Ecological Research (1994) 9, 99–107

Comparative analyses on food habits of Japanese marten, Siberian weasel and leopard cat in the Tsushima islands, Japan

MASAYA TATARA AND TERUO DOI

Department of Biology, Faculty of Science, Kyushu University 33, Fukuoka 812, Japan

Food habits of three sympatric carnivore mammals in the Tsushima islands of Japan were studied during 1986–91. Scats of the Tsushima marten (n = 1236), the Siberian weasel (n = 218) and the Tsushima leopard cat (n = 350) were collected monthly and the food items were determined by scat contents analysis. Marten was omnivorous showing a high level of diversity of food throughout the year. The important foods for marten were fruits and berries from spring to autumn, insects in summer and autumn and small mammals all year round. Leopard cat preferred to hunt wood mice and birds, and remained a flesh meat specialist throughout the year. Weasel was intermediate between marten and leopard cat, but was slightly biased towards the flesh meat eater. The three carnivores do not compete against one another for food, except for small rodents. A conflict for food between leopard cat and weasel was suggested to be more intense than that of other combinations based on diet overlapping. Marten may be characterized as an opportunistic generalist. When interspecific competitors existed, or human disturbance to the habitat occurred, the preferential flexibility of the marten to alternative food resources might become more advantageous than the other two species.

Key words: food diversity; leopard cat; scat analysis; Siberian weasel; Tsushima marten.

INTRODUCTION

Twenty-one species of wild mammals live on the Tsushima islands of Japan (Abe & Ishii 1987) and only three species of carnivores, the Tsushima leopard cat (*Felis bengalensis euptilura*), the Siberian weasel (Korean yellow weasel: *Mustela sibirica coreana*) and the Tsushima marten (*Martes melampus tsuensis*) are known there. The Tsushima leopard cat is an insular subspecies of the leopard cat (*F. bengalensis*) which widely inhabits southeast Asia, and the Tsushima marten is also an endemic subspecies of the Japanese marten (*M. melampus*) which has a different pelt color pattern (Abe & Ishii 1987).

Some studies have been made on the natural history and conservation of the leopard cat (Asahi *et al.* 1968; Inoue 1972; Yamaguchi & Urata 1976; Izawa *et al.* 1991) and the marten (Asahi & Okuhama 1971; Urata & Yamaguchi 1976; Tatara 1988; Urata 1991). The Japan Wildlife Research Center (1988) reported historical, ecological and veterinary aspects of the Tsushima leopard cat and proposed some management plans for this endangered species. Tatara and Doi (1991a,b), and Tatara (in press) reported ecological status of the Tsushima marten that contained distribution, home range use, activity pattern, behavior and diet, and proposed conservation plans of the species. However, there was no information on ecology and present status of Siberian weasel on the Tsushima islands.

The three sympatric carnivores in the islands ought to share the food resources as well as spatial and temporal habitats. The genus *Martes*, *Mustela* and *Felis* are generally recognized as flesh meat eaters who hunt vertebrate prey (Gittleman 1989). They may compete for similar prey on the islands of Tsushima. The goal of this study was to determine the diet of each species by the scat analysis and to discuss some ecological features of coexistence by examining diversity and overlapping of each carnivore's food habits.

Received 2 June 1993.
Accepted 10 September 1993.

STUDY AREAS

The Tsushima islands (34°05′–42′N, 129°10′–30′E) are situated in the Korea Strait. They are comprised of two main islands, North and South, and several smaller islands encompassing an area of approximately 708 km^2, of which 89% is mountainous and covered with forests (Fig. 1). Climate is moderately warm, with temperatures ranging from a mean of 4°C in January to a mean of 26°C in August. Little snowfall occurs there. The human population on the islands was approximately 45 600 in 1992.

The distribution range of the Tsushima leopard cat extended over the entire islands a few decades ago, but recently the range has been reduced and scattered, and the high density habitat is restricted to the narrow shore areas facing northwest on the North island (Yoneda & Izawa 1988). The Tsushima marten and the Siberian weasel, on the other hand, are distributed evenly over the two main islands (Tatara 1988; in press).

