RELATIONSHIP BETWEEN FOOD HABITS AND ACTIVITY PATTERNS OF PINE MARTENS

William J. Zielinski, Wayne D. Spencer,
and Reginald H. Barrett

Abstract.—Pine martens (*Martes americana*) consume a variety of food types annually but seasonal foraging is restricted to a subset of available prey. Winter foods include chickarees (*Tamiasciurus douglasii*), voles (*Microtus* spp.), snowshoe hares (*Lepus americanus*), and flying squirrels (*Glaucomys sabrinus*), whereas ground-dwelling sciurids (*Spermophilus* spp. and *Eutamias* spp.) comprise the bulk of the diet during the remainder of the year. Activity also is variable by season, with martens foraging at night during winter and by day during summer. Seasonal marten activity does not appear associated with optimal ambient temperature but instead appears synchronized with the activity of prey.

Predators are known to synchronize their predatory activities with the activity periods of their primary prey (Curio, 1976). Several authors have speculated that prey may be easier to detect when active (Bider, 1962; Kaufman, 1974; Curio, 1976). Examples of concurrent activity periods of predator and prey include the hunting behaviors of the pygmy owl (*Glaucidium passerium*) (Mikkola, 1970), the wildcat (*Felis silvestris*) (Schuh et al., 1971), and several marine fishes (Starck and Davis, 1966).

The annual diet of the pine marten includes many mammalian prey species, but martens are restricted seasonally to a few accessible or abundant prey (Grinnell et al., 1937; Marshall, 1946; Cowan and Mackay, 1950; Weckwerth and Hawley, 1962; Francis and Stephenson, 1972; Soutiere, 1979). If each prey species has a unique activity regime and martens benefit from synchronizing their activity with that of their prey, one would expect a considerable amount of annual variation in marten activity. Anecdotal accounts of marten activity patterns are numerous but only More (1978) has quantified activity. His results indicate that activity is indeed highly variable throughout the year. In this paper we describe and discuss the relationship between the food habits and diel activity patterns of the pine marten at Sagehen Creek, California. This work was part of a larger study designed to collect baseline habitat and diet data on a marten population prior to timber harvest. Information on habitat preferences was provided by Spencer (1981).

Study Area and Methods

The study was conducted in the 40-km^2 Sagehen Creek watershed of the Tahoe National Forest, Nevada Co., California. Elevations range from 1,880 to 2,620 m. Summers are short and dry with great diurnal temperature variations; winters are long and nocturnally cold, but often have mid-day temperatures above 0°C. Most of the 91 cm of annual precipitation falls as snow. Average winter snow pack at 1,950 m elevation is 112 cm; pack at higher elevations may be substantially deeper.

South-facing slopes are dominated by Jeffrey pine (*Pinus jeffreyi*) and mixed Jeffrey pine-white fir (*Abies concolor*). Jeffrey pine is replaced by lodgepole pine (*Pinus contorta murrayana*) on the more mesic sites below 2,050 m elevation. Red fir (*Abies magnifica*), mountain hemlock (*Tsuga mertensiana*), and western white pine (*P. monticola*) dominate above 2,050 m. Vegetation in riparian areas consists mainly of lodgepole pine with a dense ground cover of sedges (*Carex* spp.), forbs, and willow shrubs (*Salix* spp.). Large brushfields resulting from wildfire cover a third of the study area.

Fieldwork was conducted from July 1979–September 1980. Fourteen martens (7M:7F) were captured in 20 by 20 by 50-cm live traps (Tomahawk Live Trap Co., Tomahawk, WI 54587) baited with meat scraps, strawberry jam, or fish, and scented with marten lure (S. Stanley Hawbaker and Sons, Fort Loudon, PA 17224). Each animal was immobilized with ketamine-hydrochloride (Vetalar, 100 mg/ml, Parke-Davis, Detroit, MI 48233) combined with acetylpromazine maleate (Acepromazine, 10 mg/ml, Ayerst Laboratories, Inc., New York, NY 10001). Six martens (2M:4F) were fitted with 148-Mhz radio-transmitter collars (SB2, AVM Instrument Co., Dublin, CA 94566). The 26 g collars were 2–4 percent of the marten weights. Animals were monitored via Telonics receivers (Telonics Inc., Mesa AZ 85201).

