**INTRODUCTION**

One of the most important aspects of mammal ecology is nutritional condition. Together with the environment, diet composition (food items, volume of food, and nutritional content) influences spatial distribution, and social and foraging behaviour, as well as growth (Iriante et al. 1990, Gende & Quinn 2004, Zalewski & Bartoszewicz 2012). Therefore, diet can be a target of natural selection (Stephens & Krebs 1986). Studies on seasonal variation in mammalian diets at local scales have contributed to understanding of diet-related traits, such as inter- and intra-group...
competition, home range use, and population dynamics (O’Donoghue et al. 1998).

Food availability and climate vary spatially; therefore, we hypothesised that the main food items chosen by omnivorous carnivores vary across their geographic ranges in response to variation in environmental conditions (Bojarska & Selva 2012, Díaz-Ruiz et al. 2013). A study on the variation in diet with respect to environmental variation has the potential to generate interesting hypotheses.

Diets of carnivorous mammals vary over space and time in response to environmental factors (Zalewski 2005, Lozano et al. 2006, Remonti et al. 2009, Díaz-Ruiz et al. 2013). For example, small mammals are least abundant and vegetable matter and insects are more abundant in the diets of pine martens Martes martes at low latitudes (35–40°N) or low elevations (<500 m) than at higher latitudes (50–60°N) or higher elevations (>1000 m; Zalewski 2005, Zhou et al. 2011). This relationship originates from the spatial patterns of availability and diversity of primary foods (Owen 1990, Villafuerte et al. 1998) and fruits (Elder 2004, Ting et al. 2008, Moles et al. 2009). However, several researchers have failed to find any regional variations in food habits in this species (Roper & Mickevicius 1995, Virgós et al. 1999). The inconsistencies among the studies could be attributed to a lack of evaluating the relative contribution of each potential factor to animal foraging.

We studied Japanese martens Martes melampus, which are distributed widely through the Japanese archipelago (range: 31–42 °N; Ohdachi et al. 2009), but for which few studies on variation in diet have been conducted (but see Hisano et al. 2018). Specifically, we 1) tested whether environmental factors explain variations in martens’ dietary composition and its diversity, in parallel to variation in geographical factors and forest types, and 2) identified environmental factors that describe the variation in the dietary composition and its diversity.

METHODS

Literature review and standardisation

We conducted a web-based survey of dietary studies of Japanese martens. We searched ISI Web of Science (http://apps.webofknowledge.com/) and Google Scholar (http://scholar.google.co.jp/) for the keywords 'Japanese marten’’, 'Martes melampus’’, ‘diet’*, ‘feeding’*, ‘food’*, and ‘foraging’* in both English and Japanese. We only included studies that contained 1) information for multiple seasons, 2) information on the location of the study site, and 3) the frequency of occurrence (FO) of food types in the diet. We obtained data for 21 sites in 26 studies, ranging from 146 to 1800 m in elevation; nine sites were in evergreen forests and 12 sites in deciduous forests (Fig. 1).

We placed food items in eight categories: 1) mammals, 2) birds (including their eggs), 3) other vertebrates (including reptiles, amphibians, fish, and unidentified), 4) insects, 5) non-insect invertebrates (including centipedes, spiders, crustaceans, molluscs, and others), 6) fruits (including seeds), 7) other plant parts (including foliage, flowers, and branches), and 8) others (including human foods, mushrooms, and unknown). We pooled data for sites with > 1 study. We calculated the diversity of diets using the Shannon index (H’) by means of the following formula (Begon et al. 2006):

\[ H' = - \sum FO_i \cdot \log_{10} FO_i \]

where FO_i represents the frequency of occurrence of food i. This equation is biased to an unknown degree, since FO is affected both by prey size (small prey is more easily detected in scats than large prey) and by other aspects of food types that affect their detectability in scats. We omitted the study by Otani (2002) from this calculation due to the lack of information on non-fruit items in the diet.

Selection of variables

We obtained data on latitude (with 0.1° resolution) and mean elevation (m) from the source article, or from Google Earth (http://earth.google.com). We defined latitude and elevation as geographical variables.

We extracted data for each study site on the annual mean temperature (0.1°C resolution), mean annual rainfall (mm), and mean snow depth (cm) from November to March (Tsuji 2010). Except for the Ashu Experimental Forest, in which systematic weather information was available (Ando et al. 1989), we obtained weather information from the nearest weather station to each study site (http://www.data.jma.go.jp/). We used the normalised difference vegetation index (NDVI) as an index of primary productivity (Pettorelli et al. 2011). NDVI ranges between −1 and +1 (positive values: existence of plants, value is related to plant biomass; negative values: non-vegetated surfaces; Ito et al. 2005, Pettorelli et al. 2011). We downloaded 16-day composite and 250-m resolution NDVI data (MYD13Q1) for each study site from the National Aeronautics and Space Administration (NASA), Goddard Space Flight Center (http://modis-land.gsfc.nasa.gov/vi.html). For each study site, we calculated the mean values of the NDVI within a circle with a radius of 2.5 km (ca. 19.6 km²), which represents the mean home range size of Japanese martens (Tatara 1993, Kurushima 1998, Yamanashi Prefecture 2009), and we calculated the mean of 16 NDVIs from 2000, 2003, 2005, 2007, 2010, 2012, 2015, and 2017 in spring (7–22 April), summer (26 June to 11 July), autumn (30 September to 15
October), and winter (1–16 January). Using the geographical information system software ArcGIS, version 10.1 (ESRI, California, USA), we extracted the mean NDVI. We also calculated seasonal variation of NDVI (defined as maximum–minimum, represents an indicator of seasonal changes to forest productivity; Imai et al. 2017). We defined temperature, rainfall, snow depth, NDVI, and variation of NDVI as environmental variables.

