

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

Authors: Enomoto, Takaaki, Watabe, Ryoga, and Saito, Masayuki U.

Source: Journal of Vertebrate Biology, 72(23021)

Published By: Institute of Vertebrate Biology, Czech Academy of Sciences

URL: <https://doi.org/10.25225/jvb.23021>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

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

Takaaki ENOMOTO^{1*}, Ryoga WATABE² and Masayuki U. SAITO³

¹ The United Graduate School of Agricultural Sciences, Iwate University, Morioka, Japan; e-mail: t.enomoto6518@gmail.com

² Graduate School of Agricultural Sciences, Yamagata University, Tsuruoka, Japan; e-mail: hiatus7354@gmail.com

³ Faculty of Agriculture, Yamagata University, Tsuruoka, Japan; e-mail: saito.ume@gmail.com

► Received 23 February 2023; Accepted 28 March 2023; Published online 24 May 2023

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

* Corresponding Author



trophic niche differences among species is the first step in understanding community structure (Schoener 1983, Ray & Sunquist 2001, Juárez & 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 ($\times 20$) 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).

$\text{FO (\%)} = (\text{number of scats containing food category A} / \text{total number of scats}) \times 100$

$\text{RFO (\%)} = (\text{number of scats containing food category A} / \text{sum of the number of food categories in a scat}) \times 100$

$\text{PV (mean} \pm \text{SD, \%)} = [\Sigma (\text{number of grid points covered by food category A in a scat } i) / \text{total number of counted grid points of a scat } i) / \text{total number of scats}] \times 100$

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.

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

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": $0.90 \geq \alpha$, High: $0.90 > \alpha \geq 0.70$, Moderate: $0.70 > \alpha \geq 0.50$, and Low: $0.50 > \alpha$ (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

