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Annual and seasonal changes in diets of martens: evidence from stable isotope analysis

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Abstract Theory predicts that generalist predators will switch to alternative prey when preferred foods are not readily available. Studies on the feeding ecology of the American marten (*Martes americana*) throughout North America suggest that this mustelid is a generalist predator feeding largely on voles (*Microtus* sp.; *Clethrionomys* sp.). We investigated seasonal and annual changes in diets of martens in response to the changing abundance of small rodents (*Peromyscus keeni*, and *Microtus longicaudus*) on Chichagof Island, Southeast Alaska, using stable isotope analysis. We hypothesized that martens would feed primarily on small rodents during years with high abundance of these prey species, whereas during years of low abundance of prey, martens would switch to feed primarily on the seasonally available carcasses of salmon. We also hypothesized that home-range location on the landscape (i.e., access to salmon streams) would determine the type of food consumed by martens, and martens feeding on preferred prey would exhibit better body condition than those feeding on other foods. We live-captured 75 martens repeatedly, from mid-February to mid-December 1992–1994. We also obtained marten carcasses from trappers during late autumn 1991 and 1992, from which we randomly sub-sampled 165 individuals. Using stable isotope ratios and a multiple-source mixing model, we inferred that salmon carcasses composed a large portion of the diet of martens in autumn during years of low abundance of rodents (1991 and 1992). When small ro-

dents were available in high numbers (1993 and 1994), they composed the bulk of the diet of martens in autumn, despite salmon carcasses being equally available in all years. Selection for small rodents occurred only in seasons in which abundance of small rodents was low. Logistic regression revealed that individuals with access to salmon streams were more likely to incorporate salmon carcasses in their diet during years of low abundance of small rodents. Using stable isotope analysis on repeated samples from the same individuals, we explored some of the factors underlying feeding habits of individuals under variable ecological conditions. We were unable to demonstrate that body weights of live-captured male and female martens differed significantly between individuals feeding on marine-derived or terrestrial diets. Therefore, martens, as true generalist predators, switched to alternative prey when their principal food was not readily available on a seasonal or annual basis. Although salmon carcasses were not a preferred food for martens, they provided a suitable alternative to maintain body condition during years when small rodents were not readily available.

Key words *Martes americana* · Prey abundance · Food selection · Salmon · Stable isotope ratios

Introduction

Studies on the feeding ecology of the American marten (*Martes americana*) throughout North America suggest that this mustelid is a generalist predator, feeding on a large variety of prey such as small mammals, birds, invertebrates, fish, ungulate carrion, and vegetation (Martin 1994 for review). Most studies identified voles (*Microtus* sp. and *Clethrionomys* sp.) as the most common prey in diets of marten (Buskirk and MacDonald 1984; Douglas et al. 1983; Martin 1987, 1994; Thompson and Colgan 1990; Weckwerth and Hawley 1962). These studies, however, differed in their conclusion as to whether martens responded opportunistically to prey

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abundance (Campbell 1979; Gordon 1986; Soutiere 1979) or actively selected for this prey (Buskirk and MacDonald 1984; Douglas et al. 1983; Martin 1987; Thompson and Colgan 1990). Foraging theory predicts that animals will select food items that result in energy returns equal to or higher than the energy expended on locating, capturing, and consuming that food (Pyke et al. 1977), and that generalist predators will switch to alternative prey when preferred foods are not readily available (Taylor 1984). During years of low abundance of small rodents, encounter rates of martens with these prey would likely be reduced. Under such circumstances, other food items should be of increased dietary importance. Dietary specialization, through resource selection, can lead to increased vulnerability of martens and possibly to a numerical response of these predators when the availability of their principal food declines (King and Moors 1979). During our study of the ecology of martens on Chichagof Island, southeast Alaska, from 1991 to 1994, rodent populations (*Peromyscus keenii*, and *Microtus longicaudas*) fluctuated widely. We investigated seasonal and annual changes in diets of martens in response to the changing abundance of small rodents.

From late summer through autumn, spawning Pacific salmon (*Oncorhynchus* sp.) carry marine-derived nutrients into streams and rivers along the Pacific Northwest, and subsequently fertilize those systems through their decomposition and consumption (Cederholm et al. 1989; Kline et al. 1989, 1993; Piorkowski 1995; Richey et al. 1975). Salmon carcasses are easy for martens to obtain during spawning runs because other predators such as brown bears (*Ursus arctos*), bald eagles (*Haliaeetus leucocephalus*), and river-otters (*Lutra canadensis*) often leave carcasses partially eaten (Cederholm et al. 1989). We hypothesized that martens would feed principally on small rodents during years with high abundance of these prey species, whereas during years of low abundance martens would include more salmon carcasses in their diet, as these salmonids became seasonally available.

Cederholm et al. (1989) reported that <4% of all salmon carcasses were washed down stream, and most were retained in the riparian zone. Because salmon carcasses usually occur in the vicinity of streams (Cederholm et al. 1989), and martens typically exhibit intrasexual territoriality (Powell 1994), only resident martens with home ranges adjacent to salmon streams would have this resource available. Individuals without access to salmon streams would not benefit from such a resource. Therefore, we hypothesized that location of the home range on the landscape (i.e., access to salmon streams) would determine the diet of martens.

Small mustelids, including the American marten, store little body fat compared with other mammals (Harlow 1994), and show little seasonal variation in accumulation of body fat (Buskirk and Harlow 1989). Martens appear to compensate for their deficiency in accumulating fat by using several physiological (e.g., metabolism of muscle tissue) and behavioral adaptations, one of which is optimizing food intake by diet

selection (Harlow 1994). We investigated body condition of martens with different diets, and hypothesized that martens feeding on rodents would exhibit better body condition than those feeding on other foods.

We used stable isotope ratios to indicate marten diets. In nature carbon and nitrogen each occur as two stable isotopes: ^{12}C and ^{13}C ; ^{14}N and ^{15}N . Ratios of the two isotopes as compared with standards are noted as $\delta^{13}\text{C}$ for carbon and $\delta^{15}\text{N}$ for nitrogen, and are measured in parts per thousand (‰, relative to a standard; Ehleringer and Rundel 1988). The analysis of food webs using natural abundance of stable isotope ratios compares the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of tissues from predator and prey. Values of $\delta^{13}\text{C}$ differ between terrestrial and marine food sources due to differential assimilation of ^{13}C by primary producers in these ecosystems, and enable tracing food webs (Fry and Sherr 1988; Tieszen and Boutton 1988). Values of $\delta^{15}\text{N}$ increase with transfer between trophic levels and therefore reflect both diet and trophic levels (DeNiro and Epstein 1981). The specific combination of values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ result from the dietary interaction of species or individuals (Ambrose and DeNiro 1986; Gearing 1991; Hobson 1991; Schell et al. 1988; Schoninger and DeNiro 1984). Applying this technique to tissues such as blood allows repeated sampling of known individuals throughout the year (Hobson 1991; Hobson and Clark 1993). Using this technique on repeated samples from the same individuals enabled us to investigate, for the first time, some of the factors underlying feeding habits of individuals in different seasons and years, and gain better understanding of the process of diet selection in martens.

Methods

Study area

Our study area was located on Chichagof Island in southeast Alaska, United States, (Tenakee Springs at 57°52'N, 135° 18'W; Fig. 1). The island, one of the three large northern islands of the Alexander Archipelago, is part of the Tongass National Forest. The archipelago has a maritime climate; summers are cool and wet and winters are characterized by deep snow (2360 mm annual precipitation). The snow-free period extends from early May to early November at lower elevations. Vegetation at higher elevations is typically alpine tundra, and in lower elevations coastal, old-growth forest of Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) with well-developed understory (mainly *Oplopanax horridus*, *Vaccinium* sp., *Menziesia ferruginea*, and *Rubus* sp.). Our study area encompasses six streams that support an annual run of spawning Pacific salmon (*Oncorhynchus gorbuscha*, *O. keta*, and *O. kisutch*), from late summer to late autumn. Potential prey among the mammalian fauna of the island include: Keen's deer mice (*Peromyscus keenii*), long-tailed voles (*Microtus longicaudas*), red squirrels (*Tamiasciurus hudsonicus*), common shrews (*Sorex cinereus*), and Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). The resident avian fauna includes Steller's jay (*Cyanocitta stelleri*), spruce grouse (*Dendragapus canadensis*), and winter wren (*Troglodytes troglodytes*). Other song birds such as dark-eye junco (*Junco hyemalis*), robin (*Turdus migratorius*), varied thrush (*Ixoreus naevius*), hermit thrush (*Catharus guttatus*), and Swainson's thrush (*Catharus ustulatus*), arrive on the island for the breeding season in early May and depart during September.