In this study, we selected two study sites for scats sampling (Fig. 1). The Tanohama district was selected as a main study site, a site which was designated as a protected habitat for the leopard cat by the Japanese Agency of Environment in 1989. The area of the Tanohama district is approximately 20 km^2 and the natural vegetation is dominated by deciduous broad-leaved trees (e.g. *Quercus serrata, Platycarya strobilacea*). In the Tanohama area, approximately 14.2 km of farm roads and pathways were established as scat sampling routes. Additionally, the Mitake region was selected for comparison with the different environmental condition. The Mitake region is a mountainous area located in the central part of the North island and the vegetation consists mainly of primary evergreen forest (dominated by *Quercus acuta*). In the Mitake area, the scat sampling route was approximately 2.8 km of mountaineering trails.

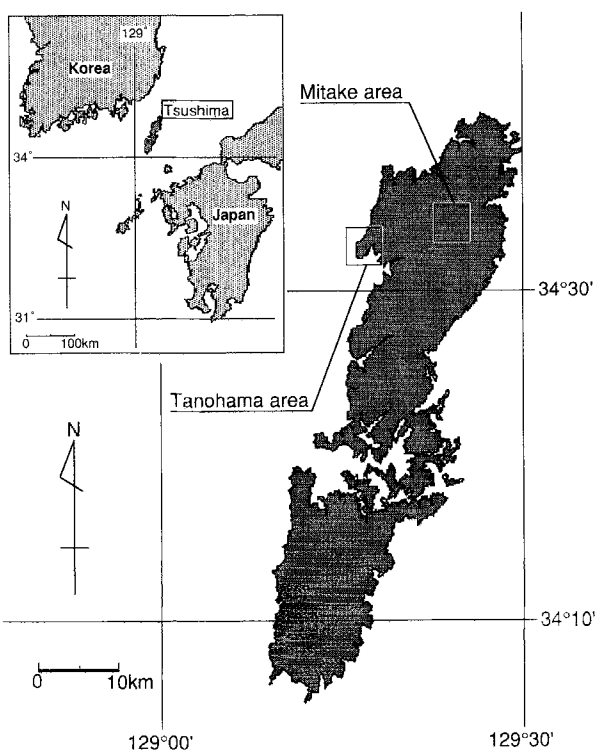

Fig. 1. Location map of the study areas on the islands of Tsushima.

METHODS

Scats of the carnivores were collected along the sampling routes which were approximately 4 m wide. Scats were collected monthly from May 1986 to August 1987 in both study areas, and then eight times at irregular intervals until March 1991 in the Tanohama area.

Leopard cat scats could be easily discriminated from the other two Mustelidae scats by size, shape, colour and smell. Marten and weasel scats could also be discriminated by size and shape, but in cases where they were quite similar in appearance, a conclusive determination was made by the empirical testing of species specific odors of scats. The double-blind test using scats from captive animals of both species under the same food condition was examined, and as a result, a probability of 99.6% (three faults in 800 attempts) was obtained. The old scats that could not be discriminated by odor and which were estimated to be defecated in a previous season were not used as samples for the present analyses.

The collected scats were soaked in water to soften them and washed through a 0.5 mm saran net. Remains were preserved in 80% alcohol for identification. Animal remains were sorted into class levels and if possible identified at species level. Plant materials were sorted to the level of species or genus. The percentage frequency of absolute occurrence of each food item was used to show the year-round diet menus of the three carnivores, and the percentage

frequency of relative occurrence of each food type was used to examine seasonal variations of the food habits. The volume frequency of each item in scats was also estimated to evaluate the importance of the food item. The diversities of foods were calculated according to the Shannon-Weaver's diversity index (H') formula, where p_i is the proportion of food item i in the total diet:

$$H' = -\Sigma(p_i) \ln (p_i) .$$

To determine the overlapping of foods among the three carnivores, we calculated the overlapping index (a_{jk}) according to Pianka (1973), where p_{ij} and p_{ik} are proportions of food item i in the total diet of species j and k, respectively:

$$a_{jk} = \Sigma(p_{ij})(p_{ik})/[(\Sigma p_{ij})^2 (\Sigma p_{ik})^2]^{1/2}.$$

If a large amount of overlapping index value is obtained, it suggests that interspecific competition for food will be intense.

Statistical analysis by means of Student's t-test was employed to determine significant differences in values of H' and a_{jk} indices among the three species in each season and throughout the year. Among H' indices, values of t between the species j and k were calculated according to Pielou (1966), where var(H') is the estimated variance of H' for the sample size n:

$$\text{var}(H') = [\Sigma p_i (\ln p_i)^2 - (H')^2]/n$$

$$t_{j-k} = (H'_j - H'_k)/[\text{var}(H'_j) + \text{var}(H'_k)]^{1/2} .$$

The same methods were applied to calculate the t values among a_{jk} indices. Probability levels of 0.05 and 0.01 were adopted to evaluate the significance of the tests.