Marten activity was monitored by recording signal variations due to movements of the animals (Sunquist and Montgomery, 1973). Most observations were from special activity monitoring sessions during which activity was recorded at 30-min intervals at one of a series of 8-element Yagi antennas (Hy-gain Electronics Corp., Lincoln, NE 68504) mounted on 6-m masts or on a 30-m communication tower located at the field station headquarters. On several occasions observations were made on foot using a 2-element Yagi antenna. These monitoring sessions were selected largely by convenience and their duration varied, but rarely exceeded 24 h. Weather data were recorded at the antenna site. Daily activity data for all individuals were pooled into 12, 2-h periods for each 2-month period of the year. Activity was defined as the percentage of observations that indicated movement.

Marten food habits were investigated by identifying scat contents. Scats were collected from trapped animals, at frequently used resting sites, and in "cubbies" erected on trees to record marten visitations (Spencer, 1981). Deposition dates were estimated and recorded for five time periods: (number of items/number of scats in parentheses), 1 December–1 March (138/91); 2 March–25 April (96/61); 26 April–1 July (125/76); 2 July–1 September (59/25); 2 September–30 November (84/47), total (502/300). Scats were processed and contents identified according to standard techniques (Korschgen, 1980).

After identification, the volumetric contribution of each item was estimated visually and these proportions multiplied by the scat volume and weight to determine relative proportions of items by volume and weight respectively. Frequency of occurrence also was recorded. Each of these indices was compared with results based on estimations of actual weight of prey eaten as calculated from feeding trials with a related mustelid, the European ferret (*Mustela furo*) (Zielinski, 1981). Because analysis of remains by percent volume of scat correlated most closely with the actual weight of prey eaten by the ferret, this method of analysis was used to describe the marten diet.

RESULTS

Food Habits

Thirty-six different food items were identified in 300 scats. Mammals were the most important foods, contributing most to the diet during the winter (Fig. 1). Human refuse, birds, insects and vegetable foods were more variable and far less important items. Rodents comprised the bulk of the mammalian prey, microtines being the most common item (Table 1). Because their remains were indistinguishable, the montane vole (*Microtus montanus*), the long-tailed vole (*M. longicaudus*), and the heather vole (*Phenacomys intermedius*) were grouped to form the microtine rodent category. The use of voles by martens was not confined to any particular season, but fluctuated throughout the year. The remaining mammalian prey were easily grouped by the season in which they predominated in the marten diet.

Winter foods.—Consumption of chickaree, snowshoe hare, northern flying squirrel, and deer mouse (*Peromyscus maniculatus*) was confined almost exclusively to winter (1 December–25 April). When microtines are included, these species constitute 73.5% of the winter diet. The use of snowshoe hare, flying squirrel, and deer mouse was relatively uniform throughout the period.

Summer foods.—Ground squirrels (golden-mantled ground squirrel, *Spermophilus lateralis*, California ground squirrel, *S. beecheyi*, and Belding ground squirrel, *S. beldingi*) and chipmunks (classified as *Eutmias* spp. since remains were not identifiable to species) formed the largest component of the diet from late spring through fall. These ground-dwelling sciurids made up 49.6% of the total and 70.6% of the mammalian category throughout summer. The two most important prey in this category were golden-mantled ground squirrels and chipmunks.

Remains of birds and insects were most prevalent in the diet during the snow-free period also. Avian remains comprised 8.7% of the spring and summer diet but only 2.7% of winter foods. The incidence and volume of insect remains in fall scats was almost 20 times greater than the average for all other seasons. During this time insects were second in importance only to microtine rodents, with yellow-jackets (*Vespula* sp., Vespidae, Hymenoptera) the only group represented.

Insectivores (shrews, *Sorex* spp., and the broad-handed mole, *Scapanus latimanus*) and pocket gophers (*Thomomys monticola*) were eaten intermittently, primarily during summer.

