

# Prey choice by marten during a decline in prey abundance

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**Summary.** We examined variation in diet choice by marten (*Martes americana*) among seasons and between sexes and ages from 1980–1985. During this period prey populations crashed simultaneously, except for ruffed grouse (*Bonasa umbellus*) which was common at the beginning and end of the study, and masked shrews (*Sorex cinereus*) which were abundant in 1983. Marten were catholic in selection of prey and made use of most available mammalian prey, ruffed grouse, passerine birds, berries, and insects. Diet niche was widest during the latter three years when prey was scarce, particularly in late winter. Diet niche breadth was negatively correlated with abundance of all common prey species. Proportion of small prey species in the diet was correlated with absolute abundance of those species, but proportion of some large prey was related to their relative abundance. Diet choice varied among years and among seasons. Berries and insects were common in summer diets while large prey, particularly varying hare (*Lepus americanus*), were more frequent in winter diet than in summer diet. We found little evidence that any small mammal species was a preferred prey. Sexual size dimorphism between the sexes did not affect prey choice, nor did age. Reduced foraging effort in winter resulted in a wider diet niche only when prey was scarce. The only prediction of optimal foraging models fully supported by our data was a wider diet niche with reduced prey abundance. However, among the three most profitable prey species choice was dependent on the absolute abundance of the most profitable type (varying hare). We suggest that marten primarily forage for large prey but employ a strategy which results in encounters with small prey as well. These small prey are eaten as they provide energy at minimal cost, between captures of large prey.

**Key words:** Prey choice – Marten – Sexual dimorphism – Prey availability – Optimal foraging

Stephens and Krebs (1986) suggested that foraging models can be used to analyze behavioural mechanisms, and list many published studies which test the predictions of foraging theory. However, few studies have examined

the predictions of foraging models as applied to the diets of terrestrial mammalian predators with the constraints imposed by natural systems (but see Erlinge 1981; Corbett and Newsome 1987; McCracken and Hansen 1987). Marten (*Martes americana*) is an example of a predator which exists in a variable environment (weather, food resources) and preys on several food types (Weckwerth and Hawley 1962; Francis and Stephenson 1972).

Several authors have criticized the assumptions of optimality models as applied to complex systems (e.g., Schluter 1981; Glasser 1984; Pierce and Ollason 1987). Many of the criticisms are challenged by Stephens and Krebs (1986), and we believe that foraging theory provides a reasonable basis to examine the mechanisms of prey selection. Models have been suggested which allow for factors that may influence foraging behaviour including learning (Hughes 1979; Greenwood 1984), reduced foraging time, for example as a result of poor weather (Lucas 1983), clumped distribution of prey (McNair 1979), and requirement for specific nutrients (Westoby 1978). All of these complications may apply in natural situations.

Optimal foraging models suggest that food choice reflects profitability or absolute abundance of prey (Royama 1970; Pulliam 1975; Charnov 1976). Other models stress the importance of switching based on relative prey abundances (Murdoch 1969; Cornell 1976; Visser 1981). Corbett and Newsome (1987) reported that prey switching in dingoes (*Canis familiaris dingo*) was a function of absolute availability of small and medium-sized prey which were controlled primarily by weather (drought/rain). They indicated that dingo foraging was not necessarily optimal (referring, we suspect to optimal foraging) but rather represented a continuum of strategies depending ultimately on weather conditions.

Here we present results of a long-term study of marten prey choice in an environment where availability of food was altered by deep snow during winter, and by fluctuating prey numbers among years. Time available for foraging by marten is reduced by extreme temperatures in winter which are below the lower critical temperature of marten (Thompson 1986; Buskirk et al. 1988) for extended periods.

Specifically, we examine the predictions of optimal foraging (Lucas 1983; Pyke 1984) and prey switching (Murdoch 1969) as affected by age (learning), sexual di-

morphism in size, weather, and prey availability. Optimal diet selection theory predicts that: 1) only the most valuable prey species should be eaten and partial preferences should not be exhibited, 2) choice of a particular prey type should reflect absolute abundance of more profitable types, and 3) a general decline in prey abundance should result in a wider diet niche. Alternatively, the prey-switching hypothesis suggests that choice of a prey species is influenced by its abundance relative to the abundance of other prey types.

We expected that age would influence prey choice by increasing handling and searching times in young marten. Increased foraging time should produce a wider diet niche in younger marten because they may not be as selective of prey as more experienced marten (Hughes 1979). A second factor which we anticipated would influence diet choice was sexual size dimorphism. Size difference between the sexes has been shown sometimes to influence diet niche in other mustelids including mink (*Mustela vison*) (Birks and Dunstone 1985), and stoats (*Mustela erminea*) (Erlinge 1979; Moors 1980). Female marten are approximately 35–40 percent smaller than males and so we predicted that they would be less capable of capturing large prey species such as varying hare (*Lepus americanus*). Finally, constraints on foraging time and prey availability in winter were expected to result in a less specialized diet compared to in summer, as predicted by the model of Lucas (1983).

