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Effects of Sex and Age on Winter Diet of American Martens in Michigan

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ABSTRACT. We investigated whether sex or age influenced winter diet in American martens (Martes americana) from the Upper Peninsula of Michigan by analyzing gut content of 151 individuals trapped during 2000–2004. We identified 433 occurrences of 10 prey species and classified them into six groups based on body size. Overall, marten diets were similar to those reported previously. Proportion of prey groups and kilocalories consumed were generally similar between male and female marten diets, as well as between juveniles and adults. Average dietary breadth (0.46) was comparatively high but within the range reported for other North American studies. Dietary overlap (0.99) was high between males and females and between juveniles and adults. Comparable diets between sexes suggest that size sexual dimorphism was unrelated to prey species consumed. Similarly, diets of juveniles and adults were comparable. Mice and voles occurred most frequently in marten diets; however, squirrels represented the greatest proportion of kilocalories consumed. Future studies of marten diet should emphasize prey abundance.

INTRODUCTION

Adult male American martens (Martes americana) are 20–40% heavier than females (Strickland et al. 1982, Buskirk and MacDonald 1989, Holmes and Powell 1994). Dimorphism of this magnitude would be expected to result in prey partitioning between sexes (Dayan and Simberloff 1994). However, several studies have reported high dietary overlap between male and female martens, suggesting little partitioning of prey species (Nagorsen et al. 1989, 1991; Andruskiw 2003). Where differences between male and female diets have been reported, males ate larger prey such as ruffed grouse (Bonasa umbellus) and snowshoe hares (Lepus americanus) while females most commonly consumed mice and voles (Poole and Graf 1996, Bul 2000).

As animals mature, foraging skills are refined (Raven et al. 2005). Consequently, juveniles are generally considered less skilled hunters than adults which may be reflected in their diets. Few studies have compared juvenile (<1 year old) and adult (>1 year old) American marten diets and those results are conflicting. Thompson and Colgan (1987) found no differences between juvenile and adult diets in north central Ontario. In contrast, juvenile martens in the Northwest Territories consumed more large prey items (e.g., snowshoe hare) than adults (Poole and Graf 1996).

Because the influence of size and age on marten diet remains conflicting and no data on marten diet are available for Michigan, our objectives were to: 1) estimate marten diet in Michigan's Upper Peninsula (UP) during early winter, and 2) compare diet by sex and age groups using frequency of occurrence and estimated caloric intake.

MATERIAL AND METHODS

The Upper Peninsula of Michigan is located on the southern shore of Lake Superior and covers an area of 42,610 km² (Latitude: 45°45'–46°49' N, Longitude: 84°15'–89°30' W). December temperatures ranged from average lows of -8°C to highs of -1°C; average precipitation during the study was 49.5 cm.

Carass Collection

Gastrointestinal (GI) tracts of trapped martens were collected by the Michigan Department of Natural Resources (MDNR) from the 2000–2004 trapping seasons as part of mandatory registration and frozen until analysis. Sex, age using cementum annuli (Arthur et al. 1992), date, and location trapped were determined by MDNR personnel and recorded for each marten. We used martens with complete information that were registered as harvested during the marten trapping season for analysis. All martens harvested during 2000–2001 (1-10 December) were used for analysis. In 2002 and 2003 (1-15 December), we sampled all females and an equal number of randomly selected males. In 2004 (1-15 December), we randomly selected 30 individuals of each sex.

Gastrointestinal Content

Because stomachs and intestines of an individual marten may contain remains from different meals (Nagorsen et al. 1989), stomach and intestinal contents were separated initially. Gastrointestinal tracts from martens were opened and scanned of their contents and contents were rinsed with 75% ethyl alcohol. We then separated hair samples into labeled containers and air dried hairs for identification (Weingart 1973).