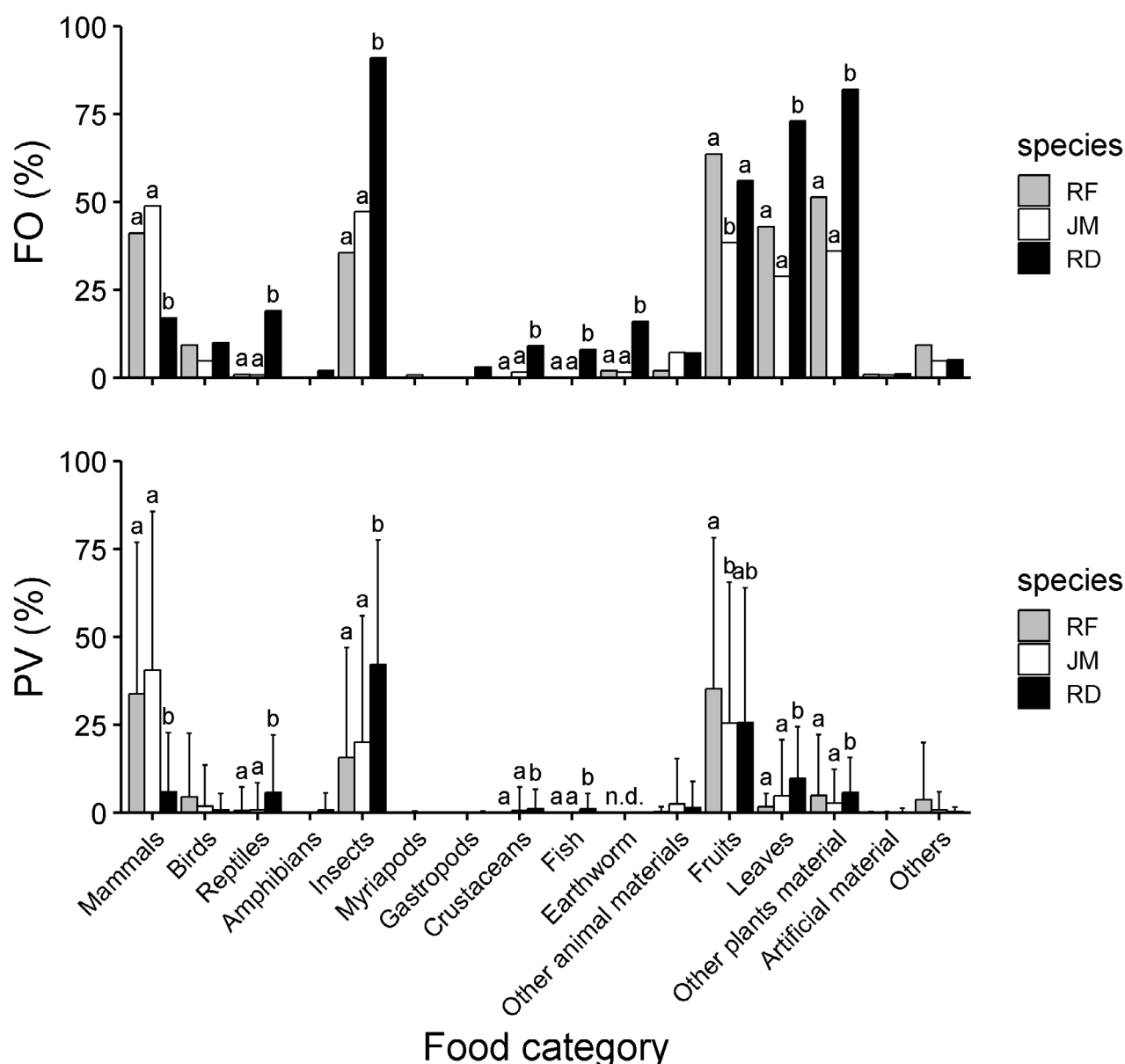


Fig. 1. Frequently of occurrence (FO, %) and per cent volume (PV, %) of each food category for the red fox (RF), Japanese marten (JM), and raccoon dog (RD) in the study area.

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	RD	RF	JM	RD
Number of samples	20	34	29	43	49	43	17	22	28	27	20	107	125	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	RD	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	RD	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

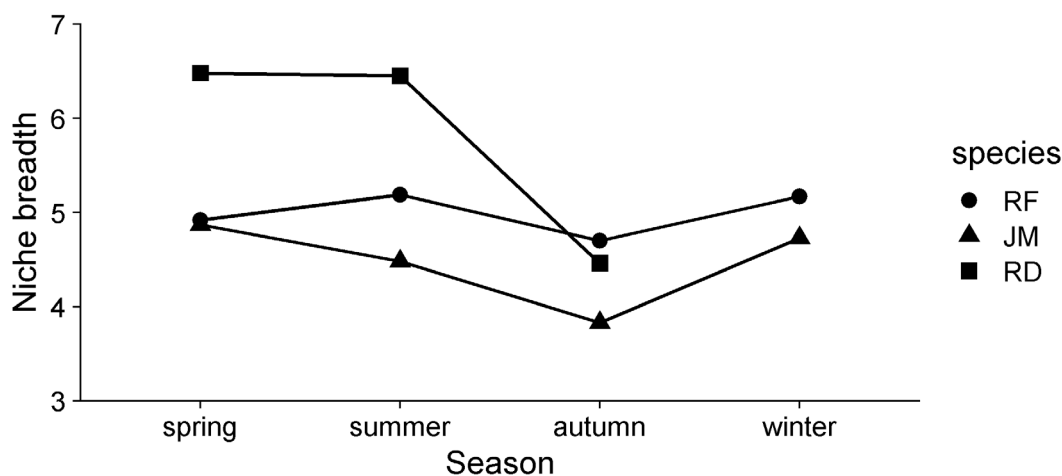


Fig. 2. Seasonal trophic niche breadth indices (B) for the red fox (RF), Japanese marten (JM), and raccoon dog (RD).

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" ($\alpha \geq 0.90$), "High" ($0.90 > \alpha \geq 0.70$), "Moderate" ($0.70 > \alpha \geq 0.50$), and "Low" ($0.50 > \alpha$).

season	Pianka's index α					
	RF-JM		RF-RD		JM-RD	
	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 ($\alpha = 0.65$; 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.

Acknowledgements

We thank the associates of Yamagata University for supporting our field survey. This study was supported by UGAS-IU Collaborative Research Grant Projects and UGAS-IU Student Research Grant Projects. The procedures of this study were in accordance with the national laws of Japan. The authors declare no competing interests.

