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RESEARCH PAPER

Seasonal variation in dietary patterns and trophic niche overlap among three sympatric medium-sized carnivores in a cool-temperate zone

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Abstract. To understand and sustain carnivore communities and ecosystems, it is important to determine the mechanisms of coexistence and potential competitive interactions among carnivores. This study examined how carnivores coexist and how climatic environmental shifts affect the potential competitive interactions among medium-sized carnivores. The seasonal trophic niche overlap of red foxes, Japanese martens, and raccoon dogs in the cool-temperate zone in Japan was evaluated, where there are distinct seasonal changes, especially from heavy snowfall. Faecal analysis of red foxes (n = 107), Japanese martens (n = 125), and raccoon dogs (n = 100) from 2019 to 2021 showed that carnivores share the main food items and their annual dietary overlap is relatively high despite the co-occurrence of carnivores. These results have indicated that the carnivores have potentially strong competitive interactions, and various competition avoidance mechanisms besides niche partitioning may facilitate the coexistence of carnivores in Japan. The study also found that the degree of trophic niche overlap varied by season, indicating that shifts in environmental conditions, particularly food abundance and snowfall, may affect potential competitive interactions among carnivore guilds.

Key words: diet, food habits, dietary overlap, red fox, Japanese marten, raccoon dog

Introduction

The competitive exclusion principle (Gause 1934, Hardin 1960) indicates that intensive interspecific competition occurs between species with similar niches. Therefore, interspecific competition affects species survival (Waggershauser et al. 2021) and distribution (Krohn et al. 1995, Hinton & Chamberlain 2022) and shapes community structure (Schoener 1983). Carnivores provide important ecosystem functions (e.g. Inagaki et al. 2020, Tochigi et al. 2022) and influence the ecosystem structure (Roemer et al. 2009). Therefore, determining the coexistence mechanisms and competitive interactions among carnivores is vital for understanding and sustaining carnivore communities and ecosystems.

Sympatric carnivores coexist through resource partitioning along spatial (e.g. Müller et al. 2022), dietary (e.g. Tsunoda et al. 2017), and temporal axes (e.g. Hayward & Slotow 2009) to avoid interspecific competition. Trophic niche partitioning, which changes food items, is one of the most important strategies for avoiding competition. Identifying

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trophic niche differences among species is the first step in understanding community structure (Schoener 1983, Ray & Sunquist 2001, Juarez & Marinho-Filho 2002, Zapata et al. 2007). Trophic niche partitioning in sympatric carnivores has been evaluated in various carnivorous guilds, especially in Europe and Africa (e.g. Tsunoda et al. 2017, Vogel et al. 2019, Müller et al. 2022). However, few studies have been conducted in the East Asian region (Zhang et al. 2011, Chiang et al. 2012). Regional and climatic changes influence carnivore diets and competitive interactions (Zhou et al. 2011, Soe et al. 2017, Zielinski et al. 2017), highlighting that trophic niche partitioning in East Asia could provide essential insights into the coexistence mechanism among carnivores.

Understanding the relationship between carnivore communities and environmental conditions is essential for ecosystem management under ongoing global environmental change (Hisano et al. 2021). Many carnivores shift their foraging strategies in response to the surrounding environment, such as food abundance and climatic conditions (e.g. Zhou et al. 2011, Soe et al. 2017, Willebrand et al. 2017, Mustonen & Nieminen 2018, Nakane et al. 2022). Therefore, these environmental changes may also affect competitive interactions among carnivores. The cool-temperate zone, to which parts of East Asia belong, has four distinct seasons with climatic shifts in temperature and precipitation. Food abundance increases in summer and autumn and decreases substantially during winter and spring (Tsukada & Nonaka 1996). Some areas in the cool-temperate zone have heavy snowfall of several meters, and the environmental conditions have changed considerably. Therefore, evaluating seasonal changes in trophic niche overlap in cool-temperate zones can provide valuable insights into the relationship between the environment and interspecific competitive interactions over food resources among medium-sized carnivores. However, few studies have evaluated seasonal changes in trophic niche partitioning among carnivores in cool-temperate zones.

The study mainly focused on red foxes (*Vulpes vulpes*), Japanese martens (*Martes melampus*), and raccoon dogs (*Nyctereutes procyonoides*), which co-occur in the cool-temperate zone of Japan (Watabe & Saito 2021, 2022, Suzuki & Saito 2023). They are likely to be potentially competitive interactions (Donadio & Buskirk 2006) because of their taxonomy, body size (Ohdachi et al. 2015), and dietary similarities (raccoon dog: Sutor et al. 2010, red fox: Hisano et al. 2021, Japanese marten: Hisano et al. 2019, Tsuji et al. 2019). Their temporal niche overlap is also relatively high (Watabe & Saito 2021, 2022, Watabe et al. 2022). Therefore, it is suitable for evaluating how trophic niche partitioning facilitates carnivore coexistence in the cool-temperate zones of Japan.