**Statistical analysis**

We analysed the FOs of eight food categories (see description above, angular transformed) by multivariate analysis of variance (MANOVA) using the two geographical variables and five environmental variables as explanatory variables. If an explanatory variable had a significant effect, we then performed a series of generalised linear models (GLMs) to search for specific food categories for which variation was related to the target explanatory variable. Since variation in FOs of mustelids often shows non-linear trends across their geographic range (e.g. Zalewski 2005), we performed a quadratic least square regression. We compared the FO of each food category and dietary diversity between two forest types (deciduous forests and evergreen forests, see Fig. 1) using t-tests. We conducted statistical analyses with R v.3.2.4 (R Development Core Team 2016). Because many researchers had pooled the samples collected in multiple seasons, we did not address seasonal variation in diets (see Zalewski 2005).

**RESULTS**

**Geographical and environmental factors and overall diet**

The geographical and environmental variables, except for annual rainfall, mean NDVI, and NDVI variation, were significantly different between the two forest types (latitude: $U = 94.0$, $P = 0.003$; elevation: $U = 102.0$, $P < 0.001$; rainfall: $U = 28.0$, $P = 0.070$; temperature: $U = 4.5$, $P < 0.001$; snow depth: $U = 93.0$, $P = 0.006$; mean NDVI:}
Table 1. Summary of the results of multivariate analyses of variance (MANOVA) and generalised linear models (GLMs) on dietary composition and dietary diversity of Japanese martens

| Variables                  | MANOVA | GLM                  | F-value | P-value | Linear          | Non-fruit | Mammals | Birds | Other vertebrates | Insects | Non-insects | Others | Hf           |
|----------------------------|--------|----------------------|---------|---------|-----------------|-----------|---------|-------|-------------------|---------|-------------|--------|--------------|
| Latitude (°)               | 0.538  | 1.18                 | 0.389   |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = −0.86,   |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | P = 0.401    |
| Elevation (m)              | 0.338  | 2.69                 | 0.065†  |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = −0.53,   |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | P = 0.605    |
| Mean temperature (°C)      | 0.232  | 4.55                 | 0.012†  |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = −0.97,   |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | P = 0.38,    |
| Rainfall (mm)              | 0.336  | 2.71                 | 0.064†  |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = 0.77,    |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | P = 0.452    |
| NDVI (mean)                | 0.455  | 1.64                 | 0.218   |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = −0.85,   |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | P = 0.405    |
| NDVI (variation)           | 0.308  | 3.09                 | 0.043†  |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = 0.94,    |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | P = 0.360    |
| Snow depth (cm)            | 0.298  | 3.25                 | 0.037†  |         | Linear          | –         | –       | –     | –                 | –       | –           | –      | t = −2.02,   |
|                           |        |                      |         |         | Quadratic       | –         | –       | –     | –                 | –       | –           | –      | t = −2.02,   |

*P < 0.10. †P < 0.05. ‡P < 0.01.
Appendix S1). Deciduous forests are found in mountainous northern regions with more snow and lower temperatures than the regions where evergreen forests are found. Clear differences in forest productivity (NDVI) were not detected (Appendix S1).

Mean FOs of fruits (64%), mammals (35%), and insects (46%) were higher than those of other dietary categories, so these three categories seemed to be the main dietary components of the Japanese martens (Appendix S1). Among the eight food categories, we found significant differences for FO Mammals ($t = -3.07, P < 0.001$, higher in deciduous forests), FO Non-insects ($t = 2.59, P = 0.019$, higher in evergreen forests), and FO Non-fruits ($t = -2.21, P = 0.040$, higher in evergreen forests; Appendix S1). None of the other dietary components or dietary diversity showed significant differences between the two forest types (FO Fruits: $t = 0.85, P = 0.407$; FO Birds: $t = -0.90, P = 0.398$; FO Other vertebrates: $t = -0.13, P = 0.902$; FO Insects: $t = -0.10, P = 0.922$; FO Others: $t = -1.21, P = 0.240$; dietary diversity ($H'$): $t = -0.71, P = 0.487$; Appendix S1).

