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RESEARCH PAPER

Utilization of cultivated fruits by Japanese martens and red foxes in a snowy environment: a comparison of feeding habits between rural and forest landscapes

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Abstract. Cultivated fruits can serve as an important winter food resource for medium-sized carnivores in rural areas that experience heavy snowfall. However, studies on the food analysis of medium-sized carnivores in heavy snowfall areas, particularly on the use of cultivated fruits, are limited. We evaluated the use of cultivated fruits by medium-sized carnivores during winter in a heavy snowfall area by comparing their feeding habits in rural and forest landscapes. We conducted faecal analysis of Japanese martens (*Martes melampus*) and red foxes (*Vulpes vulpes*) in rural and forest landscapes in north-eastern Japan during periods of snow cover. Based on a faecal analysis in the rural landscape, both Japanese martens and red foxes consumed mammals, birds, fruits, and other plant material. In the forest landscape, mammals and insects were consumed by Japanese martens and mammals, fruits, and other plant material were consumed by red foxes. Our results showed that cultivated fruits, such as persimmons and apples, were a major food source in snowy environments, suggesting a wider range of available resources and overlapping feeding habits. It has been suggested that red foxes in forest landscapes move long distances (several kilometres) to consume cultivated fruits. This study suggests that cultivated fruits may also indirectly feed wildlife, even in areas with heavy snowfall.

Key words: carnivores, cool-temperate zone, diet, feeding ecology, wildlife management, winter ecology

Introduction

An increase in agricultural activities significantly impacts wildlife ecology. Wildlife changes habitat use, foraging behaviour, and activity patterns to avoid human agricultural activities (Kuijper et al. 2016). However, the artificial introduction of crops and garbage can serve as food resources for wildlife (Reshamwala et al. 2018). The use of anthropogenic food resources causes behavioural modifications, such as habituation and alterations to population dynamics, making it easier for animals to invade human habitats (Goldyn et al. 2003). When wildlife is no longer afraid of humans, human-wildlife conflicts, such as crop damage and injuries, may increase (Herrero et al. 2005, Honda et al. 2019). To reduce the frequency of human-wildlife conflicts, it is necessary to clarify the food resource used by wildlife in rural areas.

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Many medium-sized carnivores are omnivorous, foraging various food resources, such as small mammals, insects, and fruits, depending on the environment and season (Ohdachi et al. 2015). In general, the availability of food items is limited in winter (Tsuji et al. 2019, Hisano et al. 2022). Lower winter temperatures lead to a significant decrease in food resources for carnivores, especially in cool temperate zones (Tsukada & Nonaka 1996). For example, insects, amphibians, and reptiles, which are often consumed by medium-sized carnivores, are rarely active at cold temperatures, making them difficult to catch (Yamagishi 1990). Earthworms also decrease in dominance and population density during the cold-temperate winter (Makoto & Kawakami 2019). It has been reported that the use of anthropogenic food resources (e.g. garbage, crops, and poultry) by medium-sized carnivores increased during winter (Misawa 1979, Yagami & Mizuno 1986, Sasaki & Kawabata 1994). However, it is important to examine how medium-sized carnivores utilize artificial food resources for reducing the human-wildlife conflicts.

Rural landscapes with numerous orchards and croplands provide easy access to farmland-derived anthropogenic food resources for medium-sized carnivores. In addition, fruit trees are often planted as garden trees in rural landscapes (Taira & Kawamura 2002, Lanszki 2003, Czernik et al. 2016), facilitating access to food resources other than farmland. In winter, leftover and discarded fruits may play an important role as a food resource because cultivated fruits are highly nutritious, making it an energy-efficient acquisition; abundant as a resource; and continuously available for long periods (Ishikawa 2017, Kozakai et al. 2018, 2019, Lanszki et al. 2019). Since cultivated fruits may promote the dependence of animals on them as a high-quality food source, it is necessary to evaluate their use as a food resource for reducing the human-wildlife conflicts in rural areas.