This study aimed to determine how the carnivores coexist and how environmental change affects potential competitive interaction among carnivores by evaluating the seasonal trophic niche overlap of red foxes, Japanese martens, and raccoon dogs in the cool-temperate zone in Japan. It was hypothesised that the trophic niche is generally partitioned among carnivores to avoid competition. However, the degree of niche partitioning varies with season. Therefore, it was predicted that the degree of trophic niche overlap would be relatively high in summer and autumn when various food resources increase, which reduces competition. Meanwhile, it was predicted that limited food resources and heavy snowfall highlight the competitive interactions and ecological differences, resulting in differences in foraging strategy and the degree of trophic niche overlap decreasing in spring and winter.

Material and Methods

Study area

Surveys were conducted in and around the forests in Tsuruoka City, Yamagata Prefecture, northeastern Japan. This region comprises forests, fields, rice paddies, orchards, and residential areas. The forests are predominantly deciduous broad-leaved forests which mainly consist of Japanese beeches (*Fagus crenata*) and Japanese oak (*Quercus crispula*) and planted forests of Japanese cedar (*Cryptomeria japonica*). This area has a cool-temperate climate, with an average annual temperature of 12.9 °C and an average annual precipitation of 2,191.4 mm (Japan Meteorological Agency 2022). This area has a distinct seasonal climate. Spring (April and May) has relatively low temperatures (average 13.2 °C) and the lowest precipitation, summer (June-August) has the highest temperatures (average 23.1 °C), autumn (September-November) has relatively low temperatures (average 15.4 °C) and highest precipitation, and winter (December-March) has the coldest temperatures (average 3.2 °C) with a maximum snow depth of 100-300 cm.

Faecal sampling

Fresh faecal samples were collected along roads in and around forests (38°26′-38°44′ N, 139°45′-139°58′ E; height, approximately 100-800 m a.s.l.)

from February 2019 to November 2021. Red fox and Japanese marten faeces were distinguished by their diameter (Tsuji et al. 2011, Munekane et al. 2021) and nearby tracks only during the snow season. Raccoon dog faeces were collected from their latrines in the study area only when the faecal sample was fresh and regarded as being from one defecation based on shape, odour, and colour. Unidentified samples were excluded from the analysis. All the faecal samples were stored at approximately −20 °C until faecal analysis.

Faecal analysis

The defrosted faecal samples were washed with 1 L of water using a 0.5-1 mm sieve. The remaining undigested items were evaluated using point-frame methods (Takatsuki & Tatewaki 2012, Takatsuki 2013). The remains of the red fox and raccoon dog faecal samples were spread onto a Petri dish with a 5 mm grid and the number of points the grid covered by remains was counted up to 200. For the remains of the Japanese marten faecal sample, a Petri dish was used with a 1 mm grid and counted up to 300. The remains were classified into 15 categories: mammals, birds, reptiles, amphibians, insects, myriapods, gastropods, crustaceans, fish, other animal materials, fruits, leaves, other plant materials, artificial materials, and others. To detect earthworms, 15 ml of wash water was pipetted onto a Petri dish covered with a 1 cm grid, and the earthworm chaetae were examined in 10 randomly chosen grid cells under a microscope (× 20) according to Kaneko et al. (2006) and Enomoto et al. (2018).

To evaluate the diet composition, the frequency of occurrence (FO), relative frequency of occurrence (RFO), and per cent volume (PV) was calculated for each food category, and only FO and RFO were calculated for earthworms according to Fukue et al. (2011) and Hijikata et al. (2020).

FO (%) = (number of scats containing food category A/total number of scats) × 100
RFO (%) = (number of scats containing food category A/sum of the number of food categories in a scat) × 100
PV (mean ± SD, %) = [Σ (number of grid points covered by food category A in a scat i/total number of counted grid points of a scat i)/total number of scats] × 100

Data analysis

Levins' index B (Krebs 2014) was calculated from RFO to estimate the breadth of the trophic niche for each species.

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

where, p is the RFO of food category i.

Pianka's index α (Pianka 1973) was calculated from the RFO and PV to assess the dietary overlap.

$$\alpha = [\Sigma\,(p1_i \times p2_i)]/\{[\Sigma\,(p1i)^2]^{1/2} \times [\Sigma\,(p2_i)^2]^{1/2}\}$$

Where p1 is the RFO or PV of food category i for species 1 and p2 is the RFO or PV of food category i for species 2.

