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INSECTIVORY CHARACTERISTICS OF THE JAPANESE MARTEN (*MARTES MELAMPUS*): A QUALITATIVE REVIEW

REVIEW PAPER

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Abstract. Insects are rich in protein and thus are important substitute foods for many species of generalist feeders. This study reviews insectivory characteristics of the Japanese marten (*Martes melampus*) based on current literature. Across the 16 locations (14 studies) in the Japanese archipelago, a total of 80 different insects (including those only identified at genus, family, or order level) were listed as marten food, 26 of which were identified at the species level. The consumed insects were categorised by their locomotion types, and the Japanese martens exploited not only ground-dwelling species, but also arboreal, flying, and underground-dwelling insects, taking advantage of their arboreality and ability of agile pursuit predation. Notably, immobile insects such as egg mass of Mantodea spp, as well as pupa/larvae of *Vespula flaviceps* and *Polistes* spp. from wasp nests were consumed by the Japanese marten in multiple study areas. This review shows dietary generalism (specifically 'food exploitation generalism') of the Japanese marten in terms of non-nutritive properties (i.e., locomotion ability of prey).

INTRODUCTION

Dietary generalists have capability to adapt their foraging strategies by switching to alternative foods according with fluctuations in prey abundance induced by environmental and climatic conditions (e.g., Zhou et al. 2011a; Soe et al. 2017; Hisano et al. 2019). Martens (*Martes* spp., Carnivora: Mustelidae) are one of the typical generalist feeders. They primarily consume rodents, but their main food and diet composition can vary spatially and temporally, depending on environmental conditions (Zhou et al. 2011a). For example, annual trophic diversity of martens increases with increasing temperature (or latitude) (Zalewski 2004; Zhou et al. 2011a). Seasonally, martens tend to eat fruits and invertebrates more frequently in a warmer season (summer/autumn) than a colder season (Zalewski 2004; Hisano et al. 2019). Therefore, information of martens' alternative prey (e.g., fruits, invertebrates, herptiles) is important to understand their dietary generalism and flexibility with climatic and environmental variations.

This paper focuses on insectivory of the Japanese marten (*Martes melampus*), of which life history has been relatively understudied compared to the other martens in western countries but its dietary information has recently been growing (see Hisano et al. 2019; Hisano in press). The Japanese marten is native to the three main Japanese islands of Honshu, Shikoku, and Kyushu. Although insects are usually martens' secondary prey, they have important functions for martens with both nutritive and non-nutritive aspects (*sensu*, Machovsky-Capuska et al. 2016); i.e., insects are rich in protein as well as mammals (Remonti, Balestrieri, and Prigioni 2011; Remonti et al. 2016) and they can be easily and safely accessed compared to larger and more agile rodents (see Zhou et al. 2011b; Hisano et al. 2016). Remarkably, Japanese marten populations from two out of nine study areas reviewed in Hisano et al. (2019) ate invertebrates (mainly insects) most frequently (based on the relative frequency of occurrence, RFO). Moreover, the RFO of invertebrates was one of the determinants that explained the geographical variation in diet composition of the Japanese marten (Hisano et al. 2019). Thus, insects should be essential components of the Japanese marten diet as supplementary prey. A systematic list of insect species consumed by the Japanese marten (*cf*. regional scale, Koike et al. 2012; see also Peeva, Mikov, and Georgiev 2018) would improve our knowledge on its feeding ecology. However, such insectivory inventory across the distribution range of the Japanese marten is not available despite intensive reviews on frugivory of martens as well as other medium-sized carnivores (e.g. Koike and Masaki 2008; Rosalino and Santos-Reis 2009; Kurek 2015; Takatsuki 2017; Hisano and Deguchi 2018; Hisano 2018). Here I review the literature on insectivory of the Japanese marten and discuss its characteristics with special reference to locomotion types of the consumed insects.

LITERATURE COMPILATION

I browsed peer-reviewed papers and local anecdotal (non-reviewed) reports on diet composition and insectivory of the Japanese marten, including a subspecies *M. melampus tsuensis* (Kurose, Masuda, and Tatara 2005) in the Tsushima Islands (southern Japan), as of October 2018. For this purpose, I used *Google Scholar* (https://scholar.google.com), *ISI Web of Science* (http://apps.webofknowledge.com), and *Citation Information by National Institute of Informatics* (http://ci.nii.ac.jp). To browse papers written in English or Japanese, I entered different combinations of keywords: "Japanese marten", "*Martes melampus*", "diet", "food", "insectivory", "tenn" (martens in Japanese), "Hondo-tenn" (the Japanese marten in Japanese), "Nihon-tenn" (a synonym of the Japanese marten in Japanese), "Tsushima-tenn" (the subspecies *M. melampus tsuensi* in Japanese), and "shokusei" (diet in Japanese). In addition, a regional report of author's prior knowledge (Kitahara 1985; Miyano and Ochiai 2000; Hirakawa and Sayama 2005) was also included.