RESULTS

Food items and diversity

Total numbers of the collected scats were: 1236 for marten, 350 for leopard cat and 218 for weasel. As the numbers of weasel scats and leopard cat scats collected in the Mitake area were not enough to evaluate the difference between habitats, the samples from both Tanohama and Mitake areas were combined. The difference in food habits between the two areas was examined only for the marten. The identification levels of food items were not the same for the three carnivores because of differences in digestive states. Food items of the three carnivores are listed in Table 1.

In marten diets, mammals, birds and/or their eggs, amphibians and/or their eggs, earthworms, centipedes, spiders and insects appeared as major animal food items in both the Tanohama and Mitake areas. The mammal prey eaten by the marten could not be identified to species level. In the Tanohama area, however, we could find two species of wood mice *Apodemus speciosus* and *Apodemus argenteus*, house mouse *Mus musculus*, rats *Rattus* spp. and some insectivores. The wood mice and the insectivores were also found in the Mitake area. Fish and crustaceans were occasional foods of the marten only in the Tanohama area, but not in the Mitake area. Most plant remains were of fruits and seeds such as *Elaeagnus* spp., *Ficus electa*, *Morus australis*, *Rhus* spp., *Rubus* spp., *Stauntonia hexaphylla* and *Vitis ficifolia* (Table 1). Numbers of both animal and plant items from the Mitake area were fewer than those from the Tanohama area.

The H' value for marten foods was 2.986 in the Tanohama area and 2.675 in the Mitake area (no significant difference was detected, $t = 6.24$, d.f. $= 3$, $P > 0.10$). The H' index of 2.818 for all marten samples was the highest among the three carnivores (Table 2).

In weasel diets, mammals, birds, earthworms, insects and plant fruits were found as major foods. Rodents (mainly house mice *Mus musculus* and wood mice *A. speciosus* and *A. argenteus*) ate a large portion of mammal remains and some insectivores (Soricidae and Talpidae) were also eaten (Table 1). The size of birds eaten by weasel was limited to pigeon size. Other vertebrates were not found. The number of food items identified was fewer than that found in marten scats (Table 1). The year round H' index of 1.869 for weasel diets was between marten and leopard cat H' values but biased slightly toward the latter (Table 2).

In leopard cat diets, small mammals, birds, insects and plant materials were eaten in large amounts. Almost all the mammal remains were rodents, including wood mice, house mice and rats (*Rattus rattus* or *Rattus norvegicus*), but only the remains of one insectivore was found. All the plant remains were Graminoid grass and compared to all food items eaten, plant volume was below 10%, although found in over 90% of the scats. The grass

Table 1 Year-round food items of marten, weasel and leopard cat on the islands of Tsushima, Japan based on scat analysis and expressed as average percentages of absolute occurrence from the scats