## Study area and methods

We collected data on marten diets from the fall of 1980 until February 1985. Our research was conducted in boreal forest near Manitouwadge, Ontario, Canada (49° 15' N, 85° 35' W). Rolling topography of glacial moraines supported mixed and coniferous stands of primarily black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), and white birch (*Betula papyrifera*). Poorly drained sites supported homogeneous black spruce forest. Much of the area had been logged but few marten used regeneration stands (Thompson et al. 1989).

The area was snow-covered from late October until May with average maximum snow depth in uncut forests of 90 cm with a mean of 68 cm in February. Winter minimum temperatures were often below  $-35^{\circ}\text{C}$  for extended periods from December to March.

## Indices of prey abundance

We sampled small mammal populations using snap-traps. Trap-lines were paired and located about 1 km apart in two uncut stands and in regeneration stands aged 10, 20, and 30 years. We baited traps with peanut butter and set two at each of 25 stations per line, for three consecutive nights in spring and fall. Upland and lowland habitats were sampled in all stand age classes and we calculated a mean value for each species weighted by the area of upland and lowland habitat in uncut and cutover stands. Marten populations in logged areas were about 10 percent of those in uncut forest (Thompson 1988). Therefore we weighted our small mammal abundance indices to reflect the disparity in availability to marten of small mammals between the two types of area ( $0.9 \times \text{uncut values} + 0.1 \times \text{logged values}$ ).

**Table 1.** Numbers of prey items in 1028 scats and stomachs of marten near Manitouwadge, Canada 1980–1985. Seasons: F=fall, EW=early winter, LW=late winter, SP=spring, SU=summer)

Prey item	1980			1981					1982				
	F	EW	LW	SP	SU	F	EW	LW	SP	SU	F	EW	LW
Small mammals:													
<i>Clethrionomys gapperi</i>	20	24	30	14	66	21	46	14	19	11	15	26	16
<i>Microtus</i> spp. <sup>a</sup>	3	4	8	4	20	10	13	2	2	8	8	6	5
<i>Peromyscus maniculatus</i>	10	18	15	10	66	15	32	3	9	5	13	16	12
<i>Sorex cinereus</i>	4	1	3			1	4			5	7	8	5
<i>Blarina brevicauda</i>	2		1	1	2	4	2		1			1	
<i>Phenacomys intermedius</i>	1	1	1	1	1		2		3		1	1	1
<i>Synaptomys cooperi</i>			2					1					
<i>Zapus hudsonius</i>					3			1		2		1	
<i>Napeozapus insignis</i>		2			3	1		1				2	
<i>Eutamias minimus</i>	2					1				1			
<i>Tamias striatus</i>								1	1	1			1
Lagomorphs:													
<i>Lepus americanus</i>	2	13	7		17	9	35	17	1	9	2	17	9
Sciurids:													
<i>Tamiasciurus hudsonicus</i>	1		1				2	3			1		
<i>Glaucomys sabrinus</i>								1					4
Mustelids:													
<i>Mustela erminea</i>	1	2	1	1	2		5		2	1	1		6
<i>Mustela nivalis</i>							1					1	
<i>Martes americana</i>		1	1					5					
Birds:													
<i>Bonasa umbellus</i>			1	1	1	2	3	1		2	1	4	1
Unknown passerine					1								1
Berries	1			1	62	12	1		7	15	1		
Insects	5		1		16	3			2	5	1		

<sup>a</sup> *Microtus* spp. was predominantly *M. pennsylvanicus* but may have included some *M. chrotorrhinus*

Populations of other potential prey including varying hare, red squirrels (*Tamiasciurus hudsonicus*), and ruffed grouse (*Bonasa umbellus*) were inferred from track counts on 1 km transects in each of the stand age classes (Thompson et al. 1989). Counts were replicated three times in each of December, January, and March. Our second index of red squirrel and hare populations was the number of incidental captures in live-traps set for marten in spring and fall (Thompson and Colgan 1987). We used the latter index for most analyses because it provided spring and fall values and correlation analyses showed similarity of the two indices (see Thompson et al. 1989). Comparisons of relative abundance of ruffed grouse and varying hare populations were done using track count indices because tracks were our only index of grouse numbers.

### Identification of prey

We determined prey selection from 1028 scats and carcasses which provided 1873 occurrences of mammals, birds, plants, and insects. Summer diet was determined from scats and winter diet from scats as well as stomach contents of trapped animals provided by trappers. A key (Thompson et al. 1987) was used for identifying mammal species and a reference collection aided in identification of plant and bird material. We report the data as frequency of occurrence.