We made negative impressions of hairs sampled from each marten's GI tract (Weingart 1973). We used a compound microscope at 40–400x magnification, hair identification guides (Adorjan and Kolenosky 1969, Moore et al. 1997, Andruskiw 2003), and reference slides made from museum specimens to identify prey species. In addition to hair, animal parts including portions of skulls and feet were also separated, air dried, and identified using a museum reference collection. We used hair and other animal parts to estimate the minimum number of individuals of each prey species contained in each marten GI tract. For example, if a GI tract contained hair and portions of two skulls from red-backed voles, we recorded two voles. For GI tracts containing hair only of a given species, we recorded one individual for that species.

Six prey groups were designated based primarily on body size: shrew, mice/vole, bird, chipmunk, squirrel, and grouse/hare. The shrew group included Sorex spp. and short-tailed shrews (Blarina brevicauda). The mice/vole group consisted of deer mice (Peromyscus maniculatus) and red-backed voles (Clethrionomys gapperi). The bird group included all avian species except ruffed grouse. The chipmunk group comprised eastern chipmunks (Tamias striatus), and the squirrel group included red squirrels (Tamiasciurus hudsonicus) and eastern gray squirrels (Sciurus carolinensis). Ruffed grouse and snowshoe hares comprised the grouse/hare group.

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Analyses were conducted using STATISTIX 8 (Analytical Software 2003) with significance accepted when $P < 0.05$. We estimated dietary breadth as $\frac{1}{\sum P_{ij}^2}$. We then calculated mean ingested biomass of prey groups occurring in the stomach and intestinal contents of individual martens.

We estimated kilocalories (kcal) for prey groups using mean body mass of prey species; unknown kcal values for prey species were estimated using linear regression based on kcal values from prey species reported in Cumberland et al. (2001). Two-way analysis of variance was used to compare kcal consumption of prey groups between sex and age classes. Analyses were conducted using STATISTIX 8 (Analytical Software 2003) with significance accepted when $P \leq 0.05$.

We calculated dietary breadth as $(1/\sum P_{ij}^2)/N$ where $P_i$ equals the proportion of prey group $i$ in the diet of martens in a particular sex and age class and $N$ is the number of prey groups (Nagorsen et al. 1989). Values range from zero to one, where one = prey groups consumed in identical proportions. We estimated dietary overlap using the equation:

$$\text{dietary overlap} = \frac{\sum P_{ij} \cdot \sum P_{jk}}{(\sum P_{ij}^2 \cdot \sum P_{jk}^2)^{1/2}}$$

where $P_{ij}$ is the proportion of prey group $i$ in the diet of group $j$ and $P_{ik}$ is the proportion of prey group $i$ in the diet of group $k$, and reflects similarity of diets (Nagorsen et al. 1991). Values range from zero to one, where zero = no overlap and one = identical diets.

**RESULTS**

We sampled 318 martens of which 151 contained stomach and intestinal contents used for analyses. Sex and age structure of the 151 martens included 68 females and 83 males or 47 juveniles and 104 adults. We identified 433 prey items representing ten species in our six prey groups (Table 1). The percentage of martens containing one to seven prey items was 9%, 32%, 33%, 19%, 3%, 3%, and 1%, respectively. Mean number of prey items per marten was 2.87 (standard deviation $\pm 1.52$).

Overall, marten GI tracts contained species belonging to smaller-sized prey groups. In the mice/vole group, red-backed voles were the most frequently identified prey species, occurring in 145 (96%) GI tracts and deer mice were the second most abundant (57%). In the shrew group, short-tailed shrews and Sorex species occurred in 47% and 21% tracts, respectively. In the four larger prey groups, frequencies of occurrence were 17% for eastern gray squirrels, 16% for red squirrels, 15% for birds, 12% for eastern chipmunks, 3% for snowshoe hares, and 1% for ruffed grouse.

The proportions of prey groups used by male and female martens was similar ($\chi^2 = 7.57$, 5 df, $P = 0.180$; Fig. 1). Males and females acquired similar ($F_{1, 148} = 0.03-2.75$, $P = 0.10-0.86$) amounts of kcals from all prey groups. Dietary breadth was 0.41 for males and 0.50 for females; dietary overlap between sexes was 0.98.