In cool temperate zones, winter brings colder temperatures and heavy snow to some areas. Previous studies have indicated that snow cover limits the foraging behaviour of carnivores and reduces foraging efficiency (Yagami & Mizuno 1986, Willebrand et al. 2017, Mustonen & Nieminen 2018). It is expected that snow cover will limit cultivated fruit use; however, there are examples of their use in snowy environments. Martens dug out cultivated fruits such as persimmons and apples buried in the snow (Ōtsu 1972, Czernik et al. 2016). Similarly, red foxes (*Vulpes vulpes*) dug up fruit of the hardy kiwi (*Actinidia arguta*) out of the snow and continued consuming them during the winter (Tsukada 1997). Cultivated fruits, therefore, might serve as an important winter food resource in rural areas with heavy snowfall. However, there are few studies on the food analysis of medium-sized carnivores in heavy snowfall areas, particularly on their consumption of cultivated fruits.

Here, we evaluated the use of cultivated fruits during winter in a heavy snowfall area in north-eastern Japan by comparing the feeding habits of medium-sized carnivores in rural and forest landscapes. We hypothesized that medium-sized carnivores would consume more cultivated fruits in rural landscapes than in forested landscapes in a snowy environment. If cultivated fruit is heavily used as a winter food resource by carnivores, we predicted that 1) the dietary niche breadth will be narrower in rural landscapes than in forest landscapes, and 2) the dietary similarity between carnivore species will be higher in rural landscapes than in forest landscapes. To examine these predictions, we focused on Japanese martens (*Martes melampus*) and red foxes, which are abundant in the study area (Watabe et al. 2020). Japanese martens and red foxes are omnivorous, consuming both animals and plants (Ohdachi et al. 2015). They are relatively active during the snow season (Watabe & Saito 2021), making them suitable targets for this study. We clarify the feeding habitats of Japanese martens and red foxes in rural and forest landscapes using faecal analysis and discuss the possibility of dependence on anthropogenic food resources in snowy environments, especially in terms of the use of cultivated fruits. Because red foxes and genus *Martes* individuals are widespread in the Northern Hemisphere, our results could be beneficial findings for wildlife management in other regions.

Material and Methods

Study area

This study was conducted in rural and forest landscapes in Tsuruoka City, north-eastern Japan, a cool temperate region. The study area for the rural landscape is around Nishiaraya (38° 65′ N, 139° 82′ E), approximately 250 m above sea level (Fig. 1). The area's climate is an average annual temperature is 13.5 °C, annual precipitation of 1,992 mm, and maximum snow depth of 150-200 cm (Japan Meteorological Agency 2022). The human population around Nishiaraya is approximately 500, and there are forests, rice paddies, fields, and orchards in the area. Forest roads were established in forested areas. The forest landscape utilized the area around