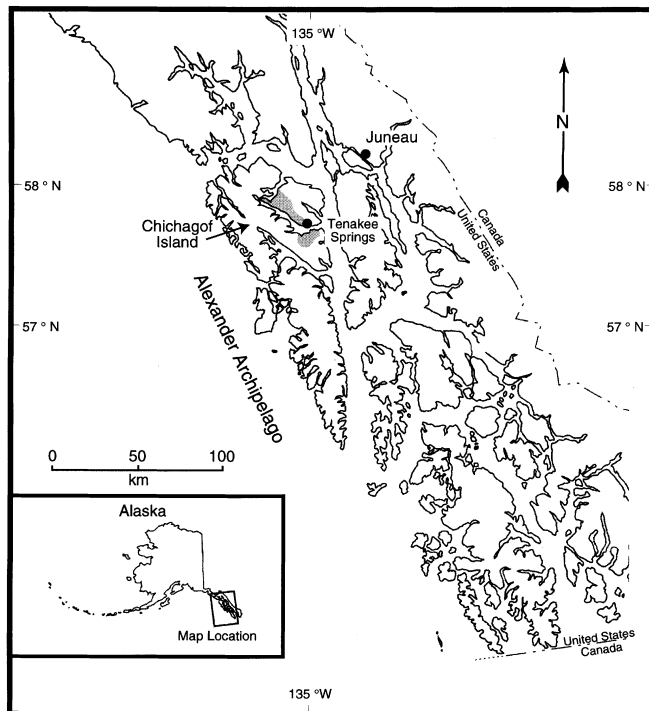


Fig. 1 Location of study area (shaded) on Chichagof Island, Southeast Alaska, USA

Sampling martens

We live-captured 75 martens repeatedly, from mid-February to mid-December in 1992–1994, using Tomahawk live traps (models 203 and 205; Tomahawk Live Trap Co., Tomahawk, Wis., USA). After immobilization with an injection of ketamine hydrochloride (15 mg/kg body weight; Aveco, Fort Dodge, Iowa) and Xylazine Hydrochloride (2 mg/kg body weight; Vedco, St. Joseph, Mich.), each individual was measured, weighed, and marked with ear tags (size 1, style 1005; National Band and Tag Co., Newport, Ky.) or a passive integrated transponder (PIT) tag (Biosonics, Seattle, Wash.). A vestigial first premolar was extracted from all newly captured martens for age determination using counts of cementum annuli (Poole et al. 1994; Matson's Laboratory, Milltown, Mont.). A blood sample of 2 ml was drawn from the jugular vein, and stored in a glass or plastic vial. Most new captures were fitted with radiocollars (Telonix, Mesa, Ariz.), and radiocollars were replaced on recaptured martens as needed. A 30-g radio collar (MOD-070 expected life of 8 months) was placed on females, and a 49-g collar (MOD-080, expected life 18 months) was placed on males. Upon recovery from sedation, we released animals at their sites of capture. Blood was centrifuged for 5 min., using a manual centrifuge, within 2 h after collection, and serum was siphoned into a separate vial. Both serum and samples of clotted blood-cells were then frozen until analysis. In later analyses, samples were pooled by season, to reflect ecological changes. For instance, summer samples were those collected from late-May to the end of August, covering the time of vegetation green-up and breeding of song birds. Autumn samples were those collected from September to late December, representing the period of the main abundance of salmon carcasses. Winter-spring samples were those collected from mid-February to early May, representing the period of snow cover.

We obtained 610 carcasses of martens from trappers on Chichagof Island during the December 1991 to January 1992 and December 1992 trapping seasons. For each marten carcass, data on site and date of capture were recorded. We determined sex, measured body length, and weight for each carcass before removal of viscera, uterus, ovaries, and premolar teeth. Carcasses of 165

martens were selected randomly for this analysis. From each of these individuals, a muscle sample of 5–10 g was excised from the hind leg for stable isotope analysis. Carcasses were subsequently aged using cementum annuli of premolar teeth (Matson's Laboratory, Milltown, Mont.).

Position of home range on the landscape

We located radiocollared martens from a small aircraft (Mech 1974; Kenward 1987) during daylight hours every 2 weeks throughout the year. The location of each marten was plotted on high-resolution, orthophoto maps (scale 1:31,680) while circling in the aircraft above the location. Error was determined by retrieving dead individuals and was estimated at 50–110 m. Aerial locations were plotted on digital versions of the orthophoto maps using geographic information system (GIS) on a personal computer to determine x, y coordinates. We estimated annual home ranges of resident martens from the radio-telemetry locations using the computer program HOME RANGE (Ackerman et al. 1990). Locations were tested for independence (Swihart and Slade 1985), and outliers were examined (Samuel et al. 1985). Locations were not significantly autocorrelated ($P > 0.05$), and therefore no locations were excluded. We used 95% minimum convex polygons (MCP) to describe home range area for each marten (Ackerman et al. 1990). This method excludes irregular excursions from the delineation of the home range area. Animals that moved over an area > 2 home ranges within any season sampled, and covered areas that were occupied by resident martens, were considered transients. Digital GIS maps of the study area were obtained from the USDA Forest Service, Tongass National Forest. These maps demarcated stream segments used by anadromous fish and beach fringe habitats. Landscape position of home range for each marten was determined by over-laying the home range plot on the GIS maps. A home range that included a segment of an anadromous fish stream or beach fringe habitat was considered to have marine resources available.

Abundance of small rodents

We monitored annual trends in abundance of Keen's deer mice, and long tailed voles by trapping along three permanent transects during autumn (September–October) of each year from 1991 to 1994. Each transect consisted of 25 stations at 15-m intervals. Two snap traps (museum specials) were placed at each station, baited with rolled oats and peanut butter, and set for 3 consecutive nights. Seasonal changes in abundance of small mammals were monitored at 7–13 trapping grids during summer (mid-May to mid-August), autumn (October to November), and spring (March to early May) from summer 1992 to autumn 1993. Each grid contained 25 Sherman live traps set in a 20×20 m arrangement, baited with rolled oats and peanut butter, and set for 3 consecutive nights. Keen's deer mice and long-tailed voles, were marked with paint on their nape and released; a sub-sample of two individuals per species per trap site was selected randomly, and euthanized with Halothane (Halocarbon, River Edge, N.J.). A muscle sample was collected from each euthanized individual for stable isotope analysis. We expressed abundance of small rodents as number caught per 100 trap nights during the three nights of sampling. Recaptures were not included in the count. All methods used in this study were approved by an independent Animal Care and Use Committee at the University of Alaska, Fairbanks.

Sampling prey

Prey samples for each season were collected after examination of marten feces collected in the same study area, as well as gastrointestinal analysis of marten carcasses (M. Ben-David, unpublished work). Muscle samples from Keen's deer mice, long tailed voles, and red squirrels were collected from small rodents trapped on the

grids, and from a companion study by T.A. Hanley (USFS, Pacific Northwest Research Station), for stable isotope analysis. The remainder of each carcass was prepared as a museum specimen (including frozen tissues) and archived at the University of Alaska Museum. Tissue samples were obtained from salmon carcasses, and deer carcasses when encountered or obtained from hunters. Adult and fledged song birds (winter wrens, dark-eye juncos, robins, and thrushes) were collected when encountered (permit ADFG 90-16). Berry samples were collected from 11 vegetation transects (500 m long) from the riparian to the upland habitats and at 100-m intervals. Additional samples of berries were collected at higher elevations and at beach fringe habitats. The berry samples included: blueberries (*Vaccinium* sp.), salmon berries (*Rubus spectabilis*), cloud berries (*R. chamaemorus*), stink current (*Ribes bracteosum*), Pacific crab apple (*Malus fusca*) and devil club (*Oplopanax horridus*).