Pianka's index ranges from 0 (no overlap) to 1 (complete overlap) and is categorised as "Extremely High": 0.90 ≥ α, High: 0.90 > α ≥ 0.70, Moderate: 0.70 > α ≥ 0.50, and Low: 0.50 > α (Zuercher et al. 2022). Fisher's exact test and Wilcoxon rank sum test were applied to the FO and PV of each food category to evaluate the dietary differences between seasons and species. The level of significance was adjusted using the Bonferroni correction. All the statistical analyses were performed using R version 4. 2. 2 (R Core Team 2022).

Results

General diet composition and seasonal pattern

A total of 332 faeces samples were analysed, of which 107 were red foxes (spring: 20, summer: 43, autumn: 17, winter: 27), 125 were Japanese martens (spring: 34, summer: 49, autumn: 22, winter: 20), and 100 were raccoon dogs (spring: 29, summer: 43, autumn: 28). Raccoon dog latrines could not be found during winter because of the heavy snow cover.

In the overall diet of red foxes, fruit, mammals, and insects were the dominant food categories (Tables 1-3). Other plant materials and leaves occurred at a relatively high frequency, but their volume was relatively low. Birds, reptiles, earthworms, other animal materials, and artificial materials were also consumed. The consumption of major food items differed significantly between seasons. Red foxes consumed more fruits in autumn than in the other seasons, and insects consumed more in summer than in spring and winter. The consumption of mammals was higher in spring and winter than in summer, and the PV in spring was higher than in autumn.

Mammals, fruits, and insects were the dominant food categories in the overall diet of the Japanese martens, similar to the red fox (Tables 1-3). Other plant materials and leaves occurred at a relatively