All the insect species exploited by the Japanese marten were then listed. To be consistent with the regional insectivory study on the Japanese marten (Koike et al. 2012), I exclusively focused on "true insects" (i.e., Insecta). When insects were not identified at the species level in the study, they were recorded as '*Genus* spp.' or 'Family spp.' (Hisano and Deguchi 2018). I then noted information of locomotion types ('arboreal mobile','flying', 'ground mobile', 'immobile', and 'underground mobile') of the insect prey based on reliable literature (Furukawa and Nakayama 1994; Kurosawa, Watanabe, and Kuribayashi 2006) and the author's prior knowledge from field observations.

INSECTIVORY CHARACTERISTICS OF THE JAPANESE MARTEN

A total of 18 publications from 14 study areas across the range of the Japanese marten were compiled (Figure 1). Among these publications, 80 different insects (including those identified to family or genus level) were recorded as marten food, 26 of which were identified at the species level (Table 1). Although information about the frequency and abundance of consumed insect species was not available, the largest number of species were eaten from taxa of Coleoptera (18 species and 21 genera from nine families) and Orthoptera (eight species and 15 genera from six families; Table 1). Moreover, Coleoptera spp. (particularly *Carabus* spp.) and Orthoptera spp.

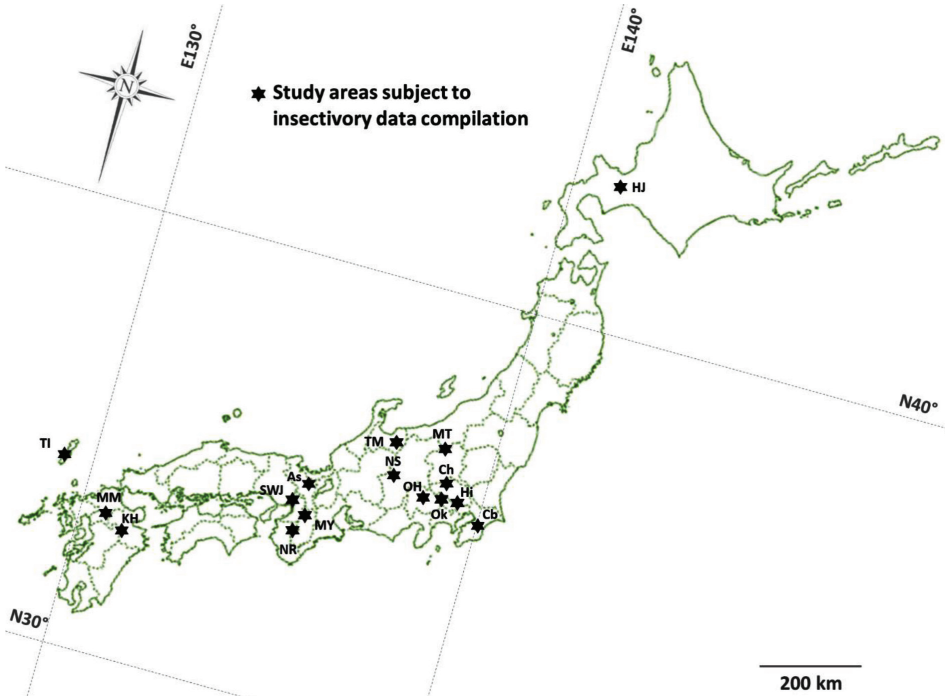

Figure 1. Geographical locations of 14 reviewed studies (16 localities) across the Japanese archipelago from which insectivory information was extracted. Dashed grey lines indicate latitude and longitude. MT: Mt. Tairappyo (Hisano et al. 2017), Ch: Chichibu (Yamagishi 1990), Ok: Okutama (Koike et al. 2012), Hi: Hinode (Nakamura, Kanzaki, and Maruyama 2001), Cb: Chiba (Miyano and Ochiai 2000), NS: Nishikoma Forest of Shinshu University (Suzuki et al. 1976, 1977), OH: Otome Highland (Adachi et al. 2016a), TM: Tateyama Mountains (Kitahara 1985), As: Ashiu (Kondo 1980), MY: Mt. Yamato-Katsuragi (Kusui and Kusui 1995, 1998), NR: Neko River (Shiratsuki 1972), KH: Kuju Highland (Arai et al. 2003), TI: Tsushima Islands (Asahi and Okuhama 1971; Tatara and Doi 1994; Okawara, Nakanishi, and Izawa 2018), SWJ: Southwestern Japan (compiled data from Prefectures of Mie, Shiga, Nara, Kyoto, Osaka, Hyogo, Ehime, Miyazaki, and Kagoshima; Shiratsuki, Asaki, and Yoshida 1973), MM: Mt. Momi (Adachi et al. 2016b), HJ: Higashi-Jozankei National Forest (Hirakawa and Sayama 2005).