Food item / Number of scats	Marten: Tanohama 975	Marten: Mitake 261	Weasel 218	Leopard cat 350
Animal materials				
Mammals total	18.8	23.3	71.5	91.6
Murids	18.3	20.8	41.5	91.6
Insectivores	0.5	2.5	30.0	0.3
Birds*	4.4	6.9	10.8	36.5
Reptiles	0.5	0.0	4.2	9.9
Amphibians*	3.1	2.3	2.4	12.4
Fishes	1.0	0.0	0.0	1.2
Earthworms	9.9	12.9	12.3	0.0
Gastropods	2.5	1.4	0.0	0.0
Crustaceans				
Sesarma haematocheir	2.1	0.0	0.0	0.0
Ligia exotica	5.7	0.0	0.0	0.0
Centipedes				
Scolopendra subspinipes	9.8	16.6	1.2	0.0
Spiders	3.2	1.9	2.1	0.0
Insects total	26.4	36.8	27.6	24.3
Coleoptera				
Harpalidae	3.3	11.7	2.1	0.0
Cicindelidae	1.3	0.0	2.1	0.0
Elateridae†	1.3	1.4	0.0	0.0
Scarabaeidae†	9.4	2.5	6.8	3.6
Silphidae	1.0	0.0	2.4	0.0
Lucanidae	0.3	0.0	0.0	0.0
Orthoptera				
Acridoidae	1.3	0.9	3.6	6.9
Tettigonioidae	0.7	0.0	0.0	4.8
Grylloidae	1.3	1.4	2.1	7.8
Mantodea*	4.5	1.9	0.0	0.0
Odonota	0.3	0.0	0.0	0.0
Hemiptera†	0.5	3.7	2.4	1.2
Hymenoptera	0.0	2.5	0.0	0.0
Lepidoptera†	1.2	10.8	6.1	0.0
Animal total	87.4	102.1	132.1	175.9
Plant materials				
Rosaceae				
Rubus hirsutus	5.3	6.9	8.5	0.0
Rubus parvifolius	4.6	5.1	5.8	0.0
Malus toringo	2.0	0.0	0.0	0.0
Prunus jamasakura	2.6	4.6	4.6	0.0
Elaeagnaceae				
Elaeagnus pungens	2.8	3.7	0.0	0.0
Elaeagnus umbellata	5.3	0.0	0.0	0.0
Elaeagnus spp.	1.1	0.9	0.0	0.0
Moraceae				
Ficus electa	2.5	3.7	3.2	0.0
Morus australis	9.5	12.9	4.6	0.0
Broussonetia kaempferi	7.2	10.1	0.0	0.0
Ebenaceae				
Diospyros kaki	5.1	0.0	0.0	0.0
Theaceae				
Eurya japonica	5.7	4.6	0.0	0.0
*Camellia japonica**	2.5	3.7	0.0	0.0
Anacardiaceae				
Rhus sylvestris	4.9	4.6	2.3	0.0
Rhus trichocarpa	5.4	3.7	1.2	0.0
Caprifoliaceae				
Viburnum erosum	4.9	6.9	3.2	0.0
Lardizabalaceae				
Stauntonia hexaphylla	11.4	12.9	4.6	0.0
Vitaeae				
Vitis ficifolia	4.9	0.0	1.2	0.0
Ampelopsis spp.	6.2	7.4	4.6	0.0
Ulmaceae				
Aphananthe aspera	2.6	2.5	0.0	0.0
Celtis sinensis	3.8	2.5	0.0	0.0
Cephalotaxaceae				
Cephalotaxus hurringtonia	1.1	0.0	0.0	0.0
Other plants‡	8.0	14.5	2.3	78.8
Plant total	109.4	111.2	46.1	78.8

*Including their eggs (or pollens and stamen parts of the flowers); †including their larvae; ‡most of them were leaves of Gramineae grass.

Table 2 Seasonal variations in diversity index (H') and overlapping (a_{jk}) relationships among diets of marten, weasel and leopard cat in Tsushima islands

	Diversity index (H')			Overlapping index (a_{jk})		
	Marten	Weasel	Leopard cat	Marten–Weasel (a_{mw})	Weasel–Leopard cat (a_{wl})	Leopard cat–Marten (a_{lm})
Spring	2.75*	1.55†	1.05‡	2.61**	4.42††	0.81‡‡
Summer	3.45*	2.24†	0.78‡	3.04**	5.05††	0.93‡‡
Autumn	2.67*	1.99†	1.39†	1.98**	4.18††	2.41**
Winter	3.02*	1.61†	1.20‡	2.35**	5.32††	2.22**
Total	2.82*	1.87†	1.26‡	2.54**	4.67††	1.96‡‡

Values in each row with superscripts are significantly different from each other ($P < 0.01$), using Student's t-test.

was considered not to be taken as food but to improve occasional intestinal disorders (Tatara & Doi 1991b). Consequently, the occurrence of the grass from the subsequent analysis of the leopard cat diet was excluded. The H' index for the leopard cat was 1.256 and was the lowest diversity in foods of the three carnivores (Table 2). There were significant differences in the diversity indices of the year round diets among the three species ($t = 5.264$, d.f. = 4, $P < 0.01$).

Seasonal changes of diets

To evaluate seasonal changes in diets for the three carnivores, the samples were divided into four seasons, spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). They were compared as the percentage frequencies of relative occurrences of seasonal food remains identified at class level (Fig. 2a–c).