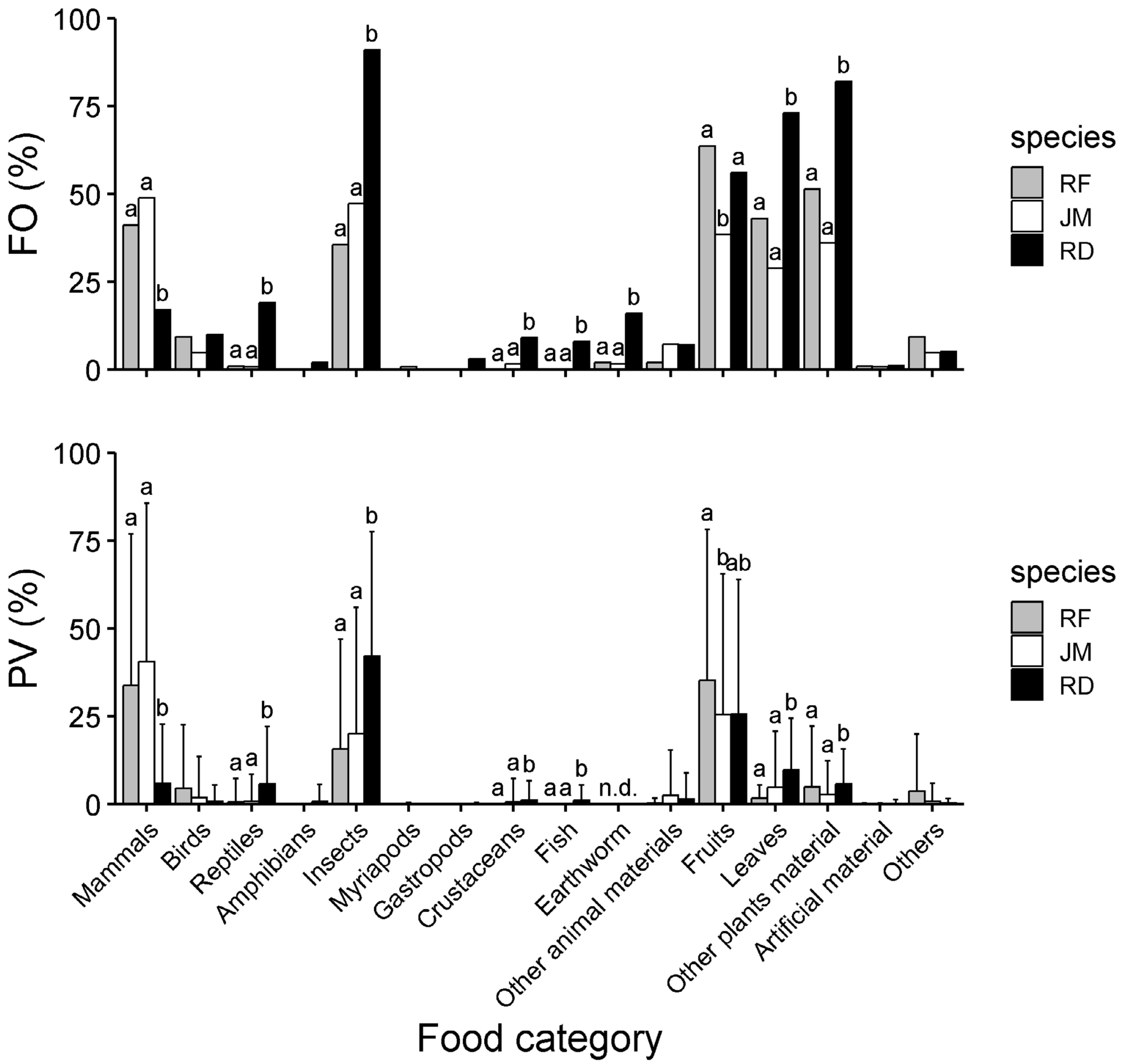

Fig. 1. Frequently of occurrence (FO, %) and per cent volume (PV, %) of each food category for the red fox (RF), Japanese marten (JM), and raccoon dog (RD) in the study area.

high frequency, but their volume was relatively low. Birds, reptiles, myriapods, crustaceans, earthworms, other animal materials, and artificial materials were also consumed. The consumption of major food items differed significantly between seasons. Japanese martens consumed more insects in summer than in the other seasons, and mammals consumed more insects in spring and winter than in summer and autumn. The consumption of fruits was higher in autumn than in other seasons, and the PV was higher in summer than spring.

Insects and fruits were the dominant food categories in the overall diet of raccoon dogs (Tables 1-3). Other plant materials and leaves occurred at a high frequency, but their volume was relatively low. Raccoon dogs consumed various food items; mammals, birds, reptiles, amphibians, gastropods, crustaceans, fish, earthworms, artificial materials, and others occurred from the faeces. The consumption of major food items differed significantly between the seasons. Raccoon dogs consumed more fruits in autumn than in spring and summer. The consumption of insects was higher in spring and summer than in autumn, and the PV in spring was higher than in summer.

Interspecific differences in the diet and trophic niche

The consumption of major food items differed significantly among carnivores (Fig. 1). Red foxes and Japanese martens consumed more mammals than raccoon dogs. In contrast, raccoon dogs consumed

Table 1. Seasonal variation in Frequency of occurrence (FO, %) of each food item and the mean number of food items per scat based on red fox (RF), Japanese marten (JM), and raccoon dog (RD) faecal samples. Boldface indicates the most frequently consumed food item for each carnivore.

Food items	Spring			Summer			Autumn			Winter		Total		
	RF	JM	RD	RF	JM	RD	RF	JM	RD	RF	JM	RF	JM	RD
Number of samples	20	34	29	43	49	43	17	22	28	27	20	107	125	100
Animal material														
Mammals	**80.0**	**79.4**	17.2	16.3	28.6	18.6	41.2	18.2	14.3	51.9	**80.0**	41.1	**48.8**	17.0
Birds	5.0	5.9	10.3	4.7	2.0	11.6	5.9	4.5	7.1	22.2	10.0	9.3	4.8	10.0
Reptiles	5.0	2.9	3.4	-	-	39.5	-	-	3.6	-	-	0.9	0.8	19.0
Amphibians	-	-	6.9	-	-		-	-	-	-	-	-	-	2.0
Insects	15.0	35.3	**100.0**	62.8	**75.5**	**100.0**	29.4	36.4	67.9	11.1	10.0	35.5	47.2	**91.0**
Myriapods	-	-	-	-	-	-	-	-	-	-	5.0	-	0.8	-
Gastropods	-	-	10.3	-	-	-	-	-	-	-	-	-	-	3.0
Crustaceans	-	-	3.4	-	2.0	16.3	-	4.5	3.6	-	-	-	1.6	9.0
Fish	-	-	17.2	-	-	7.0	-	-	-	-	-	-	-	8.0
Earthworm	-	2.9	17.2	4.7	2.0	25.6	-	-	-	-	-	1.9	1.6	16.0
Other animal materials	-	5.9	17.2	2.3	10.2	4.7	-	4.5	-	3.7	5.0	1.9	7.2	7.0
Plant material														
Fruits	25.0	8.8	34.5	**67.4**	34.7	41.9	**88.2**	**90.9**	**100.0**	**70.4**	40.0	**63.6**	38.4	56.0
Leaves	55.0	50.0	82.8	39.5	22.4	88.4	41.2	9.1	39.3	40.7	30.0	43.0	28.8	73.0
Other plants material	50.0	58.8	89.7	51.2	14.3	93.0	52.9	36.4	57.1	51.9	50.0	51.4	36.0	82.0
Artificial material	-	-	-	2.3	-	-	-	4.5	3.6	-	-	0.9	0.8	1.0
Others	20.0	8.8	13.8	9.3	4.1	2.3	5.9	-	-	3.7	5.0	9.3	4.8	5.0
The mean number of food items per scat	2.55	2.59	4.24	2.60	1.96	4.49	2.65	2.09	2.96	2.56	2.35	2.59	2.22	3.99