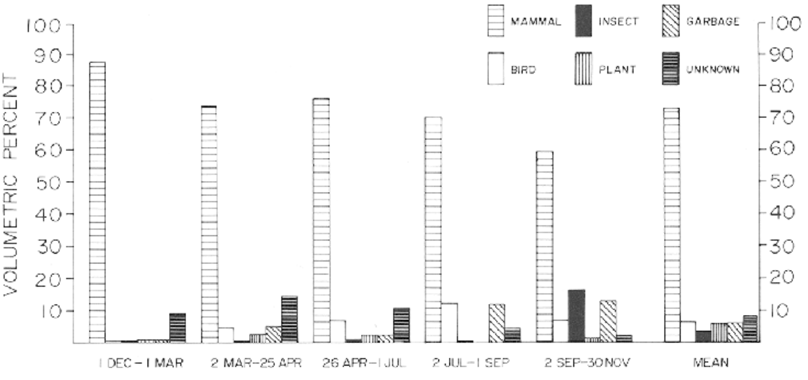

FIG. 1. Major categories of food items of martens arranged by season.

Activity

Six telemetered martens yielded 2,142 activity data points. Activity during the snow-free season (May–December) was strongly diurnal whereas winter activity was largely nocturnal (Fig. 2). Differences among mean level of activity for nocturnal and diurnal periods in each 2-month period are summarized in Table 2.

Total diel activity (diurnal and nocturnal combined) also varied by season. Martens spent a larger percentage of their time hunting and traveling during summer than winter. Total activity in January–February was similar to that in March–April but each of these periods was less than during July–August ($P < 0.05$ and $P < 0.025$ respectively). Diel activity levels in the period May–June could not be distinguished from the periods January–April or July–August.

Although data from all martens were pooled for analysis, activity patterns of individuals also were examined. Where the data were sufficient for comparison, trends in annual activity for individuals appeared similar to those produced by pooling. All individuals were largely diurnal in summer and nocturnal in winter.

Activity appeared unrelated to temperature ($r^2 = 0.29$, $P > 0.05$). Although the intensity of summer activity appeared positively correlated with temperature, winter activity seemed unrelated or often inversely related to temperature (Fig. 3). However, martens generally seemed less active at both extremely high and low temperatures.

DISCUSSION

Food Habits

Martens at Sagehen were euryphagic carnivores, with microtine rodents the most frequent food item. Similar results have been reported in all other studies of marten diets. In those studies that described food habits for an entire year (Cowan and Mackay, 1950; Newby, 1951; Lensink et al., 1955; Francis and Stephenson, 1972; Soutiere, 1979), voles comprised the bulk of the annual diet but decreased during winter due to increasing predation on squirrels and hares. However, results reported here are among few (Marshall, 1946; Hargis, 1981) documenting greater use of chickaree than voles during late winter and early spring. The use of snowshoe hare by martens also is greater than reported in most other studies.

Eutamias and *Spermophilus* were far more important constituents of the summer diet here than elsewhere, perhaps due to the greater diversity and numbers available. Observations of martens stalking and sometimes killing ground squirrels and chipmunks during this period (Zielinski, 1981) substantiate the results from scat analysis. The proportions of the remaining vertebrate foods were not substantially different than reported elsewhere.

TABLE 1.—*Seasonal diets of pine martens at Sagehen Creek 1979–1980, presented as percentage of total volume, weight, and frequency of occurrence in scats.*