### Age of marten

Marten carcasses were aged by counting cementum annuli of the second premolar (Larsen and Taber 1980). The small first premolar was extracted from live-captured marten and aged in the same manner (marten defecated in traps and so aging live animals enabled assignment of sex and age of the marten for prey items in those faeces).

1983					1984				
SP	SU	F	EW	LW	SP	SU	F	EW	LW
16	13	16	29	8	12	8	6	11	
6	7	6	8	6	2	3	2	4	1
4	5	3	13		4	4	7	10	1
6	9	20	38	11	6	7	8	12	2
		1	9	5	1			2	1
1			1	1			1		
1		1	1						
	2					3	2	1	
		3		1	2	2	1		
	1					2		1	
	2	1	1	1	3				
4	2	5	7	12	1	2			1
		1	14	5	4			5	2
	1		1	1				4	
			1	4	1	1	1	1	
			1	1					
			1	13	2			1	
4	21	4	9	7	4	10	4	16	1
	1	1	5	2			2		
14	43	11	3	3	11	27	21	12	
4	15	7	4		5	12	2		

### Prey profitability

Most authors have found that prey ranking was scaled to body weight where greatly differing prey sizes were encountered (Werner and Hall 1974; Gardner 1981; Powell 1979; MacCracken and Hansen 1987). On the basis of weight, prey rankings for our study were: varying hare > ruffed grouse > red squirrels > voles > deer mice (*Peromyscus maniculatus*) > masked shrews (*Sorex cinereus*). We defined large prey as species weighing greater than 100 g. All small forest rodents and insectivores were small prey.

### Statistical analyses and indices

We assigned seasons as spring (mid-April through May), summer (June through August), fall (September and October), early winter (November and December), and late winter (January until mid-April). We compared diet between sexes for each season in all years by chi-square analysis. For adult/juvenile diet comparisons, we pooled data into three seasons and two year groups for chi-square analyses because insufficient data existed in one year and in some seasons: summer and fall were grouped, spring was added to late winter, and early winter remained as described above; we pooled data from 1980 and 1981 as abundant food years and 1982–1985 were combined as scarce food years (see Thompson and Colgan 1987). We used multidimensional contingency table analysis (Colgan and Smith 1978) of diet, season, and year to test for two-way interactions. Seasonal diet comparisons were also performed with the data pooled as indicated.

As a comparison to the chi-square analyses, we also calculated food niche overlap using Schoener's (1970) index:

$$\alpha = 1 - 0.5 \left( \sum_{i=1}^n |P_{ij} - P_{ik}| \right)$$

where  $P_{ij}$  is the proportion of the  $i$ th prey type in the diet of age or sex  $j$ , and  $P_{ik}$  is its proportion in the diet of sex or age  $k$ . Linton et al. (1981) showed that this index produced accurate estimates of overlap for true values from 7 to 85% as long as  $n > 16$ .

We calculated electivity indices as a further means to assess preferential use of small mammal species using Vanderploeg and Scavia's (1979) index:

$$E = (W_i - 1/n) / (W_i + 1/n)$$

where  $n$  = the number of food types, and  $W_i = (r_i/p_i) / (\sum r_i/p_i)$  where  $r_i$  is the proportion of the  $i$ th food type in the diet and  $p_i$  is its proportion in the environment. Lechowicz (1982) suggested that this is the best available index because it includes a component of absolute and relative abundance, and measures a deviation from random feeding that enables ordered comparisons.

To determine how diet niche changed with absolute and relative density of food types we calculated breadth using Levin's (1968) index:

$$B = 1 / \sum (p_i^2)$$

where  $p_i$  is the proportion of the  $i$ th food in the diet sample. Our prey density indices were available for spring and fall, so correlation analyses with diet niche breadth were performed with diet data grouped into those two periods. Changes in prey populations were examined using Kruskal-Wallis tests ( $H$  statistic) among years with Dunn's multiple comparisons for between years (Zar 1984). To test for individual differences between a given year and all others we used Mann-Whitney  $U$ -tests.