For marten diets, relative occurrence of small mammal remains comprised a consistent proportion (range 8.2–16.8%; Fig. 2a) throughout the year. Birds and their eggs were eaten from winter to spring with a peak in March (14.6%). Amphibian remains were found frequently in early spring. In February amphibian remains consisted exclusively of small-sized adult *Rana tsushimensis* (9.7%). Insects were found throughout the year, but varied considerably with season. Monthly occurrence rates of insects ranged from a minimum of 10.5% in May to a maximum of 27.8% in August. Centipedes, mostly consisting of large-sized *Scolopendra subspinipes*, were eaten in summer. They were found from April to September with a peak between May and June (16.9–17.4%). Approximately half of marten foods consisted of plant materials throughout the year (38.8–53.9%). The commonest plant remains were berries and seeds occurring most frequently in April (41.0%; e.g. *Rubus hirsutus*, *Elaeagnus pungens*) and in September (47.3%, e.g. *Vitis ficifolia*, *Ficus electa*). Other plant materials showed a consistently low level of relative occurrence and were eaten occasionally, except for winter (17.5%) when pollens and stamen parts of *Camellia japonica* were

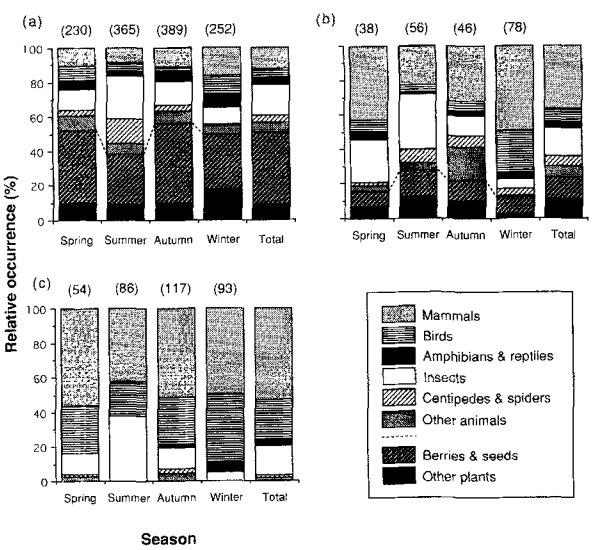

Fig. 2. Seasonal changes in diets of the three carnivores on the islands of Tsushima. (a) Japanese marten; (b) Siberian weasel; (c) leopard cat. Frequencies are expressed as percentage of relative occurrence from the scats collected during 1986–91. Occurrence of grass from the leopard cat's scats was excluded. Numbers in parentheses indicate the numbers of collected and analyzed scats in each season.

eaten selectively. In winter some of the scats were comprised entirely of those items.

For weasel, animal remains occurred more frequently than for marten throughout the year. Small mammals including rodents, shrews and moles were the most common foods for all seasons (22.6–48.9%; Fib. 2b); particularly in winter, small mammals accounted for more than 90% of the scats. Insects were common in spring and summer (24.4–31.8%). Lepidopteran larvae (caterpillars) and Coleopterae were found frequently as insect remains. Birds were commonly eaten in winter (24.5%) with most of them being small-sized perching birds. Other animals such as earthworms were found frequently in autumn (19.8%). Plant materials occurred throughout the seasons (12.8–28.6%) but occurrences were lower in weasel than in marten.

The seasonal change in leopard cat diets was characterized by high relative occurrence of mammal (range 43.1–56.7%; Fig. 2c) and bird remains (18.5–41.2%) throughout the year. Most common mammals were the two species of wood mice. Birds showed some seasonal variations with a peak in winter (41.2%) with most of these consisting of migratory waterfowls (*Anas* spp.). Insects were also dominant food items, but varied quite significantly with seasons from 5.3% in winter to 38.0% in summer. Orthopterae (grasshoppers and crickets) were major insect food items during summer and autumn. Reptiles and amphibians were eaten in autumn (2.2%) and in winter (4.9%) but were negligible for the other two seasons. For both leopard cat and marten, amphibians eaten in winter were small-sized adult *R. tsushimensis*.

Overlapping of food items among the three carnivores

Overlapping indices (a_{jk}) of the three carnivores were calculated to examine for the food segregation among them. Seasonal changes in overlapping relationship among the three species is shown in Table 2. The year round overlapping index between marten foods and weasel foods (a_{mw}), overlapping between weasel and leopard cat (a_{wl}) and that between leopard cat and marten (a_{lm}) were 2.543, 4.667 and 1.962, respectively. The overlapping index for all three combinations was significant ($t = 4.716$, d.f. = 4, $P < 0.01$). Judging from overlapping indices among the three species, the most overlap was found between leopard cat and weasel in winter, and the least overlap between marten and leopard cat in spring (Table 2). As a result, the sympatric three carnivores foraged some of the same foods but showed some degree of segregation for their food habits.