Stable isotope ratio analysis

Tissues (clotted blood-cells, muscle samples, and vegetation samples) were kept frozen until preparation for determination of stable isotope ratios. Samples were dried at 60–70°C for 48 h and then ground to fine powder using a Wig-L-Bug grinder (Crescent Dental Co.). Samples of intertidal crabs were then dissolved in 95% hydrochloric acid solution to remove calcium carbonates and re-dried. Subsequently, a sub-sample (1–1.5 mg for animal tissues and 8–10 mg for plant tissues) was weighed into a miniature tin cup (4 × 6 mm) for combustion. We used a Europa C/N continuous flow isotope ratio mass spectrometer (CFIRMS) to obtain the stable isotope ratios. Each sample was analyzed in duplicate and results were accepted only if the variance between the duplicates did not exceed that of the peptone standard ($\delta^{13}\text{C}_{\text{std}} = -15.8$, $\delta^{15}\text{N}_{\text{std}} = 7.0$, CV = 0.1).

We determined the diet source for each marten based on the combined values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. We developed a dual-isotope, multiple-source mixing model, based on the conceptual one proposed by Kline et al. (1993), to estimate the contribution of each prey item to the diet of the predator. This model uses the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value of each type of prey. This mean value (*A*, *B*, *C*, etc.) is then corrected for the enrichment in predator ratios compared with its diet (i.e., fractionation values; *A'*, *B'*, *C'*, etc.; DeNiro and Epstein 1981; Kline et al. 1993; Tieszen and Boutton 1988; Fig. 2). Euclidean distance between the corrected isotopic values of prey and each individual predator (i.e. the length of the line connecting *A'* and *P*, *B'* and *P*, and so on; Fig. 2) is then calculated by $z = \sqrt{x^2 + y^2}$. The contribution of each prey to the diet of the predator is inversely related to the distance between the corrected signature of the prey and the predator (i.e., the shorter the distance the greater the contribution). Because of this inverse relationship, the relative contribution of each prey is calculated by:

$$\% X \text{ in diet} = (PX'^{-1}/PA'^{-1} + PB'^{-1} + PC'^{-1}) \times 100,$$

where *X'* is *A'*, *B'* or *C'*.

The mixing model requires that isotopic values of all prey be significantly different from each other. This model assumes that each individual predator consumes all possible types of prey. Therefore this model will tend to overestimate the proportion of food items that are rarely consumed and underestimate the proportion of commonly used prey. Consequently, we used the model as an index of prey consumption rather than as actual proportions in the diet.

We used fractionation values of 2‰ for carbon when mammalian prey, avian prey, and berries were consumed, and 1‰ when salmon or invertebrates were consumed, based on results from feeding experiments in captivity on mink and black bears (*Ursus americanus*; Ben-David 1996; Hilderbrand et al., 1996). In these experiments fruit, mammalian food, and fish were offered in different mixtures to these two species. Differences in isotopic ratios between diet and blood were recorded, providing empirical data on assimilation of these food types in these carnivores (Ben-David

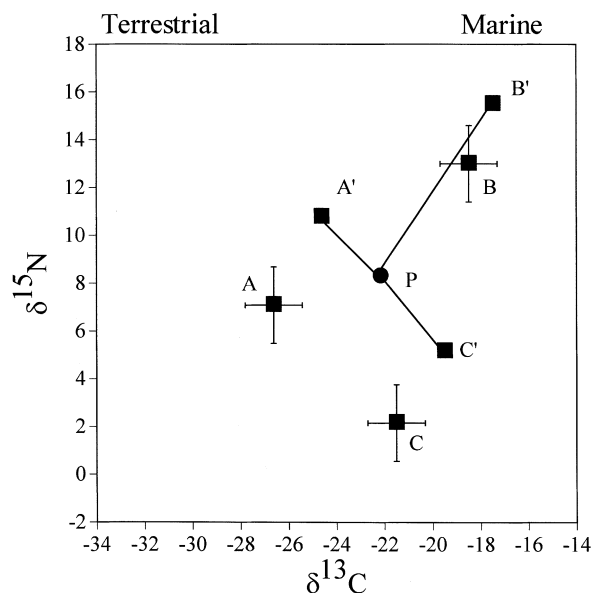


Fig. 2 Dual isotope, three-source mixing model with variable fractionation values. This model uses the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value of each prey type in a bivariate space. This mean value (*A*, *B*, *C*, and so on) is then corrected for the enrichment in predator ratios compared with its diet (i.e., fractionation values; *A'*, *B'*, *C'*, and so on). Euclidean distance between the corrected isotopic values of prey and that of each individual predator (i.e., the length of the line connecting *A'* and *P*, *B'* and *P*, and so on), is then calculated by $z = \sqrt{x^2 + y^2}$. The relative contribution of each prey to the predator's diet is inversely related to the distance between the corrected signature of the prey and that of the predator (i.e., the shorter the distance the greater the contribution)

1996; Hilderbrand et al., 1996). Also, based on the captive experiments we used fractionation values of 3‰ for nitrogen when mammalian prey, avian prey, crabs, and berries were consumed and 2‰ when salmon was consumed (Ben-David 1996). Because stable isotope values of clotted blood-cells did not differ significantly from those of muscles in experiments on captive mink (Ben-David 1996), we pooled data obtained from live animals and those of carcasses in some of our analyses.

Statistical analysis

We employed K nearest-neighbor randomization test (Ben-David 1996; Rosing et al., in press; Schilling 1986) to investigate whether stable isotope ratios of all prey types were significantly different from each other by season. In this test, the values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are treated as spatial data because the unit of measurement in both variables is equal and stable. This test uses the Bonferroni correction when all food items are compared with each other (Ben-David 1996; Rosing et al., in press). After calculating the relative contribution of each food item to the diet of each individual marten using the multiple-source mixing-model, we calculated the mean (\pm SE) for the entire sample in each season. We then explored the changes in percentages of each food item between seasons and years using Kruskal-Wallis test with multiple comparisons (Zar 1984; BMDP; Dixon 1990).

We compared abundance of small rodents between seasons and years using Pearson's χ^2 test (BMDP; Dixon 1990). Changes in stable isotope ratios of marten tissues (from live captured animals and carcasses) were investigated with one-way ANOVA with multiple comparisons (SAS 1985). To test our hypothesis that diet of martens changed in relation to abundance of small rodents, we compared the results of the stable isotope analysis with abundance

Table 1 Description of variables collected from live martens ($n = 75$) that were captured repeatedly between June 1992 and October 1994, on Chichagof Island, Southeast Alaska (total samples $n = 155$)

Variable	Definition and methods
Dependent variable	
Diet	Marine source ($> 35\%$ of diet as determined from the mixing model) coded 1, terrestrial source ($> 35\%$ of diet as determined from the mixing model) coded 0
Independent variables	
Sex	Categorical variable coded 1 for males and 2 for females
Age	Continuous variable as determined from cementum annuli
Year	Categorical variable coded 1992, 1993 and 1994 representing low, moderate, and high small rodent abundance respectively
Season	Categorical variable coded 1 for summer, 2 for autumn, and 3 for spring
Home range location	Categorical variable coded 1 for home ranges located within 150 m from salmon stream or beach fringe habitat, 2 for home ranges located further than 150 m from salmon stream or beach fringe habitat, and 3 for transient animals

of small rodents using correlation analysis (Zar 1984). To test whether the proportion of small rodents in marten diets differed in relation to their seasonal abundance we used a χ^2 goodness-of-fit test (Buskirk et al. 1996), and selection ratio (w_i) with Bonferroni confidence intervals (Manly et al. 1993). In this analysis we used the proportions of small rodents in the diet obtained from the mixing model divided by the proportion of rodents captured in 100 trap nights. Our analysis assumes that our trapping success is similar to the potential predatory success of martens (i.e., abundance represents availability), and that the availability of the sum of all other possible prey items is unlimited (D.L. Thomas, personal communication).

To identify the factors affecting diets of martens (for live-captured martens only) as represented by stable isotope ratios, we introduced the following variables to a logistic-regression model (BMDP; Dixon 1990): sex, age, year (as representative of abundance of small rodents), season (as representative of the seasonal availability of salmon, birds and berries), and home range location on the landscape (Table 1). For the step wise logistic regression, marine diets were coded 1, and terrestrial diets were coded 0 (Hosmer and Lemeshow 1989). We controlled for multicollinearity at $r > |0.45|$, and ensured that these data did not depart from a logistic-regression model with Hosmer-Lemeshow goodness-of-fit test (Hosmer and Lemeshow 1989).

To test our hypothesis that body weight will be related to prey choice and season, we used a two-way ANOVA on ranks with multiple comparisons (Conover and Iman 1988; SAS 1985) on data collected from live-captured male and female martens.