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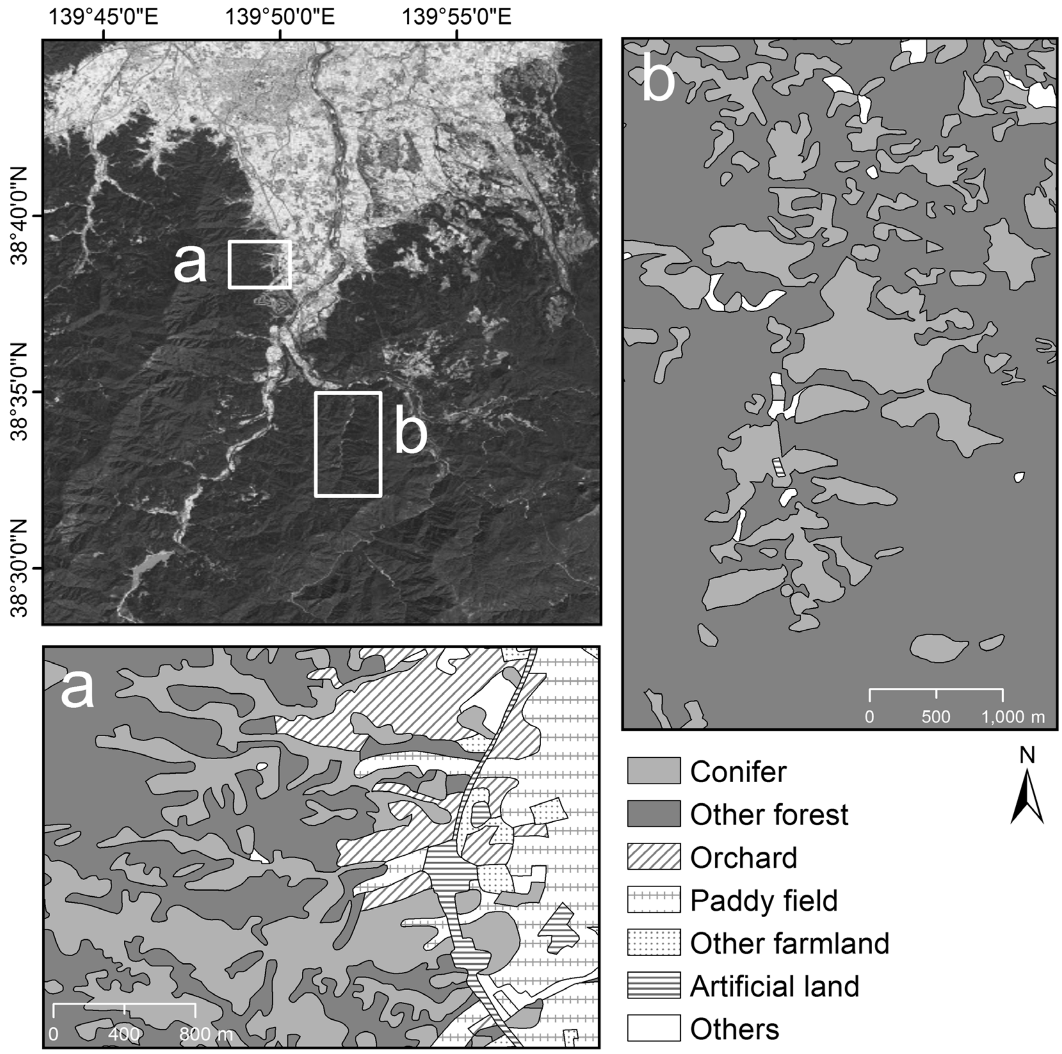

Fig. 1. Location of the study area and land use maps in rural (a) and forest (b) landscapes. The satellite image used data from the geospatial information authority of Japan. Land use data was prepared using a 1/25000 vegetation map by the Ministry of the Environment.

the Kaminagawa Experimental Forest of Yamagata University (38° 55′ N, 139° 86′ E) at an elevation of 200-410 m (Fig. 1). The climate in this region has an annual mean temperature of 10.3 °C, annual precipitation of 3,500 mm, and maximum snow depth of 200-300 cm (unpublished meteorological observation data for 2021 at the Kaminagawa Experimental Forest). An administrative building was used for management activities, but the area is otherwise uninhabited. There are settlements and farmland near the entrance to the forest, and Japanese martens and red foxes may use anthropogenic food resources in the vicinity. Therefore, the study area was chosen to be at least 1 km from the edge of the settlement to reduce the impact of anthropogenic food resources. The forest vegetation in both study areas consisted of planted forests of Japanese cedar (*Cryptomeria japonica*) and broad-leaved forests of mainly Japanese beeches (*Fagus crenata*) and Japanese oaks (*Quercus crispula*).

Faecal sampling

We collected faecal samples during snow cover from late December 2020 to early April 2021. We searched for scats within each landscape and collected one scat per individual from the snow. We did not collect scats on the ground, as they could have been excreted before the snowfall. We identified the species based on their track, size, and shape (Tsuji et al. 2011, Hisano et al. 2017). We excluded samples that were difficult to identify at species level (e.g. collapsed) from faecal analysis. The collected faecal samples were stored at about –20 °C until analysis.

Faecal analysis

We analysed the scats using the hand sorting method (Fukue et al. 2011). Frozen faecal samples were thawed, washed with water and strained using a 0.5-1 mm mesh sieve. The remains were classified into the following categories using visual observation

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or a stereomicroscope: mammals, birds, reptiles, insects, gastropods, other animal materials, seeds, fruit flesh, leaves, barks, other plant materials, artificial materials and unknown materials. After classification, each item was dried at 60 °C or 70 °C for 48 h using a drying oven (DY300, Yamato Scientific Co., Ltd., Tokyo). Each item's dry weight (g) was measured to four decimal places using a precision balance (GX-224A, A&D Company, Limited, Tokyo). Seeds were identified to the species level according to Suzuki et al. (2012), Kominami et al. (2016), and reference specimens collected by the authors. Based on this identification, the seeds were classified into four categories: cultivated fruits, wild fruits, conifers, and unknown.