Table 1. Insects consumed by the Japanese marten that were recorded in the reviewed papers.

Identified taxa		Locomotion type[a]	Study area[b]
ODONATA			
	Odonata spp.	Fly	TI, KH, Hi
DERMAPTERA			
Psalididae	*Aniscelalis maritema*	Gr	TI
PLECOPTERA			
	Plecoptera spp.	Fly	NR
ORTHOPTERA			
	Orthoptera spp.	Gr	KH, CM, Ch, MM, Hi, NR, SWJ, NS, MT, TI
Acrididae	Acrididae spp.	Gr	TI
Catantopidae	Melanoplinae spp. (subfamily)	Gr	Ok
	Atractomorpha lata	Gr	Ok
Gryllidae	Gryllidae spp.	Gr	Ok, TI, CM
	Teleogryllus emma	Gr	TI
Rhaphidophoridae	Rhaphidophoridae spp.	Gr	Ok, MM, OH, MY, TI
	Diestrammena apicalis	Gr	MY
Tettigoniidae	Tettigoniidae spp.	Gr	TI, As, SWJ
	Listroscelidinae spp. (subfamily)	Gr, Ar	Ok
	Hexacentrus japonicus	Gr	TI
	Euconocephalus thunbergi	Gr	Ok
	Gampsocleis buergeri	Gr	TI
	Parathantica spp.	Gr	TI
	Conocephalus melas	Gr	TI
Stenopelmatidae	Stenopelmatidae spp.	Gr	TI
MANTODEA			
	Mantodea spp.†	Imago: Gr Egg mass: Gr, Ar	TI, MM, OH
Mantidae	*Tenodera angustipennis*	Gr	TI
	Paratenodera ciriditalia	Gr	TI
	Acromantis japonica	Gr	TI
BLATTODEA			
Blaberidae	Blaberidae spp.*		TI
	Panesthia angustipennis spadica	Gr	TI
HEMIPTERA			
	Hemiptera spp.	–	TI, MT
Cicadidae	Cicadidae spp.**	Imago: Fly, Ar Larva: Ug, Gr, Ar	MM, OH
	Platypleura kaempferi	Fly, Ar	Ok, TI
	Graptopsaltria nigrofuscata	Fly, Ar	Ok
	Tanna japonensis	Fly, Ar	Ok
	Oncotympana maculaticollis	Fly, Ar	Ok
Scutelleridae	*Poecilocoris lewisi*	Fly, Gr, Ar	Ok
Acanthosomatidae	Acanthosomatidae spp.	Fly, Gr, Ar	Ok
Pentatomidae	Pentatomidae spp.	Fly, Gr, Ar	MN
HYMENOPTERA			
	Hymenoptera spp.	Fly	TI, CM, Ch, Hi, MY, SWJ, NS, MT
Apidae	*Apis cerana*	Fly	Ok, TI
	Xylocopa appendiculata	Fly	TI
Bombidae	*Bombus* spp.	Fly	TI
Ichneumonidae	Ichneumonidae spp.	Fly	TI
Halictidae	Halictidae spp.	Fly	TI
Vespidae	*Vespula flaviceps**	Imago: Fly Larva/pupa: Im	Ok, Cb, TM, NS, HJ
	Vespula shidai	Fly	Ok