DISCUSSION

The mammal fauna on Tsushima islands is unique compared with the mainland of Japan. Some potential competitors such as raccoon dogs, red foxes and badgers are absent; furthermore, no voles, squirrels or rabbits which are common prey species for the carnivores are present (Abe & Ishii 1987). It might be expected that the food habits of the three carnivores in Tsushima would differ from those in other inhabited ranges. The Siberian weasel on Tsushima islands tended to depend upon small mammals, birds, insects and earthworms for food. The small mammals and birds were important from winter to spring and insects and earthworms were important from summer to autumn. In general, weasels (genus *Mustela*) were recognized to be active hunters and flesh-eating specialists (Gittleman 1989; King 1989). Although the weasel in the islands of Tsushima partly showed general tendencies, it had omnivorous and opportunistic food habits especially in spring and autumn, which might be reflected by increased availability of different sorts of food resources and by reduced relative availability of small mammals caused by overlapped diet with the other sympatric carnivores.

Generally, the wild Felidae in the north temperate and boreal zone mainly depend on small mammals as predominant food resources (Kitchener 1991). The present study on the Tsushima leopard cat would support this general trend. An increase in consumption of waterfowls in winter was also noted. In this season, the abundant waterfowls immigrated into the cat habitat. Throughout the year, the Tsushima leopard cat adhered to being a flesh-meat specialist.

The boreal forest martens, including Eurasian pine marten (*Martes martes*), American marten (*Martes americana*), sable (*Martes zibellina*) and Japanese marten (*Martes melampus*) are recognized as belonging to a taxonomic 'superspecies' (Anderson 1970; Powell 1982). These *Martes* species

appear to be food generalists and reflect the variation, abundance and accessibility of local food types (Brainerd 1990). Mammals are usually the most important and dominant foods for these boreal martens (in North America: Murie 1961; Weckwerth & Hawley 1962; Buskirk & MacDonald 1984; Nagorsen *et al.* 1991; in Europe: Goszczynski 1976; Delibes 1978; Holisova & Obrtel 1982; Moreno *et al.* 1988; Clevenger 1993; in central mountainous part of Japan: Suzuki *et al.* 1977). The diversities of the foods were, however, less than that of the Tsushima marten. The Tsushima marten may become a more generalized and opportunistic forager presumably due to the overlapped food habits with other sympatric carnivores. The high diversity of the diet may be explained by the insularity of the habitat and unique composition of the competitive carnivore community. Clevenger (1993) suggested that insular environment and reduced competition might affect the increased variety of marten diet. As for Tsushima marten, only Siberian weasel and Tsushima leopard cat were possible competitors. Weasel and leopard cat were more biased toward consuming small rodents. Only marten, consequently, could expand its food to 'competitor-free' plant materials in the food resource breadth.

This study considered that the degree of food specialization and food source availability may directly affect the food segregation of the carnivores. Although food availability for each carnivore could not be determined, the food diversity of the three species reflected the degree of specialization for each food. According to the least overlapping of their diets, marten might easily coexist with other two species. On the other hand, weasel and leopard cat might compete with each other for small mammals, especially *Apodemus* species. As the leopard cat is approximately five times larger in body size (male weight) than the weasel, the cat requires more small mammals to maintain bodyweight than the weasel. Consequently, the cat is more affected than the weasel by a decrease in small mammals in the habitat.

Natural habitat in Tsushima islands has been rapidly changing in recent decades. Deciduous broad-leaved forests which are the most important habitat of *Apodemus* species (Doi & Iwamoto 1982) were fragmented and replaced by poor resource conifer plantations. Population of the leopard cat rapidly declined and recently is estimated to be less than 130 (Yoneda & Izawa 1988), but the marten population is presumed to have less of a reduction than the cat (Tatara unpubl. data). In the late 1960s, leopard cat ate small mammals, insects and birds at frequencies of 47, 20 and 22%, respectively (Inoue 1972). The same tendency has been reported by Sukigara *et al.* (1988) and in the present results. Feeding habits of the leopard cat appear to be unchanged in the past two decades. With human disturbances of its habitat the Tsushima leopard cat population will decline as a result. In the case of marten its diets in the late 1960s to early 1970s was a little different from current results in this study. Marten foraged more insects in summer (36%), more plants in winter (65%) and fewer mammals (5%) throughout the year (Asahi & Okuhama 1971). The feeding habits of marten as generalist and opportunist may enable them to adapt to the habitat disturbances.