## Results

### Diet by sex and age classes

We observed little difference in diet choice between the sexes during any season of any year ( $N = 14$  to 94 for

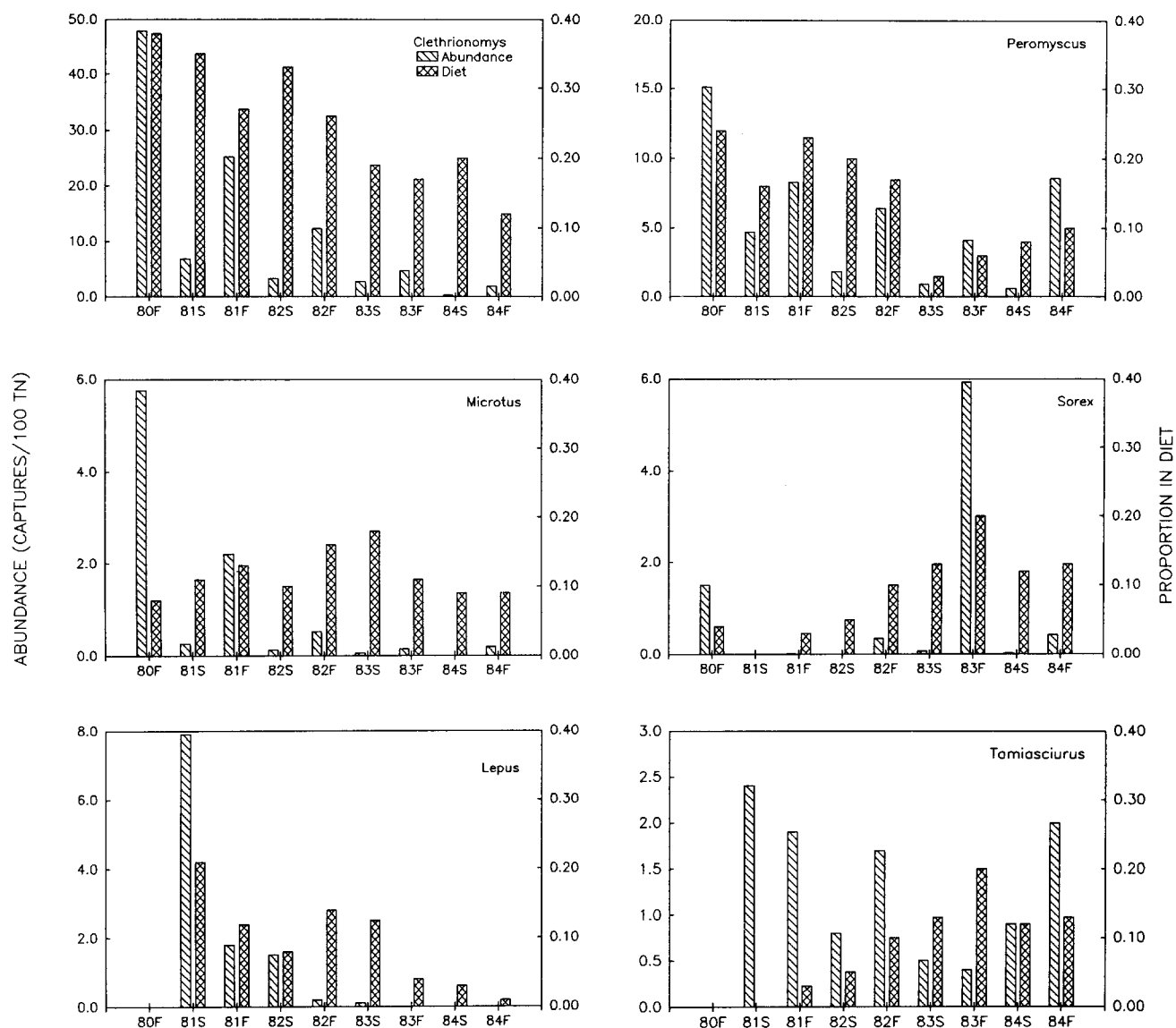


Fig. 1. Absolute abundance and proportion of major prey species in marten diet in spring (S) and fall (F) from 1980–1984, near Manitowadge, Ontario

males and 16 to 76 for females;  $X^2 = 5.7$ – $11.0$ ,  $df = 3$ – $11$ ,  $P = 0.07$ – $0.87$ ). Diet niche overlap averaged 0.72 (range 0.57–0.91) and was correlated with the chi-square values ( $r_s = -0.72$ ,  $df = 11$ ,  $P < 0.01$ ). Closest to significance was the diet in late winter 1981 with an overlap value of 0.57. Sample size for that period was low ( $N = 14$  and 16, for males and females, respectively), and most of the chi-square value resulted from fewer red-backed voles (*Clethrionomys gapperi*) in the diet sample for males. A separate analysis of proportion of varying hare in the diet of males and females showed no significant difference ( $U = 52$ ,  $P > 0.3$ ).

We found no significant difference between the diets of adults and juveniles in any year or season ( $N = 12$  to 100 for juveniles and 22 to 240 for adults;  $X^2 = 4.5$ – $10.4$ ,  $df = 5$ – $7$ ,  $P = 0.21$ – $0.95$ ), and overlap was consistently above 0.75. Prey items were pooled for all further analyses regardless of marten sex or age to increase sample sizes (Table 1, Fig. 1).