The proportions of prey groups consumed by juvenile and adult martens were similar ($\chi^2 = 4.45$, 5 df, $P = 0.487$; Fig. 2). Juveniles and adults acquired similar amounts of kcals ($F_{1, 148} = 6.37$, $P = 0.01$), with adults acquiring more kcal from this prey group. Dietary breadth was 0.51 for juveniles and 0.43 for adults; dietary overlap between age classes was 0.99.

**Table 1**

<table>
<thead>
<tr>
<th>Prey Items</th>
<th>Sex Male</th>
<th>Female</th>
<th>Juvenile</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of martens analyzed</td>
<td>83</td>
<td>68</td>
<td>47</td>
<td>104</td>
</tr>
<tr>
<td>No. of prey items</td>
<td>235</td>
<td>198</td>
<td>121</td>
<td>312</td>
</tr>
<tr>
<td>Shrew group</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sorex spp.</td>
<td>17</td>
<td>15</td>
<td>7</td>
<td>25</td>
</tr>
<tr>
<td>Short-tailed shrew</td>
<td>34</td>
<td>37</td>
<td>24</td>
<td>47</td>
</tr>
<tr>
<td>Mice/vole group</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deer mouse</td>
<td>52</td>
<td>34</td>
<td>12</td>
<td>74</td>
</tr>
<tr>
<td>Red-backed vole</td>
<td>86</td>
<td>62</td>
<td>47</td>
<td>101</td>
</tr>
<tr>
<td>Bird group</td>
<td>12</td>
<td>11</td>
<td>8</td>
<td>15</td>
</tr>
<tr>
<td>Chipmunk group</td>
<td>9</td>
<td>9</td>
<td>6</td>
<td>12</td>
</tr>
<tr>
<td>Squirrel group</td>
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<td>12</td>
<td>5</td>
<td>19</td>
</tr>
<tr>
<td>Red squirrel</td>
<td>9</td>
<td>17</td>
<td>9</td>
<td>17</td>
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<td>Gray squirrel</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>1</td>
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<tr>
<td>Grouse/Hare Group</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Snowshoe hare</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>
DISCUSSION

Diet Composition

Mice and voles were the most frequently consumed prey, consistent with other marten winter diet studies (Lensink et al. 1955, Weckwerth and Hawley 1962, Buskirk and MacDonald 1984, Strickland and Douglas 1987, Thompson and Colgan 1987, Slough et al. 1989, Buskirk and Ruggiero 1994, Poole and Graf 1996, Bull 2000, Cumberland et al. 2001). Squirrels, however, provided the largest proportion of estimated kcals. This is the second study to document gray squirrel in marten diet. Weckwerth and Hawley (1962) found gray squirrel in <0.5% of the summer and fall diets of marten in Montana in contrast to 17% of the early winter diet in this study. The variation in prevalence of gray squirrels in marten diets may be a consequence of squirrel availability, vulnerability, or seasonal differences in diet. Similarly, few diet studies have been conducted in areas where martens are sympatric with gray squirrels.

Surprisingly, eastern chipmunks occurred in 12% of martens sampled. In northern climates, chipmunks use burrows up to 10 meters long and >60 cm below ground (Whitaker and Hamilton 1998). In Michigan, chipmunks may leave their burrows during warm periods in winter; however, most remain in burrows for extended periods limiting their vulnerability to predators (Baker 1983, Whitaker and Hamilton 1998). This apparently high occurrence of chipmunks may be a consequence of chipmunks being predated while leaving their burrows during warm periods or of some martens being captured before the legal trapping season and registered as captured during this season.