In the present study, an ordinary method of scat analysis (particularly the frequency of occurrence) was used which might reflect over- or underestimates in determining the food habits of the carnivores (Uraguchi *et al.* 1987; Kitchener 1991). Temporal and spatial use of other life requisites needs to be investigated to describe other interspecific relationships (Emmons 1987). Further ecological and behavioral studies would be required to determine mechanisms and factors that enable the coexistence of these sympatric carnivores in the islands.

ACKNOWLEDGEMENTS

Special thanks to Y. Ono and other members of the Department of Biology, Kyushu University for their support and critical advice on our study. Valuable review comments were received from M. Izawa, Department of Biology, University of Ryukyus. The Japan Wildlife Research Center partly assisted the survey on scats collection. We thank the people of the Tsushima islands for their kindness and helpfulness during our field work. This study was partly supported by a Grant-in-Aid for Scientific Research (Nos 03804053 and 05454615), and by Studies for Natural Monuments in Tsushima (1988–90) from the Ministry of Education, Science and Culture, Japan.

REFERENCES

ABE H. & ISHII N. (1987) Mammals of Tsushima Island. In: *Bio-geography of the Tsushima Island*. (ed. Nagasaki Prf.) pp. 79–109 (in Japanese with English summary).

ANDERSON E. (1970) Quaternary evolution of the genus *Martes* (Carnivore, Mustelidae), *Acta Zoologica Fennica* **130**: 1–133.

ASAHI M., INOUE T., UENO Y., YAMAMOTO K. & OKUHAMA A. (1968) Small mammals in Tsushima, in relation to food habits of leopard cat. *Bulletin of Mukogawa Women's University* **16**: 19–23 (in Japanese with English summary).

ASAHI M. & OKUHAMA A. (1971) Food habit of Tsushima marten *Martes melampus tsuensis*, analyzed from their scats. *Bulletin of Mukogawa Women's University* **19**: 1–9 (in Japanese with English summary).

BRAINERD S. M. (1990) The pine marten and forest fragmentation: a review and general hypothesis. *Transactions of the International Game Biologist Congress* **19**: 421–434.

BUSKIRK S. W. & MACDONALD S. O. (1984) Food habits of marten in south-central Alaska. *Canadian Journal of Zoology* **62**: 944–950.

CLEVENGER A. P. (1993) Pine marten (*Martes martes* Linné, 1758) comparative feeding ecology in an island and mainland population of Spain. *Zeitschrift für Säugetierkunde*. **58**: 212–224.

DELIBES M. (1978) Feeding habits of the stone marten, *Martes foina* (Erxleben, 1777), in northern Burgos, Spain. *Zeitschrift für Säugetierkunde* **43**: 282–288.

DOI T. & IWAMOTO T. (1982) Local distribution of two species of *Apodemus* in Kyushu. *Researches on Population Ecology* **24**: 110–122.

EMMONS L. H. (1987) Comparative feeding ecology of fields in a neo-tropical rainforest. *Behavioral Ecology and Sociobiology* **20**: 271–283.

GITTLEMAN J. L. (1989) Carnivore group living: comparative trends. In: *Carnivore. Behavior, Ecology and Evolution* (ed. J. L. Gittleman) pp. 183–207. Chapman and Hall, London.

GOSZCZYNSKI J. (1976) Composition of the food of martens. *Acta Theriologica* **21**: 527–534.

HOLISOVA V. & OBRTEL R. (1982) Scat analytical data on the diet of urban stone martens, *Martes foina* (Mustelidae, Mammalia). *Folia Zoologica* **31**: 21–30.

INOUE T. (1972) The food habit of the Tsushima leopard cat, *Felis bengalensis* sp., analyzed from their scats. *Journal of the Mammalogical Society of Japan* **5**: 155–169 (in Japanese with English summary).

IZAWA M., DOI T. & ONO Y. (1991) Ecological study on the two species of Felidae in Japan. In: *Wildlife Conservation* (eds N. Maruyama, B. Bobek, Y. Ono, W. Regelin, L. Bartos & P.R. Ratcliffe) pp. 141–143. Japan Wildlife Research Center, Tokyo.