#### General characteristics of marten diet

Small mammals, primarily red-backed voles, meadow voles (*Microtus pennsylvanicus*), and deer mice formed the majority of prey items eaten by marten, accounting for a mean of 54% (range 28–85% for the five seasons and five years) of all prey items (Table 1). Varying hare accounted for 20% of winter occurrences (range 0–41%). Red squirrels were not frequent prey items and occurred to a maximum of 9%. Marten ate ermine and were cannibalistic in some years, as previously reported in Thompson and Colgan (1987). Passerines occurred rarely, while ruffed grouse were common prey, particularly in 1983–1984. Berries of various plants including blueberries (*Vaccinium myrtilloides*), mountain ash (*Sorbus americana*), raspberries (*Rubus* spp.), wild sarsparilla (*Aralia nudicaulis*), and juneberries (*Amelanchier* spp.) were commonly eaten when available seasonally.

**Table 2.** Density indices of important prey species and diet niche width (Levins 1968) of marten in spring (SP) and fall (F). For small mammal species values are number of animals per 100 trap-nights, for varying hare (A.) and red squirrels values are number of live-captures per 100 trap-nights, and for ruffed grouse and varying hare (B.) values are number of tracks/km in December near Manitouwadge, Ontario

Prey Species	1980	1981		1982		1983		1984	
	F	SP	F	SP	F	SP	F	SP	F
<i>Clethrionomys gapperi</i>	47.9	6.8	25.2	3.3	12.4	2.8	4.7	0.3	1.9
<i>Peromyscus maniculatus</i>	15.1	4.7	8.3	1.8	6.4	0.9	4.1	0.6	8.6
<i>Microtus</i> spp. <sup>a</sup>	7.7	0.3	2.2	0.1	0.5	0.06	0.2	0.0	0.2
<i>Sorex cinereus</i>	1.50	0.0	0.01	0.0	0.34	0.07	5.9	0.02	0.42
Total small mammals	69.3	12.5	34.0	5.8	20.5	3.9	15.7	1.1	11.4
<i>Lepus americanus</i> A.	—	7.9	1.8	1.5	0.2	0.1	0.0	0.0	0.0
<i>Lepus americanus</i> B.	68.4		23.6		9.2		4.1		1.8
<i>Tamiasciurus hudsonicus</i>	—	2.4	1.9	0.8	1.7	0.5	0.4	0.9	2.0
<i>Bonasa umbellus</i>	0.7	—	0.4	—	0.5	—	0.8	—	1.2
Marten diet niche width (B)	4.38	4.92	5.62	5.70	6.56	9.15	8.37	8.02	6.72

<sup>a</sup> *Microtus* spp. was primarily *M. pennsylvanicus* but may have included some *M. chrotorrhinus*

### Prey abundance

There was a decline in abundance of most prey species on the study area from 1980 to 1984–1985. Captures of all species of small mammals declined significantly ( $H=34.1$ – $58.6$ ,  $P<0.001$ ), with spring and fall populations progressively lower in each successive year, except for deer mice in fall 1984 (Table 2). Masked shrew was an exception to the general trend for small mammals, with highest population ( $U=5.3$ ,  $P<0.001$ ) in the fall of 1983. Varying hare and red squirrel populations also declined dramatically as indicated by both track and live-capture indices ( $H=78.7$  and  $74.2$ , respectively,  $P<0.01$ ). Track counts for ruffed grouse indicated significantly lower populations in the winter of 1981 and 1982 compared to 1984 ( $U=3.1$  respectively,  $P<0.01$ ).

For certain analyses, years were grouped into those with abundant prey, 1980 and 1981, and those when prey were generally scarce, 1982–1984. In summary, during the scarce prey years most small mammal species, varying hare, and red squirrels had low populations. The only species which were relatively more abundant during what we have referred to as scarce food years were ruffed grouse in 1984, and masked shrews in 1983 (Table 2).

### Diet choice and prey abundance

Marten diet niche was wider in the latter three years of the study when principal prey species were least abundant, and narrowest in the fall of 1980 when vole, mouse, and hare abundance was greatest (Table 2). Diet niche breadth was negatively correlated with absolute abundance of most major prey species (but not for grouse) and marginally with density of all small mammals together (Table 3).

