buskirk. 1994. Forest microenvironments and resting energetics of the American marten *Martes americanus*. Ecography 17: 249–256.

Thompson, I. D. 1986. Diet choice, hunting behaviour, activity patterns, and ecological energetics of marten in natural and logged areas. Dissertation, Queen's University at Kingston, Kingston, Ontario, Canada.

Thompson, I. D., and P. W. Colgan. 1987. Numerical responses of martens to a food shortage in north-central Ontario. Journal of Wildlife Management 51: 824–835.

Thompson, I. D., and P. W. Colgan. 1990. Prey choice by marten during a decline in prey abundance. Oecologia 83: 443–451.

Weckwerth, R. P., and V. D. Hawley. 1962. Marten food habits and population fluctuations in Montana. Journal of Wildlife Management 26: 55–74.

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ZIELINSKI, W. J., W. D. SPENCER, AND R. H. BARRETT. 1983. Relationship between food habits and activity patterns of pine martens. Journal of Mammalogy 64:387–396.

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