Table 2. Seasonal variation in Relative frequency of occurrence (%) of each food item and dietary niche breadth based on red fox (RF), Japanese marten (JM), and raccoon dog (RD) faecal samples. Boldface indicates the most frequently consumed food item for each carnivore.

Food items	Spring			Summer			Autumn			Winter		Total		
	RF	JM	RD	RF	JM	RD	RF	JM	RD	RF	JM	RF	JM	RD
Number of samples	20	34	29	43	49	43	17	22	28	27	20	107	125	100
Animal material														
Mammals	**31.4**	**30.7**	4.1	6.3	14.6	4.1	15.6	8.7	4.8	20.3	**34.0**	15.9	**22.0**	4.3
Birds	2.0	2.3	2.4	1.8	1.0	2.6	2.2	2.2	2.4	8.7	4.3	3.6	2.2	2.5
Reptiles	2.0	1.1	0.8	-	-	8.8	-	-	1.2	-	-	0.4	0.4	4.8
Amphibians	-	-	1.6	-	-	-	-	-	-	-	-	-	-	0.5
Insects	5.9	13.6	**23.6**	24.1	**38.5**	**22.3**	11.1	17.4	22.9	4.3	4.3	13.7	21.3	**22.8**
Myriapods	-	-	-	-	-	-	-	-	-	-	2.1	-	0.4	-
Gastropods	-	-	2.4	-	-	-	-	-	-	-	-	-	-	0.8
Crustaceans	-	-	0.8	-	1.0	3.6	-	2.2	1.2	-	-	-	0.7	2.3
Fish	-	-	4.1	-		1.6	-	-	-	-	-	-	-	2.0
Earthworm	-	2.3	4.1	0.9	5.2	1.0	-	2.2	-	1.4	2.1	0.7	0.7	4.0
Other animal materials	-	1.1	4.1	1.8	1.0	5.7	-	-	-	-	-	0.7	3.2	1.8
Plant material														
Fruits	9.8	3.4	8.1	**25.9**	17.7	9.3	**33.3**	**43.5**	**33.7**	**27.5**	17.0	**24.5**	17.3	14.0
Leaves	21.6	19.3	19.5	15.2	11.5	19.7	15.6	4.3	13.3	15.9	12.8	16.6	13.0	18.3
Other plants material	19.6	22.7	21.1	19.6	7.3	20.7	20.0	17.4	19.3	20.3	21.3	19.9	16.2	20.6
Artificial material	-	-	-	0.9	-	-	-	2.2	1.2	-	-	0.4	0.4	0.3
Others	7.8	3.4	3.3	3.6	2.1	0.5	2.2	-	-	1.4	2.1	3.6	2.2	1.3
Dietary niche breadth	4.92	4.87	6.48	5.19	4.48	6.45	4.70	3.83	4.46	5.17	4.73	5.75	5.91	6.44

Table 3. Seasonal variation in Percent volume (PV, mean±SD, %) of each food item based on red fox (RF), Japanese marten (JM), and raccoon dog (RD) faecal samples. Boldface indicates the highest proportion of each food item for each carnivore. "+" indicates mean value was < 0.1.