Proportion of individual prey species in the diet was

**Table 3.** Spearman correlation coefficients ( $r_s$ ) of the proportion of major prey species in the diet of marten with indices of absolute and relative abundance (captures per trap night for small mammals, *Lepus*, and *Tamiasciurus*, and track counts per km for *Bonasa*), and correlations of diet diversity with absolute abundance for spring and fall, 1980–1985 ( $N=9$  for small mammals;  $N=8$  for hare and red squirrel;  $N=5$  for ruffed grouse)

Prey Species	Proportion in diet with				Absolute abundance with	
	Absolute abundance		Relative abundance <sup>a</sup>		Diet niche	
	$r_s$	$P$	$r_s$	$P$	$r_s$	$P$
<i>Clethrionomys gapperi</i>	0.67	0.05	0.47	0.21	–0.71	0.03
<i>Peromyscus maniculatus</i>	0.65	0.05	–0.27	0.48	–0.64	0.05
<i>Microtus</i> spp. <sup>b</sup>	–0.08	0.83	–0.11	0.78	–0.73	0.02
<i>Sorex cinereus</i>	0.63	0.07	0.77	0.01	0.21	0.58
Total small mammals					–0.63	0.07
<i>Lepus americanus</i>	0.78	0.02			–0.82	0.01
<i>Tamiasciurus hudsonicus</i>	–0.31	0.45			–0.74	0.04
<i>Bonasa umbellus</i>	0.70	0.19			0.60	0.28

<sup>a</sup> Relative abundance was calculated among small mammal species

<sup>b</sup> *Microtus* spp. was primarily *M. pennsylvanicus*, but may include some *M. chrotorrhinus*

correlated with absolute abundance for red-backed voles, deer mice, and varying hare (Table 3). There was no correlation of absolute abundance of red squirrels, ruffed grouse, or meadow voles and proportion of those

species in the diet. For masked shrews, relative abundance was a slightly better predictor of occurrence in the diet than absolute abundance.

Abundance indices for varying hare, red-backed voles, deer mice, red squirrels, and meadow voles were all correlated as their populations declined simultaneously. As a result we could not ascertain from this study whether abundance of the most profitable type (varying hare) influenced use of the other species. However, predation on the second most profitable prey, ruffed grouse, was correlated with a decline in abundance of hare ( $r_s = -1.00$ ,  $P = 1.00$ ). Grouse were preyed on most heavily when hare were scarcest in 1983 and 1984. In 1980, when grouse were moderately abundant and hare were most abundant, grouse made up only 0.9% of the diet (Tables 1 and 2). Occurrence of the third most profitable large prey (red squirrel) in the diet had a weak

but also negative correlation with absolute abundance of varying hare ( $r_s = -0.61$ ,  $P = 0.10$ ).

#### Seasonal diet choice within years

Summer diet choice differed significantly from those of early and late winter, during both the abundant and scarce prey years primarily as a result of greater use of berries and insects. We also found a greater occurrence of varying hare in early and late winter diets compared to in summer, and significantly more ermine in the early winter diet than in the other two seasons (Table 4) (among season comparisons in abundant food years:  $X^2 = 134.1$ ,  $df = 28$ ,  $P < 0.0001$ ; and in scarce food years:  $X^2 = 174.6$ ,  $df = 28$ ,  $P < 0.0001$ ).

**Table 4.** Chi-square analyses, diet niche, and overlap of seasonal diet choice by marten during periods of prey abundance (AB = 1980–1981) and prey scarcity (SC = 1982–1985). Data are proportions of important prey items in the diet but chi-squares were done on count data. Asterisk refers to important cell-chi values for the abundant/scarce comparisons

Prey item	Season					
	Summer		Early winter		Late winter	
	AB	SC	AB	SC	AB	SC
Small mammals:						
<i>Clethrionomys gapperi</i>	0.28	0.16*	0.32	0.21*	0.39	0.28*
<i>Peromyscus maniculatus</i>	0.24	0.09*	0.23	0.12*	0.19	0.12*
<i>Microtus</i> spp. <sup>a</sup>	0.09	0.08	0.22	0.07*	0.09	0.09
<i>Phenacomys intermedius</i>	a <sup>b</sup>		a		0.02	0.02
<i>Zapus hudsonius</i>	0.01	0.03	a		a	
<i>Napeozapus insignis</i>	0.01	0.01	a		a	
<i>Sorex cinereus</i>	0.04	0.13*	0.02	0.18*	a	
<i>Blarina brevicauda</i>	a		0.01	0.04	0.01	0.03
Other spp. <sup>c</sup>	0.03	0.05	0.03	0.03	0.05	0.08
Lagomorphs:						
<i>Lepus americanus</i>	0.07	0.05	0.22	0.10*	0.17	0.11*
Sciurids:						
<i>Tamiasciurus hudsonicus</i>	a		0.01	0.06*	0.03	0.04
<i>Glaucomys sabrinus</i>	a		0.01	0.02	0.01	0.02
Mustelids:						
<i>Mustela erminea</i>	0.01	0.01	0.03	0.02	0.01	0.04
<i>Martes americana</i>	a		0.02	0.07*	a	
Grouse:						
<i>Bonasa umbellus</i>	0.02	0.10*	0.02	0.09*	0.01	0.07*
Berries	0.20	0.28	0.01	0.05*	a	
Diet niche (B)	5.22	6.68	4.68	7.67	4.42	7.62
Chi-square, df	107.7, 10		104.4, 12		32.4, 10	
P	0.0001		0.0001		0.001	
Overlap ( $\alpha$ )	0.70		0.61		0.73	