	1 Dec–1 Mar			2 Mar–25 April			26 Apr–1 July			2 July–1 Sept			2 Sept–30 Nov			Total		
	Vol.[a]	Wt.[b]	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.
Mammals																		
Microtus spp.	37.4	33.0	26.1	5.2	5.1	5.2	33.2	30.5	19.2	4.5	4.2	6.8	18.3	17.6	14.3	23.5	21.4	16.1
Tamiasciurus douglasii	13.9	16.9	12.3	29.8	29.5	21.9	3.5	3.5	3.2	1.1	1.0	3.4	3.1	3.3	2.4	11.3	11.5	8.1
Spermophilus lateralis				1.8	2.2	1.0	13.9	15.3	10.4	25.2	25.2	18.6	10.9	12.3	7.1	8.3	9.4	5.2
Lepus americanus	18.8	19.1	11.6	10.0	8.2	10.4	0.7	1.0	0.8	1.9	0.1	1.7	0.9	0.7	1.2	7.7	6.9	4.9
Eutamias spp.	2.7	3.2	2.2				8.6	10.2	6.4	18.8	17.9	8.5	3.0	3.1	1.2	5.4	6.2	7.0
Glaucomys sabrinus	5.6	5.2	3.6	13.1	11.1	8.3							2.0	2.1	2.4	4.6	3.8	3.0
Peromyscus maniculatus	8.5	7.6	9.4	7.8	8.4	4.2	1.0	0.8	1.6				2.1	2.4	2.4	4.5	4.2	6.3
Scapanus latimanus				3.2	2.5	3.1	5.0	5.0	3.2	5.9	6.1	6.8	7.2	6.9	2.4	3.5	3.6	2.6
Thomomys monticola	2.3	2.0	2.9				2.1	2.3	2.4	7.2	7.4	3.4	0.2	0.3	1.2	2.0	2.0	2.0
Sorex spp.							4.0	4.3	5.6				3.2	3.2	4.5	1.5	1.7	2.2
Odocoileus hemionus				0.4	0.2	1.0	1.5	0.5	0.8				5.6	5.5	4.8	1.2	1.0	1.2
Spermophilus beldingi										4.7	4.7	1.7				1.0	1.1	0.2
Spermophilus beecheyi				0.5	0.6	2.1				0.9	0.5	1.7	3.0	3.8	2.4	0.2	0.2	1.0
Spermophilus spp.							3.5	3.0	2.4							1.0	1.0	0.6
Marmota flaviventris							0.2	0.1	0.8							0.1	0.1	0.2
Erethizon dorsatum				0.1	0.1	2.1										0.1	0.1	0.4
Homo sapiens (hair)													0.2	0.2	1.7	0.1	0.1	0.2
Martes americana	0.3	0.3	2.2	0.1	0.1	2.1	0.1	0.1	2.4	0.1	0.1	1.7	0.1	0.1	2.4	0.1	0.1	2.2
Birds																		
Unidentified	0.9	1.3	2.2	4.5	4.1	6.3	6.8	5.6	11.2	12.2	11.2	15.3	7.3	8.3	14.3	5.3	5.2	8.8
Fish																		
Unidentified							0.1	0.1	0.8							0.1	0.1	0.2
Insects																		
Hymenoptera																		
Vespidae																		
Vespula sp.													16.5	14.3	15.5			
Formicidae																		
Camponotus sp.										0.2	0.4	4.9						
Coleoptera																		
Nitidulidae	0.1	0.1	2.2															
Scarabidae							0.02	0.02	1.6									
Unknown							0.04	0.04	2.4	0.4	0.8	4.1						

TABLE 1.—*Continued.*

	1 Dec–1 Mar			2 Mar–25 April			26 Apr–1 July			2 July–1 Sept			2 Sept–30 Nov			Total		
	Vol.[a]	Wt.[b]	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.	Vol.	Wt.	F.o.
Nueroptera																		
Corydalidae							0.02	0.02	1.3									
Lepidoptera																		
unknown							0.02	0.02	2.7	0.2	0.4	4.6						
Tricoptera																		
Limnephilidae																		
Psycoglypha bella	0.1	0.1	1.2															
Unknown insect	0.1	0.1	2.4	0.03	0.03	0.1												
Insect total																2.9	2.7	8.0
Vegetable																		
Saxifragaceae																		
Ribes sp.	0.07	0.07	3.2										0.1	0.09	1.8			
Leguminosae																		
Lupinus sp.	0.01	0.01	0.6															
Trifolium sp.	0.02	0.02	0.7															
Polygonaceae																		
Polygonum sp.	0.01	0.01	0.5										0.03	0.03	1.0			
Gramineae																		
Paniceae				0.01	0.01	0.7												
Rosaceae																		
Unidentified													0.04	0.04	1.0			
Rhamnaceae																		
Ceanothus velutinus				0.01	0.02	1.0												
Conifer seed							0.1	0.1	0.4				0.01	0.01	0.6			
Unidentified plant fragments	1.0	1.1	3.0	2.6	2.5	8.7	2.3	2.7	2.6				1.4	1.3	3.8			
Plant total																2.0	2.0	7.6
Human refuse	1.1	1.4	4.3	5.0	5.6	7.3	2.3	2.2	6.4	12.4	15.4	10.2	12.8	12.6	9.5	5.2	5.7	6.0
Unknown	7.2	7.6	8.7	14.5	18.4	13.5	11.0	11.8	6.4	4.5	4.8	5.1	2.1	1.9	3.6	9.1	10.3	6.7