Results

The K nearest-neighbor randomization test revealed that in each season (Figs. 3–6) the stable isotope ratios of prey were significantly different from each other, except for deer mice and voles in summer and autumn ($P > 0.2$). Therefore, we were unable to measure the contribution of voles in the diet independently of deer mice using the stable isotope analysis, in summer and autumn, and pooled them as one diet group, which we termed small rodents. In spring, isotopic ratios of voles significantly differed from those of deer-mice (K nearest-neighbor randomization test, $P < 0.001$). In this season, we calculated the relative contribution of voles and deer-mice and then summed the results for each marten to produce the relative contribution of small rodents. Similarly, there was no significant difference in the

isotopic ratios of the different species of berries ($P = 0.1643$), and we treated all species of berries as one category. Isotopic signatures of squirrels were enriched in ^{13}C (Figs. 3–6) because of enrichment in ratios of spruce seeds ($\delta^{13}\text{C} = -25.56 \pm 0.15$, $\delta^{15}\text{N} = -1.7 \pm 0.5$, $n = 38$; Ben-David 1996), rather than from consumption of marine-derived nutrients.

Diets of martens in autumn showed high variability in composition (Figs. 3 and Fig. 4). Some individuals relied heavily on salmon carcasses ($> 35\%$ of diet; Table 2), others fed mainly on small rodents ($> 35\%$ of diet; Table 2). The rest of the martens ate differing combinations of all types of food (Table 3). Berries composed $14\% \pm 0.3$ (mean \pm SE) to $31\% \pm 2.2$ of the diet, and squirrels between $15\% \pm 0.4$ and $22\% \pm 0.8$ (Table 3). The average percentages of berries in the diets of martens increased significantly between autumn 1992 and autumn

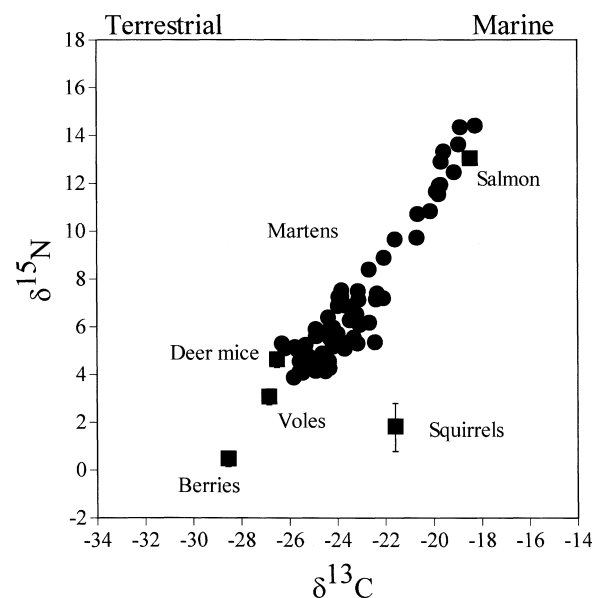


Fig. 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for live martens captured in the autumns of 1992, 1993, and 1994, on Chichagof Island, Southeast Alaska ($n = 75$). Mean values \pm SE are given for berries ($n = 8$), squirrels ($n = 8$), deer mice ($n = 26$), voles ($n = 23$), and salmon ($n = 18$)

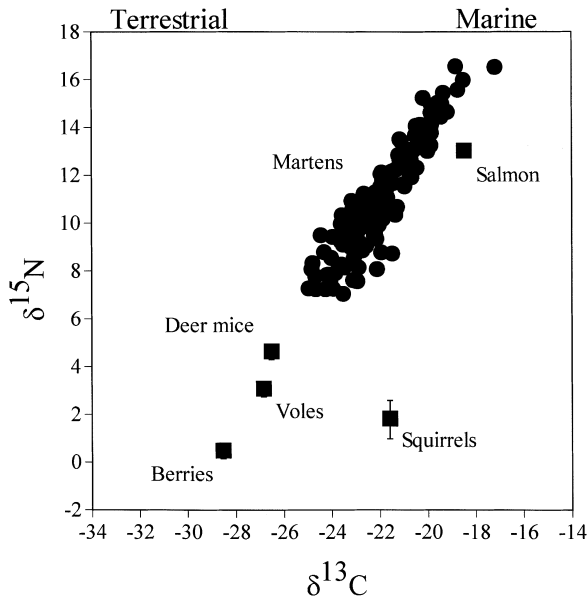


Fig. 4 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for marten carcasses collected in autumn and early winter of 1991, and autumn 1992, on Chichagof Island, Southeast Alaska ($n = 165$). Mean values \pm SE are given for berries ($n = 8$), squirrels ($n = 8$), deer mice ($n = 26$), voles ($n = 23$), and salmon ($n = 18$)

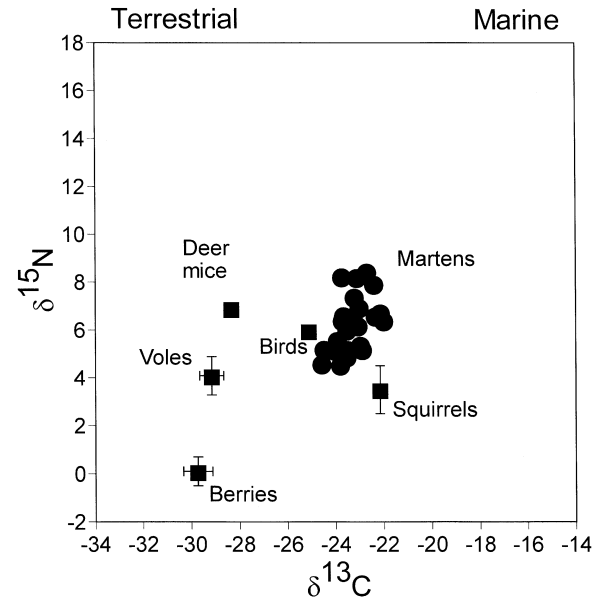


Fig. 6 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for live martens captured in summer 1992, 1993, and 1994, on Chichagof Island, Southeast Alaska ($n = 25$). Mean values \pm SE are given for berries ($n = 57$), squirrels ($n = 10$), deer mice ($n = 55$), birds ($n = 24$), and voles ($n = 5$)

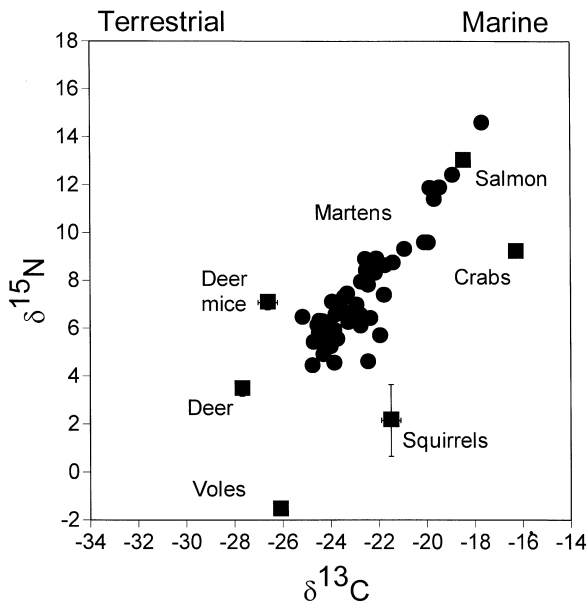


Fig. 5 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for live martens captured in spring 1993, and 1994, on Chichagof Island, Southeast Alaska ($n = 40$). Mean values \pm SE are given for deer ($n = 14$), squirrels ($n = 5$), deer mice ($n = 18$), voles ($n = 9$), salmon ($n = 18$), and crabs ($n = 20$)

1993, and between autumn 1993 and autumn 1994 (Table 3; Kruskal-Wallis, $P < 0.001$), as did small rodents (Table 3; Kruskal-Wallis, $P < 0.001$). At the same time, the average percent of salmon decreased significantly (Table 3; Kruskal-Wallis, $P < 0.001$). Percentages of squirrel in the diet significantly decreased only between autumn 1993 and autumn 1994 (Table 3; Kruskal-Wallis, $P = 0.005$).