	Identified taxa	Locomotion type[a]	Study area[b]
	Vespula schrenckii	Fly	Ok
	Polistes spp.**	Larva: Im	MM
Formicidae	Formicidae spp.	Gr	TI, NS
COLEOPTERA			
	Coleoptera spp.	–	KH, CM, Ch, MM, OH, Hi, MY, NR, SWJ, NS, MT, TI
Carabidae	Carabidae spp.	Gr	As, MN, MY, NR, SWJ, TM, NS
	Carabus albrechti	Gr	Ok
	Carabus japonicus tushimae	Gr	TI
	Leptocarabus procerulus	Gr	Ok
	Damaster fruhstorferi	Gr	TI
	Cicindelidae spp.	Gr, Fly	TI
Harpalidae	Harpalidae spp.	Gr	TI, As, MN, NS
	Pterostichus rhanis	Gr	Ok
Silphidae	Silphidae spp.	Gr, Fly	Ok, TI, MN
Lucanidae	Lucanidae spp.	Ar	TI, As, NR, SWJ, NS
	Lucanus maculifemoratus	Ar	Ok, TI
	Dorcus montivagus	Ar	Ok
	Dorcus rubrofemoratus	Ar	Ok
	Dorcus titanus castanicolor	Ar	TI
Scarabaeidae	Scarabaeidae spp.*	–	TI, MN, NS
	Trypoxylus dichotomus	Ar	Ok, TI
	Rhomborrhina japonica	Ar	TI
	Rhomborrhina unicolor	Ar	TI
	Luchno sterna	Iu	TI
	Luchno moroaa	Iu	TI
	Anomala spp.	Fly, Gr, Ar	TI
	Anomala testaceipes	Fly, Gr, Ar	TI
Elateridae	Elateridae spp.*	Gr	Ok, TI
Tenebrionidae	Tenebrionidae spp.	Gr	TI
Carambycidae	*Prionus insularis*	Gr	TI
	Arhopalus rusticus	Gr	TI
	Megopis sinica		TI
Curculionidae	Curculionidae spp.	Gr	TI
DIPTERA			
	Diptera spp.	Fly	Ch, Hi, NS, MT
Bibionidae	*Bibio* spp.	Fly	TI
LEPIDOPTERA			
	Lepidoptera spp.	Fly	TI, Ch
Hepialidae	Hepialoidea spp.	Fly	Ok
Saturniidae	Saturniidae spp.**	Imago: Fly Larva: Ar	Ok
TRICHOPTERA			
	Trichoptera spp.	Fly	Ch, NR

[a] Ar: arboreal mobile, Fly: flying, Gr: ground mobile, Im: immobile, Ug: underground mobile, Iu: information unavailable.

[b] MT: Mt. Tairappyo (Hisano et al. 2017), Ch: Chichibu (Yamagishi 1990), Ok: Okutama (Koike et al. 2012), Hi: Hinode (Nakamura, Kanzaki, and Maruyama 2001), Cb: Chiba (Miyano and Ochiai 2000), NS: Nishikoma Forest of Shinshu University (Suzuki et al. 1976, 1977), OH: Otome Highland (Adachi et al. 2016a), TM: Tateyama Mountains (Kitahara 1985), As: Ashiu (Kondo 1980), MY: Mt. Yamato-Katsuragi (Kusui and Kusui 1995, 1998), NR: Neko River (Shiratsuki 1972), KH: Kuju Highland (Arai et al. 2003), TI: Tsushima Islands (Asahi and Okuhama 1971; Tatara and Doi 1994; Okawara, Nakanishi, and Izawa 2018), SWJ: Southwestern Japan (compiled data from Prefectures of Mie, Shiga, Nara, Kyoto, Osaka, Hyogo, Ehime, Miyazaki, and Kagoshima; Shiratsuki, Asaki, and Yoshida 1973), MM: Mt. Momi (Adachi, Kiwakara, and Takatsuki 2016b), HJ: Higashi-Jozankei National Forest (Hirakawa and Sayama 2005).

* Including larvae or pupa

** Exclusively larvae

†Including egg mass

were consumed in the largest number of study areas (12 and 10 study areas, respectively; Table 1). Therefore, these two taxa could have been the common insects consumed by the Japanese marten although information about how much and how frequently the martens consumed each species of insect would be needed to confirm if this is correct. With regards to locomotion types among the insect prey, 16 species (12 genera, 10 families, and four orders) were categorised into the arboreal mobile type, 13 species (16 genera, 18 families, and eight orders) were included in the flying type, 21 species (21 genera, 20 families, and eight orders) were assigned as the ground mobile type, and one family (larvae of Cicadedae, Hemiptera) was defined as the underground mobile type (Table 1).