To evaluate the feeding habits of Japanese martens and red foxes, we calculated the frequency of occurrence (FO), relative frequency of occurrence (RFO), and percentage of dry weight (PDW) of each food item, according to Fukue et al. (2011) and Okawara et al. (2020).

FO (%) = (number of scats containing food category/ total number of scats) × 100
RFO (%) = (number of scats containing food category A/sum of the number of food categories in a scat) × 100
PDW (mean ± SD, %) = {Σ [dry weight of food category A in a scat i/total dry weight of a scat i]/total number of scats} × 100

Data analysis

We used R 4.1.1 (R Core Team 2021) for all statistical analyses. To compare feeding habitats between landscapes and species, we performed Fisher's exact test using FO and the Wilcoxon rank sum test using PDW for each food category.

To examine the dietary niche breadth of each species in each landscape, we calculated Levins' measure B (Krebs 2014) from RFO and PDW.

$$B = 1/\Sigma\, p^2_i$$

where p is the RFO or PDW of food category i.

To measure the similarity of feeding habits between landscapes in each species and between species in each landscape, we calculated Pianka's α index (Pianka 1973) from RFO and PDW.

$$\alpha = [\Sigma\, (p1_i \times p2_i)]/\{[\Sigma\, (p1_i)^2]^{1/2} \times [\Sigma\, (p2_i)^2]^{1/2}\}$$

where p1 is the RFO or PDW of food category i for species 1 or landscape 1, and p2 is the RFO or PDW of food category i for species 2 or landscape 2.

As mentioned above, faecal samples were collected at a distance of approximately 1 km or more from settlements and farmland in the study area of the forest landscape. However, according to the home range sizes (Japanese marten 0.7-2.3 km^2, red fox 1-8 km^2; Ohdachi et al. 2015) and seed dispersal distance by foxes and martens (approximately 500-1,300 m; Hovstad et al. 2009, González-Varo et al. 2013, Tsuji et al. 2016), we cannot completely exclude the possibility that they were consuming cultivated fruit. Therefore, we investigated the distance (m) from the nearest settlement or farmland to the location of the scats occurred persimmon seeds in the forest landscape.

Results

Faecal analysis

We collected 35 Japanese marten and 32 red fox scats from the rural landscape, and 37 Japanese marten and 20 red fox scats from the forest landscape. Two samples of Japanese martens in the forest landscape were excluded from the calculation of PDW because the dry weight of the remains after washing was less than 0.0001 g.

According to the FO and RFO of each food category, mammals, birds, insects, seeds, fruit flesh, and other plant materials frequently appeared in the scats of Japanese martens and red foxes in the rural landscape (Table 1). The PDW for each food category showed that mammals, birds, fruit flesh, and other plant materials were high in both Japanese martens and red fox scats in the rural landscape (Table 1). According to the FO and RFO of each food category, mammals, insects, seeds, leaves and other plant materials frequently occurred in the scats of Japanese martens in the forest landscape (Table 1). The PDW of each food category showed that mammals, insects, and other plant materials were high in the scats of Japanese martens in the forest landscape (Table 1). FO and RFO of each food category of red foxes in the forest landscape showed that mammals, seeds, fleshes, leaves, and other plant materials occurred at high frequencies in the scats (Table 1). The PDW of each food category showed that mammals, birds, fleshes, and other plant materials were high in the scats of red foxes in the forest landscape (Table 1).

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Table 1. Frequency of occurrence (FO, %), relative frequency of occurrence (RFO, %), and percentage of dry weight (PDW, mean ± SD, %) of each food item, and dietary niche breadth (Levins' measure B) based on Japanese marten and red fox faecal samples in rural and forest landscapes. Two samples of Japanese martens in the forest landscape were excluded from the calculation of PDW because the dry weight of the remains after washing was less than 0.0001 g.