Food items	Spring			Summer			Autumn			Winter		Total		
	RF	JM	RD	RF	JM	RD	RF	JM	RD	RF	JM	RF	JM	RD
Number of samples	20	34	29	43	49	43	17	22	28	27	20	107	125	100
Animal materials														
Mammals	**76.1±39.2**	**72.9±39.5**	4.9±17.4	11.7±28.2	18.0±32.8	6.7±17.0	22.4±36.6	7.9±20.7	5.4±16.7	**44.4±44.7**	**76.9±39.9**	33.7±43.2	**40.6±45.1**	5.8±16.9
Birds	0.1±0.4	1.5±8.8	0.2±0.8	2.5±13.6	0.1±0.9	1.6±6.9	0.1±0.5	3.7±17.5	-	13.4±30.3	4.6±19.7	4.4±18.1	1.9±11.6	0.8±4.6
Reptiles	3.4±15.3	2.6±15.0	0.9±4.8	-	-	12.6±23.1	-	-	-	-	-	0.6±6.6	0.7±7.8	5.7±16.4
Amphibians	-	-	2.3±8.8	-	-	-	-	-	-	-	-	-	-	0.7±4.8
Insects	5.6±19.7	2.7±6.2	**65.5±33.7**	31.1±40.2	**46.6±44.7**	**47.0±28.7**	9.8±23.1	5.9±16.5	10.5±21.8	1.9±9.1	0.4±1.3	15.6±31.3	20.1±35.9	**42.1±35.4**
Myriapods	-	-	-	-	-	-	-	-	-	-	0.2±1.1	-	+	-
Gastropods	-	-	0.2±0.8	-	-	-	-	-	-	-	-	-	-	0.1±0.4
Crustaceans	-	-	0.3±1.5	-	1.5±10.6	2.4±8.2	-	-	-	-	-	-	0.6±6.6	1.1±5.5
Fish	-	-	1.2±3.3	-	-	1.5±6.1	-	-	-	-	-	-	-	1.0±4.4
Other animal materials	-	3.8±17.3	4.6±13.6	0.3±1.7	0.7±3.5	0.2±0.8	-	3.7±17.1	-	0.4±2.1	3.2±14.1	0.2±1.5	2.5±12.9	1.4±7.5
Plant materials														
Fruits	2.1±4.1	4.8±18.2	4.6±16.8	**42.6±44.5**	24.0±39	5.3±8.5	**61.7±44.3**	**76.8±36.4**	**78.8±30.1**	31.3±41.5	7.9±21.6	**35.2±43.0**	25.5±40.1	25.7±38.3
Leaves	1.0±1.9	6.6±18.3	8.3±12.2	2.1±4.2	6.8±19.9	15.9±18.0	2.0±4.0		1.3±2.3	1.5±3.7	1.5±5.7	1.7±3.7	4.7±16.0	9.6±14.8
Other plants material	1.0±1.5	3.0±7.2	6.1±14.3	7.3±21.3	2.1±11.2	6.7±6.2	3.9±12.6	1.7±4.9	3.5±9.6	4.1±19.2	5.3±12.3	4.8±17.3	2.8±9.5	5.6±10.0
Artificial material	-	-	-	-	-	-	-	0.2±0.8	0.4±2.1	-	-	+	+	0.1±1.1
Others	10.7±30.3	2.0±9.5	0.8±2.2	2.3±9.0	0.3±2.1	0.1±0.9	-	-	-	2.9±15.1	0.2±0.9	3.6±16.2	0.7±5.2	0.3±1.3

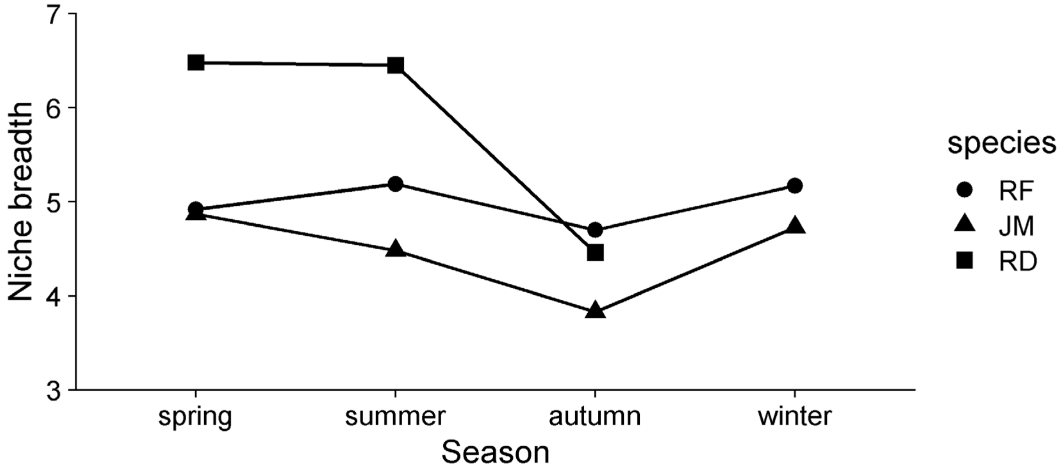

Fig. 2. Seasonal trophic niche breadth indices (B) for the red fox (RF), Japanese marten (JM), and raccoon dog (RD).

more insects than red foxes and Japanese martens. The FO of fruits in red foxes and raccoon dogs was higher than that in Japanese martens, and the PV in red foxes was higher than in Japanese martens. However, Pianka's overlap index showed a "High" overlap between raccoon dog-red fox and raccoon dog-Japanese marten calculated from PV, and the other combination showed "Extremely High" (Table 4). Raccoon dogs were more generalist than red foxes and Japanese martens because the mean number of food items per faeces and trophic niche breadth was relatively high (Tables 1, 2).