**Variables explaining variation in diet and dietary diversity**

The dietary composition of the Japanese martens across their range was significantly affected by three environmental variables: 1) mean temperature (MANOVA, $F = 4.55, p = 0.012$), 2) NDVI variation ($F = 3.09, p = 0.043$), and 3) snow depth ($F = 3.25, p = 0.037$; Table 1). The mean temperature had a significant effect on the FO Insects: forests with moderate temperature had a higher FO Insects (Fig. 2a; Table 1). The snow depth had significant effects on the FO Non-insects and FO Other vertebrates: forests with greater snow depth had a lower FO Non-insects and a higher FO Other vertebrates (Fig. 2b,c; Table 1) than those with less snow. Finally, NDVI variation had no significant effects on FOs (Table 1). On the other hand, snow depth had a significant effect on dietary diversity ($H'$): forests with moderate snow depth had lower $H'$ (Fig. 2d, Table 1).

**DISCUSSION**

Previous research has identified latitudinal and elevational variation in the diets of mammals. Omnivorous carnivores, for example, eat less fruit and shift to carnivorous diets with increasing latitude (Virgós et al. 1999, Lozano et al. 2006, Zhou et al. 2011, Díaz-Ruiz et al. 2013). Thus, latitudinal variation in forest productivity and the availability of small animals may influence the dietary preferences of these mammals and their diet composition. We found that dietary FO of mammals, non-fruits, and non-insects differed between forest types, probably due to differences in food availability (see also Hisano et al. 2018). However, we found that the forest type alone is not enough to
explain dietary variation in Japanese martens, because the FOs of two main dietary items (fruits and insects) showed no significant difference between forest types (Table 1).

We found that the two geographical variables (latitude and elevation) were not significantly related to food composition or to dietary diversity (Table 1), in contrast to the findings of other researchers, who detected positive relationships between latitude and the frequency of small animals in the diet (Zalewski 2005, Zhou et al. 2011). Thus, latitude may be a proxy for forest productivity and food availability, but may not itself affect the dietary characteristics of martens. Our results demonstrate the importance of evaluating environmental factors to which less attention has been paid, as we found that three environmental variables (mean temperature, NDVI variation, and snow depth) related to the diet of Japanese martens in different ways: martens showed higher FO Non-insects in forests with lower snow depth, higher FO Insects in forests with moderate temperature, and higher FO Other vertebrates in forests with greater snow depth (Fig. 2). This shows that analyses with multiple environmental variables provide a practical approach towards exploring variation in dietary composition. Spatial variation is likely to reflect the availability of forest-dwelling animals as food items. Forest-dwelling animals are primarily affected by the external environment that directly affects their abundance and diversity, and by forest seasonality; this may explain why NDVI variation significantly affected dietary variation.

The dietary diversity ($H'$) of martens, on the other hand, was associated with snow depth. Martens showed the lowest dietary diversity in forests with moderate snow depth. The opportunistic and generalist nature of foraging by martens might explain this phenomenon. In habitats with heavy snow depth, martens frequently eat mammals and other vertebrates, while in habitats with light snow depth they frequently eat non-insects (Appendix S1); the dietary diversity of martens increases at both ends of the snow depth spectrum. Variation in diet composition and dietary diversity of Japanese martens is shown schematically in Fig. 3. In the current study, latitude was not found to be an explanatory variable for dietary diversity, which is dissimilar from previous studies (Zhou et al. 2011, Diaz-Ruiz et al. 2013).

A phylogenetic study showed that Japanese martens originated 1.6–1.8 mya (million years ago; early Pleistocene; Sato 2013). They migrated to the Japanese archipelago from the Asian continent, and the period for their intra-species diversification is estimated at 0.3–0.36 mya (middle Pleistocene; Ohdachi et al. 2009, Sato 2013). The high plasticity in the dietary composition and diversity of martens demonstrated in this review might represent a behavioural trait that was acquired when they expanded their range into various forests with different food availability during the period of diversification. Snow depth-related dietary adaptation has also been reported in Japanese macaques *Macaca fuscata* (Tsuji et al. 2015).

In summary, we found that several environmental variables affect the food composition and dietary diversity of Japanese martens. Therefore, we need to consider the effects of environmental variables when studying foraging in omnivorous carnivores. Reviews of dietary habits across animals’ geographic ranges, in addition to long-term studies, could contribute towards improving

**Fig. 3.** A schematic chart of the variation in diet composition and dietary diversity of Japanese martens. Environmental variables increase towards the directions in which the arrows are pointing.
our understanding of animals’ behavioural plasticity, and help us to generate interesting hypotheses. In addition, in order to understand the dietary ecology of the Japanese marten more fully, it is important to test whether the geographical and environmental variables are correlated with the presence of foods in the locations we analysed. Tatara (1993) suggested that the Japanese martens in Tsushima Martes melampus tuensis prefer mature broad-leaved forest, and found that at the forest edge, the density of home ranges was correlated with home range size, which may indicate an overall environmental preference relating to food availability. However, in Akaya in Honshu (Martes melampus melampus, Hoshino et al. 2014, in the same area as Hisano et al. 2017), the martens preferred broad-leaved forest with trees of both tall and low stature, suggesting that habitat selection may be affected by the availability of suitable fruits. To answer the remaining questions about the diet of the Japanese marten, food availability and selection should be considered as next steps in field research.

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**SUPPORTING INFORMATION**

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

**Appendix S1.** Location of the study sites in the studies of Japanese martens included in this review, with diet composition and trophic diversity.