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.



Literature

- Baltrūnaitė L. 2006: Diet and winter habitat use of the red fox, pine marten and raccoon dog in Dzūkija National Park, Lithuania. *Acta Zool. Litu.* 16: 46–53.
- Barrull J., Mate I., Ruiz-Olmo J. et al. 2014: Factors and mechanisms that explain coexistence in a Mediterranean carnivore assemblage: an integrated study based on camera trapping and diet. *Mamm. Biol.* 79: 123–131.
- Broekhuis F., Cozzi G., Valeix M. et al. 2013: Risk avoidance in sympatric large carnivores: reactive or predictive? *J. Anim. Ecol.* 82: 1098–1105.
- Chiang P.J., Pei K.J.C., Vaughan M.R. et al. 2012: Niche relationships of carnivores in a subtropical primary forest in southern Taiwan. *Zool. Stud.* 51: 500–511.
- Davis C.L., Rich L.N., Farris Z.J. et al. 2018: Ecological correlates of the spatial co-occurrence of sympatric mammalian carnivores worldwide. *Ecol. Lett.* 21: 1401–1412.
- Donadio E. & Buskirk S.W. 2006: Diet, morphology, and interspecific killing in Carnivora. *Am. Nat.* 167: 524–536.
- Enomoto T., Saito M.U., Yoshikawa M. et al. 2018: Winter diet of the raccoon dog (*Nyctereutes procyonoides*) in urban parks, central Tokyo. *Mamm. Study* 43: 275–280.
- Enomoto T., Suzuki M., Honda S. et al. 2022: Early autumn diet of introduced raccoon dogs on Okushiri Island, Hokkaido, Japan. *Nat. Environ. Sci. Res.* 35: 19–22. (in Japanese with English summary)
- Fukue Y., Takeshita T. & Nakanishi N. 2011: Diet analysis methods to assess the food habits of carnivore in Japan – I. Canidae, Mustelidae, Felidae. *Mamm. Sci.* 51: 129–142. (in Japanese)
- Gause G.F. 1934: Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* 79: 16–17.
- Hardin G. 1960: The competitive exclusion principle: an idea that took a century to be born has implications in ecology, economics, and genetics. *Science* 131: 1292–1297.
- Hayward M.W. & Slotow R. 2009: Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *S. Afr. J. Wildl. Res.* 39: 109–125.
- Hijikata K., Minami M. & Tsukada H. 2020: Food habits and habitat utilisation of the Japanese badger (*Meles anakuma*) in a grassland/forest mosaic. *Mamm. Study* 45: 229–242.
- Hinton J.W. & Chamberlain M.J. 2022: Evidence of reduced abundance, density, and survival of coyotes under federal management for red wolf recovery. *Ecosphere* 13: e4216.
- Hisano M., Evans M.J., Soga M. et al. 2021: Red foxes in Japan show adaptability in prey resource according to geography and season: a meta-analysis. *Ecol. Res.* 37: 197–214.
- Hisano M., Newman C., Deguchi S. et al. 2019: Thermal forest zone explains regional variations in the diet composition of the Japanese marten (*Martes melampus*). *Mamm. Biol.* 95: 173–180.
- Ikeda K., Endo A. & Iwamoto T. 2006: Estimating deer density by the pellet count method in south-west Japan. *Forest Pests* 55: 169–176. (in Japanese)
- Inagaki A., Allen M.L., Maruyama T. et al. 2020: Vertebrate scavenger guild composition and utilisation of carrion in an East Asian temperate forest. *Ecol. Evol.* 10: 1223–1232.
- Japan Meteorological Agency 2022: Climate data of Tsuruoka in 2022. Downloaded on 22 December 2022. http://www.data.jma.go.jp/obd/stats/etrn/view/nml_amd_ym.php?prec_no=35&block_no=0263&year=&month=&day=&view=p1
- Juarez K.M. & Marinho-Filho J. 2002: Diet, habitat use, and home ranges of sympatric canids in central Brazil. *J. Mammal.* 83: 925–933.
- Kaneko Y., Maruyama N. & Macdonald D.W. 2006: Food habits and habitat selection of suburban badgers (*Meles meles*) in Japan. *J. Zool.* 270: 78–89.
- Krebs C.J. 2014: Ecological methodology, 3rd ed. Benjamin-Cummings Publishing Company, San Francisco, USA.
- Krohn W.B., Elowe K.D. & Boone R.B. 1995: Relations among fishers, snow, and martens: development and evaluation of two hypotheses. *For. Chron.* 71: 97–105.
- Kumagai N. & Saito M.U. 2022: Seasonal changes in the food habits of raccoon dogs in a cool temperate forest on the Japan Sea side around the Tohoku region. *Tohoku J. For. Sci.* 27: 1–10 (in Japanese with English summary)
- Masuda R. 2018: Carnivores in Japan: mammals at the top of the ecosystem. University of Tokyo press, Tokyo, Japan. (in Japanese)
- Munekane H., Minami M. & Takatsuki S. 2021: Food habits of Japanese marten (*Martes melampus*) in a larch forest in the montane zone of Nagano Prefecture, central Japan. *Mamm. Sci.* 61: 39–47. (in Japanese with English summary)
- Mustonen A.M. & Nieminen P. 2018: A review of the physiology of a survival expert of big freeze, deep snow, and an empty stomach: the boreal raccoon dog (*Nyctereutes procyonoides*). *J. Comp. Physiol. B* 188: 15–25.
- Müller L., Briers-Louw W.D., Amin R. et al. 2022: Carnivore coexistence facilitated by spatial and