[a] Original data in ml.
[b] Original data in g.

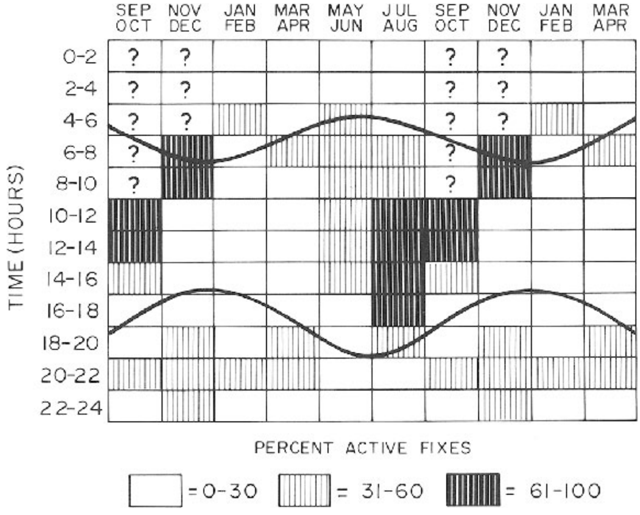

FIG. 2. Diel activity of martens at Sagehen Creek from July 1979–September 1980 (Pacific Standard Time). The four columns on the right duplicate the four on the left and are included for continuity. Undulating lines indicate approximate time of sunrise and sunset and question marks denote cells with insufficient data.

Insects were most important in early fall, with yellow-jackets comprising 98.0% of the total insect volume in scats. These wasps occupy colonial subterranean nests at Sagehen and as their remains were never found singly in scats, martens probably fed upon them at nests. Seeds or plant fragments never exceeded 3.0% of the diet during any season at Sagehen and thus were less important than reported elsewhere.

Marten Foraging Dynamics

The marten's annual diet appears very catholic. However, the diet is better understood as a series of seasonal diets where martens specialize on a few of the many prey available annually. Patterns of specialization on alternative prey seem dependent on the availability of the most frequent prey, voles. For this reason, marten foraging behavior is best described in terms of the use of voles. We suggest that the peaks in vole use that occurred in early winter and late spring can be explained by considering the seasonal availability and net caloric value of the larger alternative prey.

The use of chickarees began to exceed that of voles as winter snows made voles less available. Chickarees became more accessible as they began using terrestrial cone caches and subnivean dens (Layne, 1954; Murie, 1961). Without the necessity for arboreal pursuit, predation on chickarees is probably more energetically rewarding during the winter. Chickarees captured on the ground most likely represent a much greater energy gain per capture than do voles. Studies of captive fishers (*Martes pennanti*) (Davison et al., 1978) and coyotes (*Canis latrans*) (Litvaitis

TABLE 2.—*Percentage of time martens were active* ($\bar{X} \pm$ SE) during diurnal, nocturnal, and diel periods by 2-month periods.

Period[a]	Diurnal	Nocturnal	Total diel
1 Jan–Feb	26.8 ± 2.5	20.2 ± 5.7	23.0 ± 3.4
2 Mar–Apr	19.4 ± 4.5	20.9 ± 4.8	20.2 ± 3.1
3 May–Jun	39.2 ± 4.0	8.9 ± 2.7	29.1 ± 5.0
4 Jul–Aug	53.9 ± 8.6	13.4 ± 1.1	40.4 ± 7.9

[a] Incomplete data set in period Sept–Dec precludes averaging.