Table 2 Proportions of martens that include $> 35\%$ of salmon in their diet, and $> 35\%$ of small rodents in their diet. Samples collected on Chichagof Island, Southeast Alaska from 1991 to 1994. Percentages of prey in the diet are calculated by the multiple-source mixing model

Year	<i>n</i>	Proportion of martens
Small rodents		
1991	39	0.41
1992	133	0.46
1993	40	0.65
1994	28	0.93
Salmon		
1991	39	0.28
1992	133	0.39
1993	40	0.10
1994	28	0.00

In spring (Fig. 5), 91% of 56 martens ate a combination of small rodents, winter-killed deer carcasses, and squirrels. Some martens (9%, $n = 56$), however, had a stable isotope signature characteristic of a marine-derived diet (Fig. 5). The average percent of deer carcass and small rodents in the diet increased in spring 1994 (Table 3; Kruskal-Wallis, $P < 0.05$), corresponding to a significant decrease in the percentage of salmon (Table 3; Kruskal-Wallis, $P = 0.029$). Percent of crabs in the diet was low and did not differ between years (Table 3; Kruskal-Wallis, $P = 0.567$).

Martens ($n = 25$) fed on varying combinations of small rodents, berries, squirrels, and birds in summer (Fig. 6). The average percentage of berries increased significantly in summer 1994 compared with the previous two summers (Table 3; Kruskal-Wallis, $P = 0.015$). Similarly, a significant increase occurred in

Table 3 Relative contribution (mean \pm SE) of prey item to the diet of martens (n), captured on Chichagof Island, Southeast Alaska, during 1992–1994. Percentages were calculated using the multi-source mixing model. Letters represent significant difference in percent between seasons at $\alpha = 0.05$ (Kruskal-Wallis test with multiple comparisons)

	Percent in diet of martens					
	Summer 92		Summer 93		Summer 94	
	$n = 8$		$n = 7$		$n = 9$	
	%	SE	%	SE	%	SE
Berries	13 ^a	2.1	15 ^a	2.1	22 ^b	2.0
Small rodents	18 ^a	1.4	17 ^a	0.8	21 ^b	0.4
Birds	47 ^a	5.5	33 ^b	3.4	30 ^b	1.8
Squirrels	22 ^a	2.4	35 ^b	2.5	27 ^c	0.8

	Autumn 91		Autumn 92		Autumn 93		Autumn 94	
	$n = 39$		$n = 133$		$n = 40$		$n = 28$	
	%	SE	%	SE	%	SE	%	SE
Berries	15 ^a	0.5	14 ^a	0.3	20 ^b	1.2	31 ^c	2.2
Small rodents	37 ^a	2.9	34 ^a	1.4	40 ^b	2.2	45 ^b	2.6
Salmon	29 ^a	2.5	33 ^a	1.7	13 ^b	1.7	7 ^c	0.2
Squirrels	20 ^a	0.8	19 ^a	0.4	22 ^a	0.8	15 ^b	0.4

	Spring 93		Spring 94	
	$n = 21$		$n = 35$	
	%	SE	%	SE
Deer carcasses	26 ^a	2.7	32 ^b	1.9
Small rodents	33 ^a	1.6	37 ^b	0.9
Salmon	14 ^a	3.5	8 ^b	0.7
Squirrels	17 ^a	1.2	16 ^a	0.7
Crabs	8 ^a	0.6	9 ^a	0.6

the percentage of small rodents in summer 1994 (Table 3; Kruskal-Wallis, $P = 0.027$). Although the percentage of birds decreased between summer 1992 and 1993 (Table 3; Kruskal-Wallis, $P = 0.011$), no change occurred between summer 1993 and 1994 (Table 3). Squirrels, however, increased in the diet between summer 1992 and summer 1993, but decreased in 1994 (Table 3; Kruskal-Wallis, $P < 0.001$).

Numbers of small rodents in our study area differed significantly between years (χ^2 test, $df = 3$, $P < 0.001$). In 1991, rodent numbers were in decline, especially long-tailed voles (Fig. 7), and reached a minimum in 1992. In 1993, rodent numbers recovered to a moderate level and in 1994 rodents were abundant (Fig. 7). Our analysis showed that stable isotope ratios of marten tissues (live-captured and trapper caught) differed significantly between years (ANOVA; $P < 0.001$) (Fig. 7). The proportion of squirrels in autumn diets did not significantly differ between 1991, 1992, and 1993 and decreased significantly in 1994 (Table 2), suggesting that the enrichment in $\delta^{13}\text{C}$ values in martens tissues resulted from incorporation of salmon carcasses in the diet. The high correlation ($r = -0.988$) between the isotope ratios of carbon for marten tissues and abundance of small rodents suggests that during years of low abundance of small rodent (1991 and 1992) martens switched to feed mainly on salmon carcasses (Fig. 7). Nonetheless, when

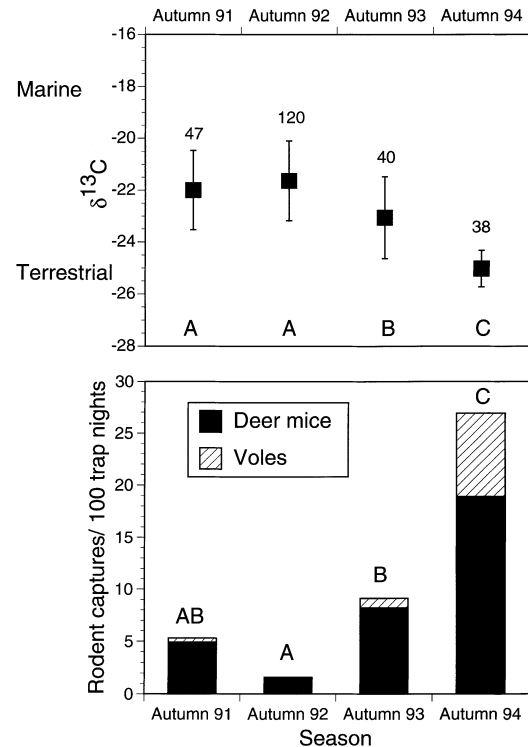


Fig. 7 Mean \pm SE values of $\delta^{13}\text{C}$ for marten carcasses and live martens captured in autumn 1991–1994, on Chichagof Island, southeast Alaska (top), and number of small rodent captures/100 trap nights during the same period (bottom). Letters represent statistical difference at $\alpha = 0.05$ (χ^2 test for abundance of small rodents; one-way ANOVA with multiple comparisons for stable isotope ratios). Sample sizes are given above SE

small rodents were available in high numbers (1993 and 1994) martens reduced their consumption of salmon carcasses, although these foods were as available to them as in previous years.

Seasonal changes in food availability resulted from several ecological phenomena. Breeding song birds arrived on our study area in early summer and departed in early autumn of each year. In addition, most species of berries produced fruits during summer (July–August). Only blueberries, berries of stink current and crab apples were available to martens in autumn (early October). Salmon carcasses became available to martens in late summer (August), and the spawning run extended into late November of each year. Winter-killed deer became available to martens in January, while carcasses from hunter kills were available as early as October. Numbers of small rodents changed significantly between seasons (χ^2 test, $df = 4$, $P < 0.001$) in 1992 and 1993. This difference was a result of change in numbers between summer and autumn (Fig. 8), but no significant difference occurred between autumn and spring or spring and summer (Fig. 8). This suggests that the rodent population in our study area experienced an increase in numbers because of reproduction during summer, and little winter mortality in these years. Using the multi-source mixing model, we determined the percentage of small rodents in the diets of live-captured martens, in summer

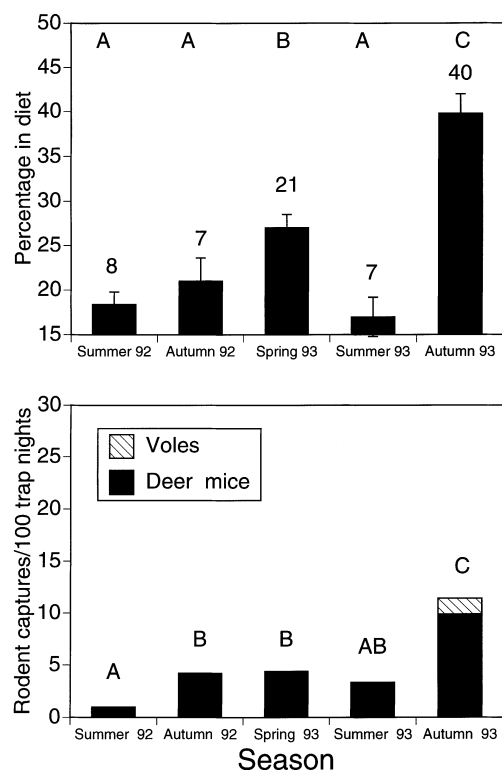


Fig. 8 Proportion of small rodents in the diet of live martens captured in summer 1992 to autumn 1993, on Chichagof Island, Southeast Alaska (*top*), and number of small rodent captures/100 trap nights during the same period (*bottom*). Letters represent statistical difference at $\alpha = 0.05$ (χ^2 test for abundance of small rodents; Kruskal-Wallis with multiple comparisons for percentages in diet). Sample sizes are given above SE

1992 to autumn 1993. These proportions differed significantly (Kruskal-Wallis, $P < 0.0001$). Multiple comparisons revealed that a significant increase occurred between autumn 1992 and spring 1993, followed by a significant decrease in summer 1993 (Fig. 8). In autumn 1993, the mean percentage of small rodents in the diet significantly increased compared with spring or summer 1993 (Fig. 8).