JAPAN WILDLIFE RESEARCH CENTER (1988) *Research Report on Environmental Habitat of the Tsushima Leopard Cat*. Japan Wildlife Research Center, Tokyo. 106 pp. (in Japanese).

KING C. M. (1989) The advantages and disadvantages of small size to weasels, *Mustela* species. In: *Carnivore. Behavior, Ecology, and Evolution* (ed. J. L. Gittleman) pp. 302–334. Chapman and Hall, London.

KITCHENER A. (1991) *The Natural History of the Wild Cats*. Christopher Helm. London. 280 pp.

MORENO S., RODRÍGEZ A. & DELIBES M. (1988) Summer foods of the pine marten (*Martes martes*) in Majorca and Minorca, Balearic Islands. *Mammalia* **52**: 289–291.

MURIE A. (1961) Some food habits of the marten. *Journal of Mammalogy* **42**: 516–521.

NAGORSEN D. W., CAMPBELL R. W. & GIANNICO G. R. (1991) Winter food habits of marten, *Martes americana*, on the Queen Charlotte Islands. *Canadian Field Naturalist* **105**: 55–59.

PIANKA E. R. (1973) The structure of lizard communities. *Annual Review of Ecology and Systematics* **4**: 53–74.

PIELOU E. C. (1966) The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**: 131–144.

POWELL R. A. (1982) *The Fisher: Life History, Ecology, and Behavior*. University of Minnesota Press, Minneapolis. 217 pp.

SUKIGARA S., YONEDA M. & IZAWA M. (1988) Food habits investigation of the Tsushima leopard cat. In: *Research Report on Environmental Habitat of the Tsushima Leopard Cat*. pp. 79–82. Japan Wildlife Research Center, Tokyo (in Japanese).

SUZUKI S., MIYAO T., NISHIZAWA T. & TAKADA Y. (1977) Studies on mammals of the Mt Kiso-komagatake, Central Japan Alps. III. Food habit of the Japanese marten in upper part of low and in sub-high mountainous zone on eastern slope of the Kiso-komagatake. *The Journal of Faculty of Agriculture, Shinshu University* **14**: 147–176 (in Japanese with English summary).

TATARA M. (1988) Home range utilization and food habits of the Tsushima marten *Martes melampus tsuensis* (Mammalia, Mustelidae). Unpublished MSc thesis, Department of Biology, Kyushu University.

TATARA M. (in press) Ecology and conservation status of Tsushima martens, *Martes melampus tsuensis*. In: *Martens, Sables, and Fishers: Biology and Conservation* (eds S. W. Buskirk, A. S. Harestad, M. G. Raphael & R. A. Powell) Cornell University Press, Ithaca, New York.

TATARA M. & DOI T. (1991a). The present ecological status of the Tsushima marten. In: *Wildlife Conservation* (eds N. Maruyama, B. Bobek, Y. Ono, W. Regelin, L. Bartos & P. R. Ratcliffe) pp. 144–147. Japan Wildlife Research Center, Tokyo.

TATARA M. & DOI T. (1991b) The Tsushima marten. In: *Reports of Studies for the Natural Monuments in Tsushima*. pp. 105–126. Nagasaki prf. miscellaneous reports (in Japanese).

URAGUCHI K., SAITOH T., KONDOH N. & ABE H. (1987) Food habits of the feral mink (*Mustela vison* Schreber) in Hokkaido. *Journal of the Mammalogical Society of Japan* 12: 57–647.

URATA A. (1991) Ecology of the Tsushima marten. *Transactions of the Nagasaki Biological Society* **38/39**: 73–83 (in Japanese).

URATA A. & YAMAGUCHI T. (1976) Mammals in Tsushima. In: *Life in Tsushima*. pp. 155–166. Nagasaki Biological Society, Nagasaki (in Japanese).

WECKWERTH R. P. & HAWLEY V. D. (1962) Marten food habits and population fluctuations in Montana. *Journal of Wildlife Management* **26**: 55–74.

YAMAGUCHI T. & URATA A. (1976) The Tsushima leopard cat. In: *Life in Tsushima*. pp. 167–179. Nagasaki Biological Society, Nagasaki (in Japanese).

YONEDA M. & IZAWA M. (1988) Density and number of the Tsushima leopard cat. In: *Research report on Environmental Habitat of the Tsushima Leopard Cat*. pp. 76–78. Japan Wildlife Research Center, Tokyo (in Japanese).