Food category	Rural landscape (around Nishiaraya)						Forest landscape (around the Kaminagawa Experimental Forest)					
	Japanese marten			Red fox			Japanese marten			Red fox		
	FO	RFO	PDW	FO	RFO	PDW	FO	RFO	PDW	FO	RFO	PDW
	n = 35	n = 35	n = 35	n = 32	n = 32	n = 32	n = 37	n = 37	n = 35	n = 20	n = 20	n = 20
Animal materials												
Mammals	37.1	10.1	16.4 ± 0.3	37.5	8.5	14.4 ± 0.3	75.7	21.2	58.3 ± 0.4	60.0	13.2	13.6 ± 0.2
Birds	34.3	9.3	6.2 ± 0.1	53.1	12.0	9.0 ± 0.2	18.9	5.3	2.2 ± 0.1	20.0	4.4	7.6 ± 0.2
Reptiles	0.0	0.0	0.0 ± 0.0	0.0	0.0	0.0 ± 0.0	2.7	0.8	2.8 ± 0.2	0.0	0.0	0.0 ± 0.0
Insects	37.1	10.1	7.1 ± 0.2	25.0	5.6	3.0 ± 0.1	48.6	13.6	10.4 ± 0.2	15.0	3.3	0.7 ± 0.0
Gastropods	0.0	0.0	0.0 ± 0.0	3.1	0.7	0.1 ± 0.0	5.4	1.5	0.9 ± 0.0	0.0	0.0	0.0 ± 0.0
Other animal materials	8.6	2.3	0.3 ± 0.0	6.3	1.4	2.2 ± 0.1	0.0	0.0	0.5 ± 0.0	5.0	1.1	1.9 ± 0.1
Plant materials												
Seeds	60.0	16.3	2.6 ± 0.0	81.3	18.3	2.9 ± 0.1	35.1	9.8	0.7 ± 0.0	95.0	20.9	1.4 ± 0.0
Fruit flesh	74.3	20.2	45.5 ± 0.4	87.5	19.7	37.5 ± 0.3	8.1	2.3	2.0 ± 0.1	75.0	16.5	24.4 ± 0.3
Leaves	14.3	3.9	0.7 ± 0.0	34.4	7.7	3.4 ± 0.2	40.5	11.4	1.5 ± 0.0	50.0	11.0	0.3 ± 0.0
Barks	5.7	1.6	0.2 ± 0.0	0.0	0.0	0.0 ± 0.0	5.4	1.5	0.1 ± 0.0	10.0	2.2	0.2 ± 0.0
Other plant materials	82.9	22.5	18.0 ± 0.2	93.8	21.1	27.4 ± 0.3	89.2	25.0	16.3 ± 0.3	100.0	22.0	45.0 ± 0.3
Artificial materials	5.7	1.6	0.0 ± 0.0	9.4	2.1	0.0 ± 0.0	0.0	0.0	0.0 ± 0.0	0.0	0.0	0.0 ± 0.0
Unknown	8.6	2.3	2.9 + 0.2	12.5	2.8	0.1 ± 0.0	27.0	7.6	4.4 ± 0.1	25.5	5.5	5.0 ± 0.2
Dietary niche breadth B	-	6.72	3.62	-	6.76	4.04	-	6.56	2.64	-	6.57	3.84

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Comparison of the feeding habits between landscapes in each species

Comparing the use of each food item by Japanese martens between landscapes, fruit flesh was significantly more abundant in samples from the rural landscape ($P < 0.05$), while mammals and leaves were significantly more abundant in samples from the forest landscape ($P < 0.05$) for both FO and PDW. Seeds were significantly greater in the PDW of samples from the rural landscape ($P < 0.05$). No significant differences were found for the other food items consumed by the Japanese martens ($P \geq 0.05$). For red foxes in the forest landscape, the FO of birds was significantly more abundant ($P < 0.05$). Other plant materials and unknown materials were significantly more abundant in PDW in samples from the forest landscape ($P < 0.05$), indicating significant differences among different food items consumed by Japanese martens.