<sup>a</sup> *Microtus* spp. was predominantly *M. pennsylvanicus* but may have included some *M. chrotorrhinus*

<sup>b</sup> a indicates that too few items occurred to include the species individually in the analysis, and that the species is included in the 'Other spp.' category

<sup>c</sup> Also includes: *Synaptomys cooperi*, *Tamias striatus*, *Eutamias minimus*, and *Mustela nivalis*

**Table 5.** Electivity indices (Vanderploeg and Scavia's E, 1979) for small mammal prey species of marten, from 1980 to 1984, near Manitouwadge, Canada (F = fall, SP = spring)

Prey species	1980	1981		1982		1983		1984	
	F	SP	F	SP	F	SP	F	SP	F
<i>Clethrionomys gapperi</i>	0.09	0.04	−0.63	0.03	−0.38	−0.64	−0.21	−0.04	0.09
<i>Peromyscus maniculatus</i>	0.43	−0.13	−0.02	0.08	−0.27	−0.79	−0.58	−0.69	−0.63
<i>Microtus</i> spp. <sup>a</sup>	0.23	0.75	0.79	0.67	0.57	0.75	0.75	− <sup>b</sup>	0.55
<i>Sorex cinereus</i>	0.64	−	−	−	0.68	0.69	−0.25	0.79	0.68
<i>Blarina brevicauda</i>	−	−	−	−	−	−	−0.30	−	−0.31
<i>Napeozapus insignis</i>	−	0.05	−	−	−	−	−	−0.48	0.39

<sup>a</sup> *Microtus* spp. was predominantly *M. pennsylvanicus* but may have included some *M. chrotorrhinus*

<sup>b</sup> indicates 0 in either the trapped sample or in the diet sample

In scarce prey years, differences among seasons in diet choice included: more masked shrews and marten eaten in early winter, while red squirrels and short-tailed shrews (*Blarina brevicauda*) occurred more in the diet from both winter seasons compared to in summer.

Diet breadth decreased from summer to winter during years of abundant prey, while during years with scarce food it was highest in winter (Table 4). Widest diet niche was found in late winter 1983 (8.96) and the lowest occurred in late winter 1980 (3.91).

#### Seasonal diet choice among years

Diets were different between years when food was abundant and years when prey was scarce, with diet niche breadth consistently widest for each season during scarce food years (Table 4). There was a significant two-way interaction between year and seasons ( $X^2 = 178.1$ ,  $df = 28$ ,  $P < 0.001$ ) suggesting that diet choice was highly dependent on availability as abundance changed between years and among seasons. In summers when prey were abundant, we found more red-backed voles and deer mice, and fewer masked shrews and ruffed grouse in the diet compared to summers with scarce prey (the latter two species were relatively more common in our 'scarce prey years'). During early winter of abundant prey years, red-backed voles, deer mice, and meadow voles occurred significantly more often, while masked shrews, red squirrels, marten, and ruffed grouse were observed less in the diet than during scarce prey years. In late winter, red-backed voles and deer mice were more common, and ruffed grouse less common in abundant food years compared to scarce prey years. Overlap in prey choice between the two year groups was lowest in early winter (0.61) and averaged 0.68 for all three seasons.

#### Electivity of small mammals

Neither of the two most common small mammal species, red-backed voles and deer mice, were preferred by marten (Table 5), and electivity for those two species was clearly not influenced by abundance. Meadow voles may be a preferred prey species, as were masked shrews in some years. However, electivity for the latter two species was not consistent in those years when populations were highest, in the fall of 1983 for shrews and in 1980 for meadow voles. Two other small mammal species for which there were sufficient data, short-tailed shrew and woodland jumping mouse (*Napeozapus insignis*), also were not preferred.

#### Discussion

Marten exhibited a high diet diversity and ate almost all possible mammalian prey species in their environment (they were not observed to prey on skunks [*Mephitis mephitis*] or ground hogs [*Marmota monax*]). We observed changes in diet choice with season and absolute and relative abundance of prey species. Other studies have commented on the catholic nature of diet choice in marten and its seasonality (Weckwerth and Hawley 1962; Zielinski et al. 1983; Buskirk and MacDonald 1984). A generalist strategy, such as we observed for marten, is predicted for predators that exploit prey which fluctuate in abundance (Emlen 1968; Schoener 1971), and for predators that search as opposed to pursue their prey (Schoener 1971). Generalizing is probably favoured in marten because they forage by searching a small home range, and encounter several sizes of prey which vary in availability by season and year.