Comparing these percentages with the seasonal abundance of small rodents revealed that while the percentage of rodents increased in the diet of martens between summer 1992 and autumn 1993, following the trend of increase in the small rodent population, selection, represented by selection ratios of $w_i > 1$ (χ^2 goodness-of-fit test, $df = 4$, $P < 0.05$; Manly et al. 1993), occurred only during summer 1992, autumn 1992, and spring 1993 (Table 4). In summer 1993 and autumn 1993, martens fed on small rodents in relation to their availability. Similarly, comparing selection ratios for all martens (live-trapped as well as carcasses), in autumn revealed that selection for small rodents occurred only when abundance was low (Table 5).

To identify the factors affecting diets of martens (for live-captured martens only) as represented by the stable isotope ratios, we introduced the following variables to a logistic regression model (BMDP; Dixon 1990): sex, age,

Table 4 Selection ratios of small rodents (w_i), Bonferroni confidence intervals and direction of selection (Manly et al. 1993), for martens live-trapped on Chichagof Island, Southeast Alaska, from summer 1992 through autumn 1993

Season	Selection Ratio	CI	Direction
Summer 1992	9	2.90–15.10	+
Autumn 1992	4	1.23–6.77	+
Spring 1993	6.6	2.27–10.93	+
Summer 1993	4.25	0.95–8.53	0
Autumn 1993	3.01	0.75–5.27	0

Table 5 Selection ratios of small rodents (w_i), Bonferroni confidence intervals and direction of selection (Manly et al. 1993), for all martens trapped on Chichagof Island, Southeast Alaska, in autumn 1991, autumn 1992, autumn 1993, and autumn 1994

Season	Selection Ratio	CI	Direction
Autumn 1991	7.4	3.17–11.83	+
Autumn 1992	11.3	5.94–16.66	+
Autumn 1993	3.01	0.75–5.27	0
Autumn 1994	1.67	–0.21–3.55	0

Table 6 Logistic regression model $P(y = j) = (e^{\beta_0} + e^{\beta_1 \times 1} + e^{\beta_2 \times 2} \dots) / (1 + e^{\beta_0} + e^{\beta_1 \times 1} + e^{\beta_2 \times 2} \dots)$ where j is 0 or 1: coefficients, SE, and odds ratio for factors affecting diet selection (marine coded 1, terrestrial coded 0) in martens repeatedly captured between June 1992 and October 1994 on Chichagof Island, Southeast Alaska

Variable		Coefficient	SE	Odds ratio
Season	(1)	–9.34	0.05	–18.3
	(2)	–10.31	0.46	–22.4
Year	(1)	7.98	1.17	6.85
	(2)	9.49	1.16	8.17
Home range	(1)	2.7	1.11	2.43
	(2)	0.59	0.48	1.24
Constant	(1)	1.94	1.07	1.82

year (as representative of abundance of small rodents), season, and home range location on the landscape (Table 1). The logistic-regression model identified year, season, and home range location as the variables best separating marine from terrestrial diets ($P < 0.001$; Table 6). The model correctly classified 77% of all individuals to their respective dietary group (69% marine and 79% terrestrial). This result suggested that home range location (i.e., access to salmon streams) determined whether martens included salmon in their diet during years in which abundance of small rodents was low and in seasons when this resource was available (Fig. 9). During years and seasons in which abundance of small mammals was high, home range location was not an important factor in determining diets of martens in our study area (Fig. 9). Age and sex did not enter the model as they did not improve the fit of the model, suggesting that these variables did not significantly contribute to the differences in diets of martens.

In investigating differences in body weights of martens (Fig. 10), we noted a significant effect of season but

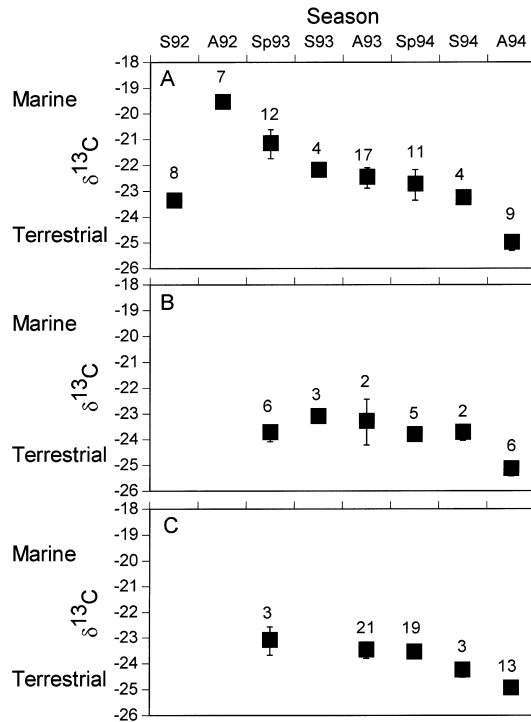


Fig. 9 Mean \pm SE values of $\delta^{13}\text{C}$ for live martens captured from summer 1992 to autumn 1994, on Chichagof Island, Southeast Alaska, in home ranges with access to salmon streams (A), without access to salmon streams (B) and transient animals (C). Sample sizes are given above SE

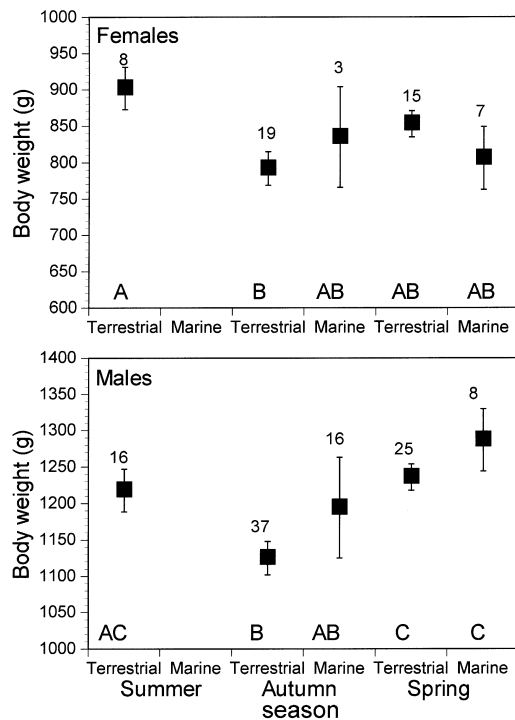


Fig. 10 Mean \pm SE of body weight (g) for female (top) and male (bottom) martens, on Chichagof Island, Southeast Alaska, by diet group (terrestrial vs. marine) in summer, autumn and spring 1992 to 1994. Sample sizes are given above SE

no significant effect of diet for males (ANOVA on ranks, overall $P = 0.0003$; season effect $P = 0.0002$, diet effect $P = 0.1755$). Multiple comparisons revealed that body weights of males were significantly lower in autumn compared with those in spring ($P < 0.05$). Female martens showed a marginal difference in body weights (ANOVA on ranks, overall $P = 0.0842$), and only the season effect was significant ($P = 0.0435$, diet effect $P = 0.5563$). Multiple comparisons revealed that body weights of females were significantly lower in autumn compared with those in summer ($P < 0.05$).

Discussion

When analyzing diet composition from isotopic ratios of consumer and food tissues, it is important to note that isotopic ratios are in part determined by metabolic pathways (Kreuger and Sullivan 1984; Schwarcz 1991; Ambrose and Norr 1993; Tieszen and Fagre 1993). In general, when a consumer assimilates structural lipids and proteins from one source but derives most of its energy from another source (such as carbohydrates), the later will be underestimated when the consumer tissues are analyzed (Schwarcz 1991; Tieszen and Fagre 1993). Therefore, diet quality and composition are likely to affect the results from our mixing model. We have, however, used fractionation values obtained from captive experiments on mink and black bears (Ben-David 1996; Hilderbrand et al., 1996) which should reduce the bias in our mixing model. In addition, because we have introduced to the mixing model only those foods that were identified in marten feces and gastrointestinal tracts (M. Ben-David unpublished work) we have reduced the problems of overestimating the proportion of food items that are rarely consumed.