Comparison of the feeding habits between species in each landscape

Interspecific comparisons in the rural landscape showed no significant difference in food items for either FO or PDW ($P \geq 0.05$). In the interspecific comparison of the FO for each food item in samples from the forest landscape, insects were significantly more abundant in Japanese martens ($P < 0.05$), and seeds and fruit flesh were significantly more abundant in samples from red foxes ($P < 0.05$). There were no significant interspecific differences in the FO of the other food items in the forest landscape ($P \geq 0.05$). For the PDW of each food item, mammals and insects were significantly more abundant in samples from Japanese martens ($P < 0.05$). Seeds, fruit flesh, and other plant materials were significantly more abundant in samples from red foxes in the forest landscape ($P < 0.05$).

Occurrence of seeds

The seeds occurring in the two landscapes were persimmons, apples, grapes (cultivar), kiwifruits, *Stachyurus praecox*, *Rhus javanica*, Japanese cedar, Japanese cypress (*Chamaecyparis obtuse*), and unknown (Table 2). Persimmons, apples, grapes, and kiwifruits were classified as cultivated fruits; *S. praecox* and *R. javanica* as wild fruits; Japanese cedar and Japanese cypress as conifers; and unknown as others. Cultivated fruit seeds appeared more frequently in the scats of Japanese martens in the rural landscape and in red foxes in the rural and forest landscapes. The FO of persimmons was particularly high (Table 2). Conifer seeds were abundant in both landscapes and both species (Table 2).

In the forest landscape, the range of distances from the nearest settlement or farmland to the location where scats were samples was 914-5,124 m for Japanese martens and 1,279-4,741 m for red foxes. The location of scats containing persimmon seeds from the nearest settlement or farmland in the forest landscape was 4,084 m for Japanese martens and 1,917, 2,034, 2,744, 2,785, and 4,111 m away for red foxes.

Dietary niche breadth

The dietary niche breadth calculated from the RFO was the narrowest for Japanese martens in the forest landscape and the widest for red foxes in the rural landscape (Table 1). Dietary niche breadth by PDW was the narrowest for Japanese martens in the forest

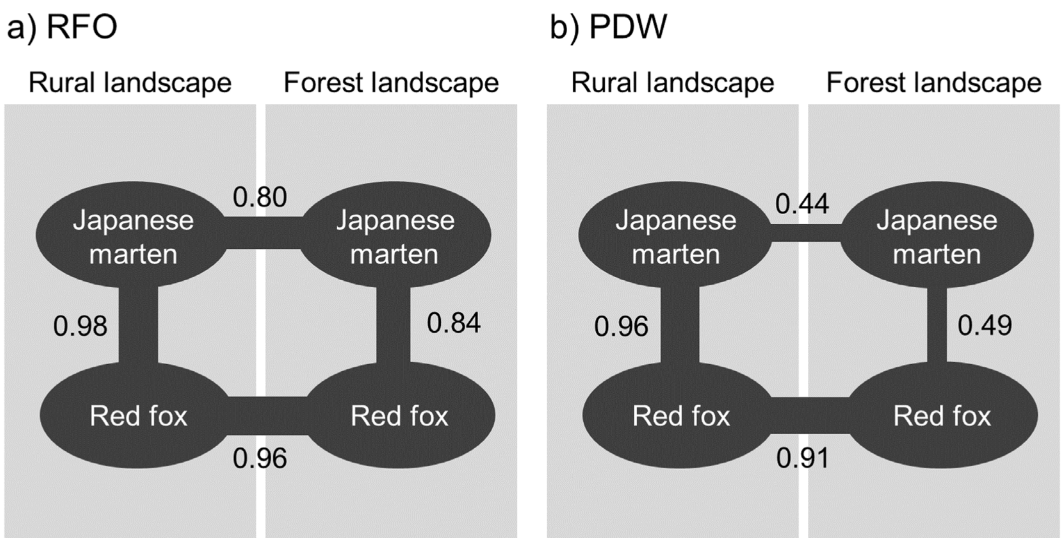

Fig. 2. Pianka's index (α) of feeding habits between landscapes for each species and between species in each landscape; (a) relative frequency of occurrence (RFO) of food items; (b) percentage of dry weight (PDW) of food items.

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Table 2. Frequency of occurrence (FO, %) of seeds in Japanese marten and red fox faecal samples in rural (around Nishiaraya) and forest (around the Kaminagawa Experimental Forest) landscapes.