- dietary partitioning and fine-scale behavioural avoidance in a semi-arid ecosystem. *J. Zool.* 317: 114–128.
- Nagasaki K., Nakamura H., Shinohara A. et al. 2022: A comparison of summer insectivory among four sympatric mesocarnivores on Izushima, a small island in northern Japan. *Mammalia* 87: 110–121.
- Nakane A., Enomoto T. & Saito M.U. 2022: Utilization of cultivated fruits by Japanese martens and red foxes in a snowy environment: a comparison of feeding habits between rural and forest landscapes. *J. Vertebr. Biol.* 71: 22028.
- Noma N. 1997: Mutualism between plants and birds/mammals by seed dispersal in Yakushima Island. *Primate Res.* 13: 137–147. (in Japanese with English summary)
- Ohdachi S.D., Ishibashi Y., Iwasa M.A. et al. 2015: The wild mammals of Japan, 2nd ed. *Shoukadoh Book Sellers, Kyoto, Japan.*
- Otani T. 2003: Seed dispersal and predation of fleshy-fruited plants by Japanese macaques in the cool temperate zone of northern Japan. *Mamm. Study* 28: 153–156.
- Palomares F. & Caro T.M. 1999: Interspecific killing among mammalian carnivores. *Am. Nat.* 153: 492–508.
- Pereira P., Alves da Silva A., Alves J. et al. 2012: Coexistence of carnivores in a heterogeneous landscape: habitat selection and ecological niches. *Ecol. Res.* 27: 745–753.
- Pianka E.R. 1973: The structure of lizard communities. *Annu. Rev. Ecol. Syst.* 4: 53–74.
- Polis G.A., Myers C.A. & Holt R.D. 1989: The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20: 297–330.
- R Core Team 2022: R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.*
- Ray J. & Sunquist M. 2001: Trophic relations in a community of African rainforest carnivores. *Oecologia* 127: 395–408.
- Roemer G.W., Gompper M.E. & Van Valkenburgh B. 2009: The ecological role of the mammalian mesocarnivore. *Bioscience* 59: 165–173.
- Schoener T.W. 1983: Field experiments on interspecific competition. *Am. Nat.* 122: 240–285.
- Soe E., Davison J., Süld K. et al. 2017: Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox *Vulpes vulpes*: a quantitative review. *Mammal Rev.* 47: 198–211.
- Sutor A., Kauhala K. & Ansorge H. 2010: Diet of the raccoon dog *Nyctereutes procyonoides* – a canid with an opportunistic foraging strategy. *Acta Theriol.* 55: 165–176.
- Sutou M. 2005: The Bibionidae (Diptera) of the Akasaka Imperial Gardens and the Tokiwamatsu Imperial Villa, Tokyo. *Mem. Natn. Mus. Nat. Sci.* 39: 269–272. (in Japanese with English summary)
- Suzuki M. & Saito M.U. 2023: Forest road use by mammals revealed by camera traps: a case study in northeastern Japan. *Landsc. Ecol. Eng.* 19: 289–296.
- Takatsuki S. 2013: Applicability of the point-frame method for food habit analysis for various mammals. *Mamm. Sci.* 53: 89–98. (in Japanese with English summary)
- Takatsuki S. & Tatewaki T. 2012: Applicability of the point-frame method as a food habit analysis method for omnivorous mammals: a case study on medium-sized carnivores. *Mamm. Sci.* 52: 167–177. (in Japanese with English abstract)
- Tochigi K., Steyaert S.M., Naganuma T. et al. 2022: Differentiation and seasonality in suitable microsites of seed dispersal by an assemblage of omnivorous mammals. *Glob. Ecol. Conserv.* 40: e02335.
- Tsuji Y., Ito T.Y. & Kaneko Y. 2019: Variation in the diets of Japanese martens *Martes melampus*. *Mammal Rev.* 49: 121–128.
- Tsuji Y., Uesugi T., Shiraishi T. et al. 2011: Faecal size criteria to discriminate Japanese marten (*Martes melampus*) and Japanese weasel (*Mustela itatsi*). *J. Jpn. Assoc. Zoo. Aqu.* 52: 8–15. (in Japanese with English summary)
- Tsukada H. & Nonaka N. 1996: Foraging behavior of red foxes *Vulpes vulpes schrencki* utilising human food in the Shiretoko National Park, Hokkaido. *Mamm. Study* 21: 137–151.
- Tsunoda H., Raichev E.G., Newman C. et al. 2017: Food niche segregation between sympatric golden jackals and red foxes in central Bulgaria. *J. Zool.* 303: 64–71.
- Vanak A.T., Fortin D., Thaker M. et al. 2013: Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* 94: 2619–2631.
- Vogel J.T., Somers M.J. & Venter J.A. 2019: Niche overlap and dietary resource partitioning in an African large carnivore guild. *J. Zool.* 309: 212–223.
- Waggershauser C.N., Ruffino L., Kortland K. et al. 2021: Lethal interactions among forest-grouse predators are numerous, motivated by hunger and carcasses, and their impacts determined by the demographic value of the victims. *Ecol. Evol.* 11: 7164–7186.