Our results suggest that martens in our study area principally fed on small rodents in autumn when those were available in high numbers (1993 and 1994), despite salmon carcasses being as available to them as in other years (1991 and 1992). In addition, some individual martens fed principally on small rodents even in years of low abundance of this prey (Table 2). While salmon carcasses did not differ from small rodents in their amino acid composition (M. Ben-David, unpublished work) there could have been a difference in quantity and composition of lipids. In many fish species, lipids are in the form of wax esters (Nevenzel 1970), which may be harder for martens to assimilate. In addition, consumption of large quantities of salmon may create a deficiency in vitamin E (Robbins 1993). Therefore, salmon carcasses may be of less nutritional value to martens than small rodents.

Several studies concluded that martens responded opportunistically to the abundance of voles (Campbell 1979; Soutiere 1979; Gordon 1986), whereas others have shown selection for this prey (Douglas et al. 1983; Buskirk and MacDonald 1984; Martin 1987; Thompson and Colgan 1990). This contradiction could stem from

the fact that many of these studies addressed diet as a secondary objective and differed in their evaluation of prey abundance and estimation of selection. On the other hand, it is possible that these studies observed martens at different levels of prey availability and therefore some observed selection, and others only an opportunistic response. Interpretation of the results from our analysis of selection ratios is limited because of the assumptions associated with the mixing model, the assumption that our rodent trapping represents availability, as well as our inability to measure the availability of all foods in each season. Nonetheless, our results suggest that martens increased the consumption of small rodents during years when those became more abundant. The proportion of small rodents in the diet was not disproportionate to the abundance in years of high small rodents numbers, but in years of low abundance, martens included more than expected of this prey in their diet. This conclusion is supported by data from feeding trials conducted on wild martens, caught in our study area, and held in captivity for two to three weeks (R.W. Flynn, unpublished work). In these feeding trials martens showed preference for voles when offered equal quantities of voles, deer mice, salmon, deer, and berries (R.W. Flynn, unpublished work).

In spring, carcasses of winter-killed deer seemed to be an important component in the diet of martens, composing 26–32% of the diet in that season. Nagorsen et al. (1989) reported deer remains in 20% of gastrointestinal tracts of martens obtained from trappers in winter on Vancouver Island, British Columbia, suggesting that this food was important for insular populations of martens in the Pacific Northwest. In spring, marine-derived foods were less available to martens in our study area because the salmon runs end in mid- to late November. Nonetheless, some carcasses of salmon may remain available as they thaw from the snow on stream banks or because they were cached by martens (Henry et al. 1990) or other predators such as mink (*Mustela vison*) (Ben-David et al., in press). Other possible marine-derived foods were intertidal organisms exposed at low tide; we observed remains of salmon as well as crab shells in marten feces collected in spring (M. Ben-David, unpublished work). Other studies have shown that island-inhabiting martens fed on intertidal organisms in winter (Nagorsen et al. 1989, 1991), as did other species of mustelids (Ben-David et al. 1996; Bowyer et al. 1994).

In summer, isotopic ratios suggest that squirrels and birds became important components in the diet of martens, even in summers with high numbers of small rodents (1993 and 1994). During that season nestlings and juvenile squirrels are encountered at a higher rate and are easier to capture than voles or deer mice (Zielinski et al. 1983). Therefore, martens likely responded to the increase in availability of these prey. In addition, the availability of berries in summer affects dietary composition of martens as they compose 13–22% of the diet. Berries are an important seasonal food in diets of martens throughout their range (Simon

1980; Hargis and McCullough 1984; Martin 1987; Nagorsen et al. 1989). That martens included other foods in their diet even in years of high abundance of small rodents suggest that these carnivores may need to augment their diet with other foods to fulfill other dietary requirements (Robbins 1993).

The logistic-regression model revealed that one important factor affecting diet composition in martens was the location of their home range on the landscape. Individuals with access to salmon streams were more likely to feed on salmon carcasses during years of low abundance in small rodent. This agrees with the prediction based on the optimal foraging theory (Pyke et al. 1977) that during years of low abundance of rodents, encounter rates of rodents will be reduced and other foods, such as salmon carcasses will be consumed to a larger extent. The logistic-regression model (year, season, and home range) correctly classified 77% of all individuals to their respective dietary group (terrestrial vs. marine – based on isotopic ratios). This suggests that although prey abundance (i.e., year and season), and home range location are important factors in determining diets of martens, additional factors such as differences in predatory specialization or imprinting can contribute to diet selection by martens.

We were unable to demonstrate that body weights of live-captured male and female martens differed significantly between individuals feeding on marine-derived or terrestrial diets. This finding contradicted our hypothesis that those martens feeding on rodents would exhibit better body condition than those feeding on other foods. Thus, switching to alternative prey seems to enable martens to maintain body condition in spite of a decline in preferred prey numbers. Nonetheless, we did record a significant change in body weights of male and female martens between seasons. Harlow (1994) demonstrated that martens partly compensate for their deficiency in accumulating body fat by metabolism of muscle tissue. Hobson et al. (1993) demonstrated that $\delta^{15}\text{N}$ enrichment occurs when animals are nutritionally stressed and therefore $\delta^{15}\text{N}$ alone might not closely reflect the diet. Whether the isotopic ratios observed in this study were influenced by muscle metabolism is unclear and merits further investigation. Also, an investigation of the factors that may affect the seasonal changes in body weights such as food availability, reproductive activity, dispersal, or changes in general levels of activity is required.

Our results suggest that martens, as true generalist predators, switch to alternative prey when preferred food is not readily available on a seasonal or annual basis. Such a short-term functional response could reduce the long-term numerical decline in predator populations, which usually follows shortages in availability of preferred foods (Taylor 1984). Thompson and Colgan (1987) recorded a numerical decline in a marten population in Northcentral Ontario following a decline in the local population of voles. Similarly, Weckwerth and Hawley (1962) reported a decline in numbers of martens in Montana following a decline in abundance of prey.

Although marten numbers in our study area changed among years, the relationship between this numerical response and the availability and quality of foods still requires clarification.