Name	Category	Rural landscape		Forest landscape	
		Japanese marten n = 35	Red fox n = 32	Japanese marten n = 37	Red fox n = 20
Persimmons	Cultivated fruit	25.7	53.1	2.7	25.0
Apples	Cultivated fruit	0.0	6.3	0.0	5.0
Grapes (cultivar)	Cultivated fruit	0.0	6.3	0.0	0.0
Kiwifruits	Cultivated fruit	2.9	0.0	0.0	0.0
Stachyurus praecox	Wild fruit	0.0	0.0	2.7	0.0
Rhus javanica	Wild fruit	0.0	0.0	0.0	10.0
Japanese cedar (*Cryptomeria japonica*)	Conifer	42.9	34.4	27.0	65.0
Japanese cypress (*Chamaecyparis obtuse*)	Conifer	0.0	0.0	2.7	10.0
Unknown	Other	0.0	12.5	2.7	15.0

landscape and widest for red foxes in the rural landscape (Table 1). Dietary niche breadth calculated from both RFO and PDW was narrower in the forest landscape, and the dietary niche breadth of Japanese martens was narrower than that of red foxes in both landscapes.

Similarity of feeding habits

Regarding the similarity of feeding habits by RFO and PDW, the similarity index α was relatively high between Japanese martens and red foxes in the rural landscape and between red foxes in the rural landscape and red foxes in the forest landscape (Fig. 2). The similarity index α for the other combinations was relatively low (Fig. 2).

Discussion

Faecal analysis revealed that fruit flesh was frequently consumed by Japanese martens and red foxes in the rural landscape and red foxes in the forest landscape (Table 1). These results suggest that fruits are important food sources in winter. Since it is difficult to identify the species of fruit flesh after mastication and digestion, we identified fruit species based on the seeds that appeared in the same sample. These results support the hypothesis that Japanese martens use more cultivated fruit in rural landscapes than in forest landscapes in snowy environments. For red foxes, fruit use was observed in both landscapes, and no significant differences were detected. However, the occurrence of fruit flesh and cultivated fruit seeds was higher in the rural landscape (Tables 1 and 2), which supports the hypothesis to some extent. In landscapes with artificially planted fruit trees, Japanese martens and red foxes consumed cultivated fruits, which were probably abundant as fruit waste, even when covered with snow more than 100 cm in depth. Indeed, the authors found several holes in the snow leading to the ground in the rural landscape in this study, red foxes and Japanese martens likely dug through the snow to access the fruit as suggested by previous studies (Ōtsu 1972, Tsukada 1997, Czernik et al. 2016).

For Japanese martens and red foxes, the dietary niche breadth was wider in the rural landscape than in the forest (Table 1). This result does not support the first prediction. The abundant and easy availability of cultivated fruit should have narrowed the niche breadth in the rural landscape. However, in the study area, limited access due to snow cover may have hindered reliance on cultivated fruit. A previous study conducted in the mountains of south-western Yamagata Prefecture (Ōtsu 1972) suggested limited access to wild fruits due to heavy snowfall and low resource availability. In the rural landscape in this study, because of the snow cover, Japanese martens and red foxes do not appear to have easy access to cultivated fruits. However, where access to some cultivated fruits is possible, even with heavy snowfall, Japanese martens and red foxes appear reliant on cultivated fruits as one of their main food sources. The presence of cultivated fruits that can serve as food in snowy environments within their movement range may not be a full substitute for other naturally occurring food resources, such as mammals, birds, and insects, but it may broaden the variety of food items they consume.

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The similarity in feeding habits between Japanese martens and red foxes in the rural landscape was high. In contrast, it was low between Japanese martens and red foxes in the forest landscape (Fig. 2). This result supports our second prediction. However, it may be difficult to regard our results as a purely interspecific comparison in the forest landscape because red foxes use cultivated fruits relatively more in the forest landscape. Nevertheless, the similarity of feeding habits in the rural landscape was extremely high compared to previous studies comparing the winter diet of red foxes and marten species in other regions (Brangi 1995, Padial et al. 2002, Lanszki et al. 2007). Although previous studies in Japan have shown different trends in the winter diets of Japanese martens and red foxes (Suzuki et al. 1976, Misawa 1979, Koganezawa & Kurokawa 1983, Tsuji et al. 2014), there is no doubt that the feeding habits of the two species were similar in the rural landscape of this study. Since both martens and red foxes increase their use of anthropogenic food resources in habitats that are more affected by human activities (e.g. Lanszki 2003, Reshamwala et al. 2018, Lanszki et al. 2019), it is likely that the presence of anthropogenic food resources, such as cultivated fruits, in our study area increased the similarity in feeding habits between species.