Male and Female Diets

Although male martens are probably more capable of killing larger prey than females (Dayan et al. 1989, Poole and Graf 1996, McDonald 2002), diet was similar between sexes in this study. Dietary breadth for males and females was within the range of previous studies of marten winter diet in North America (range = 0.19–0.69; Nagorsen et al. 1989). However, only Nagorsen et al. (1989) reported higher dietary breadth (0.69) than this study. Poole and Graf (1996) suggested that low dietary breadth during winter may reflect low prey species abundance and diversity. The number of prey species available in the UP in early winter is low (Baker 1983) compared to that found in other studies (Cowan and Mackay 1950, Weckwerth and Hawley 1962, Buskirk and MacDonald 1984, Hargis and McCullough 1984, Nagorsen et al. 1989, Nagorsen et al. 1991, Poole and Graf 1996, Bull 2000, Cumberland et al. 2001). However, many studies used different classification schemes for prey groups (Cowan and Mackay 1950, Quick 1955, Weckwerth and Hawley 1962, Koehler and Hornocker 1977, Zielinski et al. 1983, Nagorsen et al. 1989). To address variation in prey groupings across studies, we reclassified data from other studies (Cowan and Mackay 1950, Quick 1955, Nagorsen et al. 1989) into the six prey groups used in this study and recalculated dietary breadth. Recalculated dietary breadths were reduced slightly in previous studies (0.05–0.19), further demonstrating comparatively high dietary breadth observed in this study.

In contrast to our prediction, dietary overlap between sexes was high (0.98), suggesting little partitioning of prey (Nagorsen et al. 1989).

Figure 1. Proportion of prey groups and proportion of kilocalories of prey groups in male (83) and female (68) American marten gastrointestinal tracts in the Upper Peninsula of Michigan, December 2000–2004.

Figure 2. Proportion of contents and proportion of kilocalories of prey groups in male (83) and female (68) American marten gastrointestinal tracts in the Upper Peninsula of Michigan, December 2000–2004.
Comparison of Diet Techniques

Although frequency of occurrence may facilitate comparisons across diet studies, kilocalories consumed were a better indicator of the importance of large prey species. Small prey species (voles, mice, and shrews) represented a small amount of the total ingested kcals and the importance of larger prey species (i.e., squirrels, grouse, and hares) was more pronounced. For example, squirrels were consumed less frequently than small mammals; however, squirrels provided more kcal than other prey groups. Similarly, in New Brunswick, three large prey species (grouse, snowshoe hare, and squirrel) comprised only 31% frequency of occurrence in martens' diet (Cumberland et al. 2001). When minimum caloric intake was calculated for those same marten diets, these three prey species comprised about 95% of total calories consumed. Frequency of occurrence is used often to estimate diet; however, this technique may underestimate the relative contribution of larger prey species to predator fitness (Cumberland et al. 2001). We support Cumberland et al. (2001) in recommending use of estimated calories consumed over frequency of occurrence when assessing carnivore diets, particularly when body size of prey species varies markedly.

A limitation of this study and numerous other diet studies is the lack of information on prey abundance and vulnerability, both

Age Related Diets

We suspected that juvenile marten diets would differ from adults due to limited hunting experience. However, juvenile and adult diets in this study were similar as also found in Ontario (Thompson and Colgan 1987). In contrast, Poole and Graf (1996) determined that juvenile martens consumed more large prey than adults. As martens mature, improved hunting skills should increase diversity of potential prey species and decrease competition with juveniles (Raven et al. 2005). High dietary overlap of prey species between age classes suggests juvenile marten hunting skills may have been comparable to adults by early winter. Similarly, limited partitioning of prey between juveniles and adults could be attributed to low diversity of prey species (Nagorsen et al. 1989). Juveniles and adults acquired similar kcals from all prey groups except the mice/voles group. Factors influencing this are unknown; a comparative study of prey abundance was not performed.

Figure 2. Proportion of prey groups and proportion of kilocalories of prey groups in juvenile (47) and adult (104) American marten gastrointestinal tracts in the Upper Peninsula of Michigan, December 2000–2004.
seasonally and across years. To better understand prey selection or diet choice in carnivores, incorporating estimates of prey availability (e.g., Cote et al. 2008) and considering other factors that may influence diet choice (e.g., prey detectability) is critical.

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LITERATURE CITED