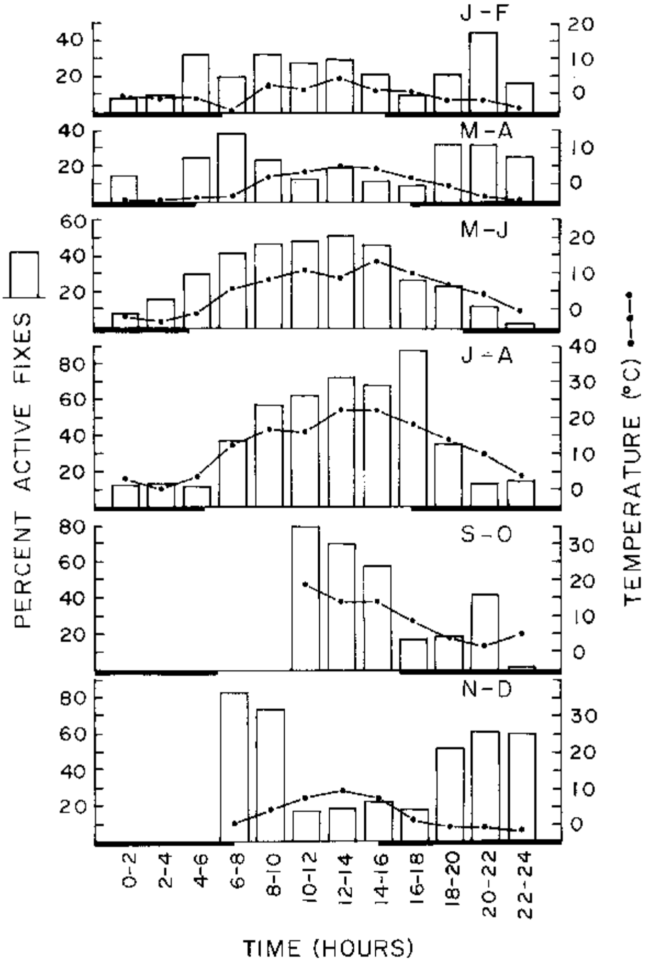

FIG. 3. Relationship between seasonal marten activity and temperature. Bold lines indicate periods of darkness.

and Mautz, 1976) indicated that large prey have higher percentages of digestible protein than do small prey. Snowshoe hares and flying squirrels also were prevalent food. Whether this was a response to poor availability of the preferred voles or a reaction to increased vulnerability of the larger prey is uncertain.

Use of voles by martens increased with the spring snow melt, peaking in late spring–early summer. By mid-summer, ground squirrels and chipmunks had almost completely replaced voles in the diet. We believe that the availability of ground squirrels (particularly the more vulnerable juveniles), overwhelmed the abundance of voles at this time. As with chickarees, once ground squirrels exceeded a threshold of availability they were probably more energetically profitable to martens than were voles.

Activity

Activity patterns are not consistent over the marten's range. Martens have been found to be diurnal in winter and crepuscular in summer (More, 1978), crepuscular throughout the year

(Markley and Bassett, 1942) and nocturnal during winter (Marshall, 1942, this study). However, all authors agreed that total diel activity was greater in summer than winter.

Reduced winter activity by mammalian carnivores is considered an adaptation to cold and food stress and has been noted in ursids, procyonids and mustelids (Ewer, 1973). Captive badgers (*Taxidea taxus*) thermoregulate behaviorally by limiting above ground activity during cold periods (Harlow, 1979). Food was less abundant at high elevations during winter in our study area, air temperatures were colder, and deep snows made travel more difficult. Each of these factors provided energetic reasons to minimize activity. Martens also minimize time spent above the snow surface by resting in subnivean dens during winter (Pullianien, 1980; Spencer, 1981). The thermodynamic advantages of this behavior have been discussed by Formozov (1963).