Red foxes showed little change in feeding habits despite changes in the landscape and consumed a variety of food items (Tables 1, Fig. 2). In previous studies, red foxes consumed a large amount of animal material, such as small mammals and hares, in winter forest landscapes (Misawa 1979, Koganezawa & Kurokawa 1983). However, in this study, red foxes in both landscapes used plant materials, including cultivated fruit (Tables 1 and 2). In the forest landscape, red foxes sometimes used cultivated fruit 1-4 km away. The home range of red foxes is estimated at 1-8 km^2 (Ohdachi et al. 2015). Considering the distance travelled based on the home range size, red foxes may travel extensively to consume cultivated fruits. Cultivated fruits may be an attractive food resource that influences the feeding habits of red foxes on a spatial scale of approximately 4 km. These results suggest that the presence of cultivated fruit may influence the feeding habits of medium-sized carnivores at the landscape scale.

Japanese cedar seeds appeared in faecal samples most frequently in this study (Table 2), however, we could not determine whether they were recognized as a food resource by the carnivores. Possibilities for the occurrence of cedar seeds in the diet include 1) accidental foraging (e.g. consumption while foraging for other foods or secondary foraging through prey), and 2) foraging as food resources. Regarding the former, the number of seeds appeared high as accidental consumption while foraging for other foods. In addition, secondary foraging could be ruled out, given that most of the seeds in this study were undamaged. As for the latter, Kusui & Kusui (1998) indicated the possibility of conifer needle consumption by Japanese martens during low fruit production periods, though cedar seeds were not mentioned. The occurrence of these seeds indicates that carnivores probably ate the cones of Japanese cedars. Since cedar cones and seeds contain trace amounts of lipids and minerals (Kida & Oikawa 1978), carnivores may forage to obtain nutrients during winter when food resources are limited. Raccoon dogs (*Nyctereutes procyonoides*), which are a common medium-sized carnivore in Japan, have been reported to utilize acorns with low tannin astringent (Omori & Hosoi 2021), though the use of cedar cones has not been reported (Takatsuki 2018). Further investigation is needed to determine whether Japanese martens and red foxes can utilize cedar cones as a food resource.

This study revealed that cultivated fruits are widely used as food resources by medium-sized carnivores, even in snowy environments during the winter. It has also been suggested that red foxes move long distances to consume cultivated fruits in forest landscapes, indicating that cultivated fruits are particularly attractive when food resources are scarce. This finding suggests that cultivated fruits may also indirectly feed wildlife, even in areas with heavy snowfall. However, our results on the feeding habits of Japanese martens and red foxes represent a snapshot for a single year, and the sample size is also limited. Because winter weather conditions vary with year, further evaluation over multiple years would be needed to confirm the results of this study as robust. Nevertheless, our results do indicate the potential importance of agricultural crops for medium-sized carnivores in snowy environments. If wildlife invades human habitats to use anthropogenic products, not only agricultural crops, a stable supply of food resources may contribute to increased survival rates and population size and promote human habituation (Abe 1975, Herrero et al. 2005, Fehlmann et al. 2021). This may increase the risk of wildlife damage and infectious diseases (Bradley & Altizer 2007, Honda et al. 2019). Managing agricultural products in winter, even in snowy regions, is expected to reduce the impact on wildlife ecology and human-wildlife conflicts.

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Author Contributions

A. Nakane and M.U. Saito designed the study, A. Nakane conducted data collection and analyses, and all authors wrote the manuscript. All authors have accepted responsibility for the entire content of this submitted manuscript and have approved its submission.

Data Availability Statement

The datasets generated and/or analysed during the current study are available from the corresponding author upon reasonable request.

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