- Watabe R. & Saito M.U. 2021: Diel activity patterns of three sympatric medium-sized carnivores during winter and spring in a heavy snowfall area in northeastern Japan. *Mamm. Study* 46: 69–75.
- Watabe R. & Saito M.U. 2022: Winter weather conditions result in temporal niche overlap among three sympatric medium-sized carnivores in northeastern Japan. *Behav. Ecol. Sociobiol.* 76: 164.
- Watabe R., Tsunoda H. & Saito M.U. 2022: Evaluating the temporal and spatio-temporal niche partitioning between carnivores by different analytical method in northeastern Japan. *Sci. Rep.* 12: 11987.
- Willebrand T., Willebrand S., Jähren T. et al. 2017: Snow tracking reveals different foraging patterns of red foxes and pine martens. *Mammal Res.* 62: 331–340.
- Zapata S.C., Travaini A., Ferreras P. et al. 2007: Analysis of trophic structure of two carnivore assemblages by means of guild identification. *Eur. J. Wildl. Res.* 53: 276–286.
- Zhang L.J., Wang A.M., Yuan L. et al. 2011: Preliminary comparison of diet composition of four small sized carnivores at Saihanwula Nature Reserve, Inner Mongolia. *Acta Theriol. Sin.* 31: 55–61. (in Chinese with English summary)
- Zhou Y.B., Newman C., Buesching C.D. et al. 2011: Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *J. Biogeogr.* 38: 137–147.
- Zielinski W.J., Tucker J.M. & Rennie K.M. 2017: Niche overlap of competing carnivores across climatic gradients and the conservation implications of climate change at geographic range margins. *Biol. Conserv.* 209: 533–545.
- Zuercher G.L., Owen R.D., Torres J. et al. 2022: Mechanisms of coexistence in a diverse Neotropical mammalian carnivore community. *J. Mammal.* 103: 618–638.

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>).