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References

- Ackerman B, Leban F, Samuel MD, Garton EO (1990) User's manual for program HOME RANGE (Forestry and Wildlife Range Experimental Station Technical report 15). University of Idaho, Moscow
- Ambrose SH, DeNiro MJ (1986) The isotopic ecology of East African mammals. *Oecologia* 69:395–406
- Ambrose SH, Norr L (1993) Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert JB, Grupe G (eds) Prehistoric human bone – archaeology at the molecular level. Springer, Berlin Heidelberg, New York, pp 1–38
- Ben-David M (1996) Seasonal diets of mink and marten: effects of spatial and temporal changes in resource abundance. PhD thesis, University of Alaska, Fairbanks
- Ben-David M, Bowyer RT, Faro JB (1996). Niche separation by mink and river otters: coexistence in a marine environment. *Oikos* 75:41–48
- Ben-David M, Hanley TA, Klein DR, Schell DM (in press) Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. *Can J Zool*
- Bowyer RT, Testa WJ, Faro JB, Schwartz CC, Browning JB (1994) Changes in diets of river otters in Prince William Sound, Alaska: effects of the Exxon Valdez oil spill. *Can J Zool* 72:970–976
- Buskirk SW, Harlow HJ (1989) Body-fat dynamics of the American marten *Martes americana* in winter. *J Mammal* 70:191–193
- Buskirk SW, MacDonald SO (1984) Seasonal food habits of martens in Southcentral Alaska. *Can J Zool* 62:944–950
- Buskirk, SW, Ma Y, Xu L, Jiang Z (1996) Diets of, and prey selection by, sables (*Martes zibellina*) in Northern China. *J Mammal* 77:725–730
- Campbell TM (1979) Short-term effects of timber harvests on pine marten ecology. MSc thesis, Colorado State University, Fort Collins
- Cederholm CJ, Huston DB, Cole DL, Scarlett WJ (1989) Fate of coho salmon (*Oncorhynchus kisutch*) carcasses in spawning streams. *Can J Fish Aquat Sci* 46:1347–1355
- Conover WJ, Iman RL (1988) Rank transformations as a bridge between parametric and non-parametric statistics. *Am Stat* 35:24–130
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosochim Acta* 45:341–351
- Dixon WJ (1990) BMDP statistical software manual. University of California Press, Berkeley
- Douglas RJ, Fisher LG, Mair M (1983) Habitat selection and food habits of marten, *Martes americana*, in the Northwest Territories. *Can Field-Nat* 97:71–74
- Ehleringer JR, Rundel PW (1988) Stable isotopes: history, units, and instrumentation. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological Research (Ecological Studies 68). Springer, Berlin Heidelberg New York, pp 1–16
- Fry B, Sherr EB (1988) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. In: Rundel PW, Ehleringer JR, Nagy KA (eds) Stable isotopes in ecological research (Ecological Studies 68). Springer, Berlin Hiedelberg New York, pp 196–229
- Gearing JN (1991) The study of diet and trophic relationships through natural abundance $\delta^{13}\text{C}$. In: Coleman DC, Fry B (eds) New York Carbon isotope techniques. Academic Press, pp 201–218
- Gordon CC (1986) Winter food habits of the pine marten in Colorado. *Great Basin Nat* 46:166–168
- Hargis CD, McCullough DR (1984) Winter diet and habitat selection of martens in Yosemite National Park. *J Wildl Manage* 48:140–146
- Harlow HJ (1994) Trade-offs associated with size and shape of American martens. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) Martens, sables, and fishers biology and conservation. Cornell University Press, Ithaca, pp 391–403
- Henry SE, Raphael MG, Ruggiero LF (1990) Food caching and handling by marten. *Great Basin Nat* 50:381–383
- Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996). Use of stable isotopes to determine diets of living and extinct bears. *Can J Zool* 74:2080–2088
- Hobson KA (1991) Use of stable carbon and nitrogen isotope analysis in seabird dietary studies. PhD thesis, University of Saskatchewan, Saskatoon
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* 95:388–394
- Hobson KA, Clark RG (1993) Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk* 110:638–641
- Hosmer DW, Lemeshow S (1989) Applied logistic regression. Wiley, New York
- Kenward RE (1987) Wildlife radio tagging. Academic Press, London
- King CM, Moors PJ (1979) On co-existence, foraging strategies and the biogeography of weasels and stoats (*Mustela nivalis* and *Mustela erminea*) in Britain. *Oecologia* 39:129–150
- Kline TC, Goering JJ, Mathisen OA, Poe PH (1989) Recycling of elements transported upstream by runs of Pacific salmon. I. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in Sashin creek, Southeastern Alaska. *Can J Fish Aquat Sci* 47:136–144
- Kline TC, Goering JJ, Mathisen OA, Poe PH (1993) Recycling of elements transported upstream by runs of Pacific salmon. II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in the Kvichak River, Bristol Bay, Southwestern Alaska. *Can J Fish Aquat Sci* 50:2350–2365
- Kreuger HW, Sullivan CH (1984) Models for carbon isotope fractionation between diet and bone. In: Turnland JR, Johnson PE (eds). Stable isotopes in nutrition ACS symp ser 258, American Chemical Society, Washington DC pp 205–220
- Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals. Chapman and Hall, London
- Martin SK (1987) The ecology of the pine marten (*Martes americana*) at Sagehen Creek, California. PhD thesis, University of California, Berkeley
- Martin SK (1994) Feeding ecology of American marten and fishers. In: Buskirk SW, Harestad AS, Raphael MG, Powell RA (eds) Martens, sables, and fishers: biology and conservation. Cornell University Press, Ithaca, pp 297–315
- Mech LD (1974) Current techniques in the study of elusive carnivores. In: Kjerner I, Bjurholm P (eds) National Swedish En-

- Environmental Protection Board. Stockholm. XI th International Congress of Game Biologists, Stockholm, Sweden, pp 315–322
- Nagorsen DW, Morrison KF, Forsberg JE (1989) Winter diets of Vancouver Island marten (*Martes americana*). *Can J Zool* 67:1394–1400
- Nagorsen DW, Campbell RW, Giannico GR (1991) Winter food habits of marten, *Martes americana*, on the Queen Charlotte Islands. *Can Field-Nat* 105:55–59
- Nevenzel JC (1970) Occurrence, function and biosynthesis of wax esters in marine organisms. *Lipids* 5:308–319
- Piorkowski RJ (1995) Ecological effects of spawning pacific salmon on several Southcentral Alaskan streams. PhD thesis, University of Alaska, Fairbanks
- Poole K, Matson G, Stirckland MA, Magoun A, Graf R, Dix L (1994) Age and sex determination for American martens and fishers. In: Buskirk SW, Harestad A, Raphael M, Powell R (eds) *Martens, sables and fishers: biology and conservation*. Cornell University Press, Ithaca, pp 204–223
- Powell RA (1994) Structure and spacing of *Martes* populations. In: Buskirk SW, Harestad A, Raphael M, Powell R (eds) *Martens, sables and fishers: biology and conservation*. Cornell University Press, Ithaca, pp 101–121
- Pyke GH, Pulliam HR, Charnov EL (1977) Optimal foraging: a selective review of theory and tests. *Q Rev Biol* 52:137–154
- Richey JE, Perkins MA, Goldman CR (1975) Effects of kokanee salmon (*Onchorhynchus nerka*) decomposition on the ecology of a subalpine stream. *J Fish Res Bd Can* 32:817–820
- Robbins CT (1993) *Wildlife feeding and nutrition*, 4th edn. Academic Press, New York
- Rosing MN, Ben-David M, Barry R (in press) Analysis of stable isotope data: a *K* nearest-neighbor randomization test. *J Wildl Manage*
- SAS (1985) *SAS User's Guide*. SAS Institute, Cary
- Schell DM, Saupe SM, Haubenstock N (1988) Natural isotope abundance in bowhead whale (*Balaena mysticetus*) baleen: markers of aging and habitat usage. In: Rundel PW, Ehleringer JR, Nagy KA (eds) *Stable isotopes in ecological research* (Ecological Studies 68). Springer, Berlin Heidelberg New York, pp 260–269
- Schilling MF (1986) Multivariate two-sample tests based on nearest neighbors. *J Am. Stat Assoc* 81:799–805
- Schoninger MJ, DeNiro MJ (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim Cosmochim Acta* 48:625–639
- Schwarz HP (1991) Some theoretical aspects of isotope paleodiet studies. *J. Archol. Sci.* 18:261–275
- Samuel MD, Pierce DJ, Garton OE, Nelson LJ, Dixon KR (1985) Identifying areas of concentrated use within the home range. *J Anim Ecol* 54:711–719
- Simon T (1980) An ecological study of the pine marten in the Tahoe National Forest. MSc thesis, California State University, Sacramento
- Soutiere EC (1979) Effects of timber harvesting on marten in Maine. *J Wildl Manage* 43:850–860
- Swihart RK, Slade NA (1985) Testing for independence of observations in animal movements. *Ecology* 66:1176–1184
- Taylor RJ (1984) *Predation*. Chapman and Hall, London
- Thompson ID, Colgan PW (1987) Numerical responses of martens to a food shortage in Northcentral Ontario. *J Wildl Manage* 51:824–835
- Thompson ID, Colgan PW (1990) Prey choice by marten during a decline in prey abundance. *Oecologia* 83:443–451
- Tieszen LL, Boutton TW (1988) Stable carbon isotopes in terrestrial ecosystem research. In: Rundel PW, Ehleringer JR, Nagy KA (eds) *Stable isotopes in ecological research* (Ecological Studies 68). Springer, Berlin Heidelberg New York, pp 167–195
- Tieszen LL, Fagre T (1993) Effects of diet quality and composition on the isotopic composition of respiratory CO₂, bone collagen, bioapatite, and soft tissues. In: Lambert JB, Grupe G (eds) *Prehistoric human bone – archaeology at the molecular level*. Springer, Berlin Heidelberg New York, pp 127–156
- Weckwerth RP, Hawley VD (1962) Marten food habits and population fluctuations in Montana. *J Wildl Manage* 26:55–74
- Zar JH (1984) *Biostatistical analysis*. Prentice-Hall, New Jersey
- Zielinski WJ, Spencer WD, Barrett RD (1983) Relationship between food habits and activity patterns of pine martens. *J Mammal* 64:387–396