Carnivores shared the main food items, and trophic niche overlap was high in the annual diets, while their trends differed between seasons. In spring, raccoon dogs consumed insects, mainly comprising larvae of Bibionidae (Table S1). They consumed more insects than red foxes and Japanese martens, while red foxes and Japanese martens consumed more mammals than raccoon dogs (Tables 1-3). The trophic niche overlap varied according to combination (Table 4). Based on RFO, overlap indices showed "Moderate" for raccoon dog-red fox, "High" for raccoon dog-Japanese marten, and "Extremely High" for red fox-Japanese marten. Based on PV, the indices showed "Low" for raccoon dog-red fox and raccoon dog-Japanese marten and "Extremely High" for the red fox-Japanese marten. Raccoon dogs have a wider dietary breadth than red foxes and Japanese martens. In summer, raccoon dogs consumed insects more frequently than red foxes and Japanese martens and consumed more volume than red foxes. However, red foxes consumed more fruits than raccoon dogs and Japanese martens and more frequently than Japanese martens. The trophic niche overlap indices showed

Table 4. Pianka's index (α) on dietary overlaps among red fox (RF), Japanese marten (JM) and raccoon dog (RD) in each season, 3season(spring-autumn) and yearly based on the relative frequency of occurrence (RFO) and per cent volume (PV). Trophic niche overlap was categorised as "Extremely High" (α ≥ 0.90), "High" (0.90 > α ≥ 0.70), "Moderate" (0.70 > α ≥ 0.50), and "Low" (0.50 > α).

	Pianka's index α					
	RF-JM		RF-RD		JM-RD	
season	RFO	PV	RFO	PV	RFO	PV
spring	0.97	0.99	0.67	0.15	0.76	0.13
summer	0.89	0.89	0.85	0.65	0.78	0.87
autumn	0.93	0.96	0.95	0.96	0.96	1.00
winter	0.89	0.86	-	-	-	-
3season	0.95	0.98	0.92	0.76	0.90	0.77
yearly	0.95	0.96	-	-	-	-

"High" between all combinations, except for raccoon dog-red fox (α = 0.65; Moderate) based on PV (Table 4). Raccoon dogs had a broader diet than red foxes and Japanese martens, similar to that in spring (Table 2, Fig. 2). In autumn, carnivores commonly consumed fruits (mainly *Actinidia arguta*; Table S1), and there were no significant interspecific differences in the consumption of the main food categories (Tables 1-3). The trophic niche overlap was "Extremely high" in all combinations (Table 4). The trophic niche breadths of all the carnivores were the narrowest throughout the year (Table 2, Fig. 2). In winter, red foxes consumed more fruit than Japanese martens, while Japanese martens consumed more mammals than red foxes (Tables 1-3). The trophic niche overlap indices were "Extremely High" based on RFO and "High" based on PV (Table 4). Red foxes had a wider dietary range than Japanese martens (Table 2, Fig. 2).

Discussion

The study identified a high degree of overlap in the overall diets of carnivores (Table 4). This result does not support the hypothesis that clear trophic niche partitioning occurs among sympatric carnivores. The degree of trophic niche overlap in this study was higher than that in a previous study (e.g. Baltrūnaitė 2006) evaluated among red foxes, raccoon dogs, and pine martens (*Martes martes*) in Lithuania. High dietary overlap is an important factor promoting interspecific competition (Polis et al. 1989, Palomares & Caro 1999). Therefore, carnivores have potentially strong competitive relationships in Japan.

Despite the lack of clear trophic niche partitioning, carnivores co-occur in the cool-temperate zone of Japan (Watabe & Saito 2021, 2022, Suzuki & Saito 2023). A high niche overlap has been identified among sympatric carnivores, which suggests that niche partitioning is not the only competition avoidance strategy in carnivore guilds (Vanak et al. 2013, Davis et al. 2018). Various factors such as limitation of resources besides food (e.g. den), roadkill, and weather conditions may suppress low population density, resulting in a high abundance of food resources for carnivores. Fine-scale avoidance or partitioning (Broekhuis et al. 2013, Nagasaki et al. 2022, Watabe et al. 2022) and landscape heterogeneity (Pereira et al. 2012, Müller et al. 2022) also facilitate coexistence among sympatric carnivores. Therefore, they may coexist without dividing their primary food resources. The study showed no clear trophic niche partitioning, which many previous studies have reported in medium and large carnivore communities in Africa and Europe (e.g. Tsunoda et al. 2017, Vogel et al. 2019, Müller et al. 2022), suggesting that the carnivore guild was facilitated by various factors besides niche partitioning in the cool-temperate zone in Japan.