Reduction in winter activity may also be related to prey size. Chickarees and snowshoe hares (winter diet) both provide more food per capture than do small rodents (summer diet). A marten would probably need to hunt less when feeding upon larger prey. A similar relationship between prey size and amount of activity was suggested by Wakeley (1974) for ferruginous hawks (*Buteo regalis*). Extended occupation of dens by martens (occasionally exceeding 20 h) and food remains discovered in dens suggested that martens at Sagehen may have cached surplus food in dens, as found by Murie (1961).

Relationship of Activity Patterns to Food Habits

Marten activities and ambient temperatures were poorly correlated. During winter, martens were most active when temperatures were coldest. However, most activity during the snow-free period of the year was diurnal when air temperatures were hottest. This behavior appears energetically maladaptive and is contrary to the general trend of predator inactivity during midday in summer (e.g., Farrell and Wood, 1968; Ables, 1969; Schaller, 1972). Equally surprising was the predominance of nocturnal activity during winter when minimum temperatures averaged −10°C. Marten metabolism has not been studied in detail, but evidence from related mustelids indicates that this is well below thermoneutrality (Farrell and Wood, 1968; Davison et al., 1978). Chappell (1980) found that most arctic mammals (the least weasel, *Mustela nivalis*, included) could save an average of 30% of thermoregulatory costs if they were diurnal during winter. More (1978) also believed that winter diurnality of martens in Alberta was best explained in terms of thermoregulatory advantages. If this advantage holds true at Sagehen Creek, martens are not exploiting it.

We suggest that marten activity is not associated with optimal temperature but is roughly synchronized with that of prey. Because prey can be detected more easily when they are active, martens can minimize prey search time if they hunt during prey activity bouts. Prey also may be more vulnerable when active. Martens are diurnal in summer, as are the ground squirrels and chipmunks which represent 70% of the summer diet. Conversely, martens are nocturnal in winter, as are the snowshoe hare, flying squirrel, and deer mouse that represented 51% of the diet at this time (Johnson, 1926; Hatfield, 1940; De Coursey, 1960; Mech et al., 1966). Microtine rodents, which are a very important early winter food, also are chiefly nocturnal during this time (Hatt, 1930; Davis, 1936; Calhoun, 1945).

As a diurnal winter prey item the chickaree is an exception to synchronized predator and prey activity periods. It is possible that chickarees are killed during short diurnal activity bouts, but more compelling evidence suggests that martens are killing chickarees at rest during darkness. During winter chickarees occupy subnivean dens that are often associated with their cone caches (Layne, 1954; Zirul, 1970). Thirty kilometers of snow-tracking at Sagehen has shown that martens focus attention to these sites when foraging (Zielinski, 1981). Spencer (1981) found chickaree middens at 76% of the winter marten dens at Sagehen. Thus, martens may prey upon the squirrels and then occupy their dens. In addition, snow-tracking indicated that arboreal travel by martens was extremely rare (two occasions in 30 km of tracking; Zielinski, 1981) and much less than would be expected if martens were pursuing chickarees through the trees during the day. Others also have suggested that the nocturnal use of subnivean dens by red squirrels

(*Tamiasciurus hudsonicus*) predisposes them to marten predation at this time (de Vos, 1951; Quick, 1955; Murie, 1961). Apparently, the nocturnal activity of marten in winter maximizes contact with hares, flying squirrels, deer mice, and to a lesser degree voles; all of which are active at night, and also maximizes contact with inactive chickarees, which are in subnivean dens.

Despite the burgeoning interest in optimal foraging theory (see Pyke et al., 1977, for review), investigations of optimal time to initiate foraging have been virtually ignored. When to forage seems no less important an optimality decision than where to forage, how long to stay there, or what size and caloric value of prey to select. Martens apparently have optimized foraging time by expressing a flexibility of activity that permits adaptation to prey activity regimes after the prey exceed an availability threshold. Because they exhibit flexibility in their activity patterns and a diversity of hunting techniques (Zielinski, 1981) many of the foods that martens find acceptable also are available to them throughout the year. These characteristics undoubtedly have led to the success of the pine marten as a food generalist at Sagehen Creek.

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Department of Forestry and Resource Management, University of California, Berkeley, CA 94720 (present address of Zielinski: Department of Zoology, North Carolina State University, Raleigh, NC 27650).
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