Partitioning of prey based on sexual size dimorphism as suggested for some mustelids by Brown and Lasiewski

(1972) and Shubin and Shubin (1975) and discussed by Moors (1980), was not supported by our study for marten. Female predation on hare was not different from the rate observed for males, nor did it increase in summer when a preponderance of young hare in the population could have enhanced capture success rates by female marten. Further, we believe that if sexual size dimorphism were to influence the segregation of food resources, then clear differences in diet choice between the sexes should have been seen during years when prey were scarce, yet such was not the case. Our observation that juvenile and adult diets were similar indicates that young marten were as opportunistic as adults. It is probable that sufficient time is spent learning to hunt with the female that juveniles are proficient hunters by the time of fall dispersal.

We observed two opposite trends in seasonal diet breadth depending on prey densities. Lucas' (1983) hypothesis that reduced time to forage should result in wider diet choice was supported during winters when prey were scarce. However, during winters when prey were abundant marten diet niche breadth was narrow, primarily resulting from their heavy use of varying hare. The ability to capture a highly profitable prey likely reduced the dependence on small prey which are subnivean and therefore less available than species which are active on the snow surface. Greater use of hare in winter than in summer by marten was also observed by Cowan and Mackie (1962), Raine (1983), and Bateman (1986). In winters when all prey including hare were scarce, diet niche was high as marten were forced to increase their use of alternate prey species.

Marten foraging strategy appears complex and our data support only one of the predictions of optimal foraging theory. We observed that a reduction in prey abundance from 1982–1985 resulted in a wider diet niche in comparison to 1980–1981 when common prey species were abundant. Diet niche breadth was negatively correlated with absolute abundance of all common prey except masked shrews. Despite the more diverse diet with reduced prey abundance, no new species were added to the diet. Instead increased use was made of species which were seldom used in 1980 and 1981 including ruffed grouse, red squirrels, other marten, and berries.

The second prediction of optimal foraging tested here was that least profitable prey types should be omitted from the diet when the more valuable types are sufficiently abundant. Marten showed a wide variety in prey selection even when large prey were abundant, including eating many low-value small mammal prey including masked shrews which weigh less than 5 g. Therefore our data clearly do not support this hypothesis.

A third prediction of optimal foraging, that inclusion of a particular prey in the diet should not be influenced by its own abundance but rather by the absolute abundance of prey types of higher value, was not supported when all prey species were considered. The proportion of low-value voles and mice was highest in the diet when varying hare and red squirrels were abundant compared to the level seen when hare and squirrels were scarce. However, predation on the three most profitable prey,

when considered alone, conformed to the prediction. Predation was dependent on absolute abundance for varying hare, while ruffed grouse and red squirrels only became common in the diet after the hare population had crashed. Corbett and Newsome (1987) and McCracken and Hansen (1987) reported support for this third prediction in canids.

We observed little support for frequency-dependent diet models. Switching was suggested for masked shrews where relative density predicted their occurrence in the diet of marten.

None of the abundant species of small forest rodents was a preferred prey suggesting that marten do not favour one small mammal species over another. Electivity for meadow voles and masked shrews are suspect because of inconsistent results when their populations were highest. There were possible trap biases for shrews (Pucsek 1969), and a clumped distribution of meadow voles in forest habitats may have resulted in under-sampled numbers through trapping (Buskirk and MacDonald 1984). In previous long-term diet studies of marten where small mammal occurrence in the diet and in the environment can be compared (Weckwerth and Hawley 1962; Francis and Stephenson 1972), there was also no electivity or frequency dependent selection for common small mammal species, again with the exception of meadow voles (our calculations).

Despite the fact that marten could capture large prey types, there was a consistently high number of occurrences of small prey in the diet. We suggest that the hunting strategy of marten was a constant attempt to maximize inclusion of large prey in their diet, particularly varying hare, and that small prey were captured proficiently but incidentally. Support for our suggestion lies first in the observation that there was no diet preference among common small mammal species despite differences in profitability. Secondly, marten used large prey depending upon absolute abundance of the most profitable species. Marten hunt by searching under logs, stumps, rocks, and in crevices and holes in the snow cover, and also spend considerable time foraging in habitats that are only frequented by varying hare (Thompson 1986). During these searches for high-value prey, low-value prey (mice, voles, and shrews) are also encountered. Handling time for small prey is probably minimal, and therefore little time searching for larger prey is lost as a result of taking small prey. Stephens and Krebs (1986) stated that an abundance of low-value prey could compensate for their low value. We believe that marten were behaving in a manner somewhat analogous to dingoes reported by Corbett and Newsome (1987) by employing a hunting strategy which ensures that some food is captured (regardless of size) between less frequent kills of large prey. Such behaviour is particularly efficient during periods when large species are less available or more difficult to capture.

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