The study results indicated that the overall dietary overlap was high. However, the degree of overlap varied with the season (Table 4). This result partially supports the study hypothesis and suggests that seasonal shifts influence and change competitive relationships. There was an especially high dietary overlap in autumn when carnivores consumed fruits regularly in relatively high quantities. Fruit abundance is highest and ripens best in autumn in cool-temperate deciduous broadleaf forests (Tsukada & Nonaka 1996, Noma 1997). The fruit most consumed by carnivores was *A. arguta* (Table S1), which was the most frequent fruit in previous research on mammalian diet in autumn (e.g. Otani 2003, Enomoto et al. 2022, Kumagai & Saito 2022). This finding suggests that *A. arguta* is abundant, given that it can be consumed by multiple mammalian species in the cool-temperate zone in Japan. Therefore, a high abundance of fruits may cause high dietary overlap in autumn, and fruits, especially *A. arguta*, are essential food resources for many species.

In contrast, the study results have shown decreased trophic niche overlap between raccoon dogs and other carnivores in spring and significant interspecific differences in the proportion of major food items between Japanese martens and red foxes in winter (Tables 1-4). Dietary partitioning can be caused by a decrease in food resources to avoid competitive interactions (e.g. Barrull et al. 2014). There were substantial decreases in major food resources in spring and winter in the cool-temperate zone (Tsukada & Nonaka 1996). Therefore, these seasonal decreases may cause low trophic niche overlap.

Heavy snowfall as a seasonal environmental change may also cause the different foraging strategies of each carnivore to adapt their ecology and morphology, resulting in interspecific differences in diets. Interestingly, high consumption of insects (mainly larvae of Bibionidae; Table S1) by raccoon dogs in spring was identified. In a previous study conducted in the same district but with a low snowfall area (Kumagai & Saito 2022), raccoon dogs consumed a high frequency of mammals (FO: 80%) in spring. This difference suggests that snow conditions change the foraging strategy of raccoon dogs. Raccoon dog foraging is restricted to snow (Mustonen & Nieminen 2018). Therefore, raccoon dogs might not actively hunt and search for small mammals and mammal carcasses to avoid a negative energy balance under spring residual snow conditions in heavy snowfall areas. Meanwhile, larvae of Bibionidae, which form groups in the soil and feed on fallen leaves and animal faeces (Sutou 2005, Ikeda et al. 2006), were often seen around raccoon dog latrines in the study area, and raccoon dogs could eat them easily. Therefore, heavy snowfall may affect the foraging strategies of raccoon dogs, resulting in interspecific dietary differences. Japanese martens used mammals significantly more than red foxes, whereas red foxes used fruits significantly more than Japanese martens in winter. This result suggests that heavy snow cover may highlight differences in the ability and morphology to get fruits buried in snow cover, resulting in differences in the interspecific diet between red foxes and Japanese martens. Red foxes, which dig their own dens, may dig snow and access fruits under snow cover more readily than Japanese martens, which use gaps in fallen trees and tree hollows as dens (Masuda 2018). The study findings emphasise that the degree of trophic niche overlap between carnivores may be affected by food abundance and climatic environment shifts, especially heavy snowfall.

Conclusions

This study has shown that carnivores share the main food items, and their annual dietary overlap is high in the cool-temperate zone of Japan. This result indicated that medium-sized carnivores have potential competitive interactions. Furthermore, high potential competitive carnivores coexisting with a high dietary overlap suggest that various factors besides niche partitioning in this area may facilitate coexistence among carnivores. Few studies have evaluated trophic niche partitioning among carnivore guilds in the East Asian region. Therefore, the findings of this study could provide important information for understanding the coexistence mechanisms among carnivores. The study findings have also shown that the combinations of potential competitive interactions change with the season, which may be affected by food abundance and environmental change based on climatic shifts, especially snow cover. Environmental changes, particularly global climate change, may affect the trophic niche and competitive relationships among carnivorous guilds. Long-term dietary surveys and evaluation of population dynamics are needed to clarify how environmental changes affect the interspecific relationships and community structure of carnivores.

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Author Contributions

T. Enomoto and M.U. Saito designed the study, T. Enomoto and R. Watabe conducted data collection, T. Enomoto conducted data 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.

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Supplementary online material

Table S1. Seasonal variation in the frequency of occurrence (FO, %) of insects and fruits based on red fox (RF), Japanese marten (JM), and raccoon dog (RD) faecal samples (https://www.ivb.cz/wp-content/uploads/JVB-vol.-72-2023-Enomoto-et-al.-Table-S1.pdf).