The present review revealed that the Japanese marten preyed upon highly diverse insect taxa across its range. Remarkably, it is also suggested that the marten can hunt insects with various types of locomotory ability – not only ground-dwelling (e.g., Carabidae) but also arboreal (e.g., Lucanidae, Cicadidae) insects. Indeed, martens are able to hunt even more agile arboreal mammals such as squirrels (*Sciurus* spp.) and dormice (Gliridae spp.) (Lanszki, Zalewski, and Horváth 2007; Zalewski 2007; Hisano et al. 2014, 2017). The ability of martens to climb trees allows them to forage for prey inhabits arboreal (three-dimensional; *sensu* Koike et al. 2012) habitats, and consumption of arboreal insects was greater for martens compared to other sympatric medium-sized carnivores (*Meles anakuma*, *Vulpes Vulpes japonica*, *Nyctereutes procyonoides*; foraging in two-dimensional habitats) in central Japan (Koike et al. 2012). Moreover, Japanese martens consumed a substantial number of flying insect species (e.g., Hymenoptera, Diptera) although they could also have caught them when these insects were on the ground. This is not surprising, considering martens' ability to hunt swifter small birds. This study also found that larvae of Cicadedae, which are underground-dwelling, most likely to have been caught by martens when these larvae emerged above ground as they were eaten during summer (Adachi et al. 2016a, b). As for hypogean insect prey, there is record that stone martens (*M. foina*) consumed *Gryllotalpa gryllotalpa* (Hisano et al. 2016); however, such evidence was not found for the Japanese marten from the reviewed literature. Interestingly, the Japanese marten also consumed immobile insects such as egg mass of Mantodea (Table 1). Immobile food items are abnormal given that martens usually hunt active prey, but they are assumed to be an important protein source in winter (Adachi et al. 2016a, b). Pupa and/or larvae of *Vespula flaviceps* and *Polistes* spp. from wasp nests were another example of immobile prey, which were consumed in summer. Bears (*Ursus* spp.) and crested honey buzzards (*Pernis ptilorhynchus*) are the common consumers of Vespidae (Koike et al. 2012), but the present review clarified that these wasps and their nests can be attacked by the Japanese marten in a wide range of geographical areas (observed in six locations; Table 1).

Other than these characteristics in locomotion types, it is notable that the Japanese marten ate both soft (e.g., Orthoptera, Hymenoptera) and hard bodied (e.g., Coleoptera with elytra) insects. In addition, this review found that martens could even eat tiny insects including Formicidae (e.g., <5–10 mm).

Having evolved a lean and elongate body (see Brown and Lasiewski 1972), martens are suited to arboreality and agile pursuit predation (Nieminen et al. 2007; Newman et al. 2011). The Japanese marten makes good use of this ability to hunt not only small mammals and birds, but also insects with various locomotion types (i.e., non-nutritive properties; *sensu*, Machovsky-Capuska et al. 2016). Insect prey is thus essential for the Japanese marten as a substitute source of protein that can be obtained with fewer difficulties, particularly in summer when their abundance reaches its seasonal peak (see Hisano et al. 2017, 2019), or alternatively when mammalian prey and fruits are relatively scarce [mammals are consumed most frequently in spring (Hisano et al. 2019), and fruits are generally eaten in autumn and winter (Hisano et al. 2017, 2019)].

TOWARDS THE FUTURE RESEARCH INTO THE MARTEN INSECTIVORY

As information of frequency or abundance of insect occurrence for each taxon was unavailable from the reviewed studies, it was not possible to quantitatively assess insectivory of the Japanese marten in relation to its preys' locomotion types (see also Hisano and Deguchi 2018). Moreover, in comparison with the previous study that reviewed fruit species consumed by the Japanese marten (Hisano and Deguchi 2018), the accuracy of species identification was substantially lower for this study [(i.e., fewer insects were identified at the species level (26 species/80 insect taxa compiled *vs* 121 species/140 fruit taxa compiled; Hisano and Deguchi 2018)]. Some insect species inhabit specific habitats and geographical areas, being restricted by environmental factors (e.g., climate, soil moisture, microtopography), and thus these species can be useful as indicators for habitat type or quality (Koike et al. 2012). Therefore, identifying consumed insects at the species level can help understand habitat preference of the Japanese marten (Koike et al. 2012). To enhance insect species identification, it is recommended to (i) collect specimens from the study area (see Hisano et al. 2016, 2017); (ii) employ DNA barcoding techniques (Valentini et al. 2009); and (iii) collaborate with insect taxonomists.

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