

1 Selected discipline: Ecology (Original paper)

2 **A comparison of visual and genetic techniques for identifying Japanese marten**  
3 **scats - enabling diet examination in relation to seasonal food availability in a**  
4 **sub-alpine area of Japan**

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24 We compare the veracity of visual diagnostic criteria to DNA diagnostic techniques,  
25 including newly designed primers, to discriminate Japanese marten (*Martes melampus*)  
26 faeces from those of other sympatric carnivore species. Visual criteria proved > 95%  
27 reliable for fresh, odouriferous scats in good condition. Based upon this verification,  
28 we then examine if and how Japanese marten diet differs among seasons at high  
29 elevation study site (1,500-2,026 m). We also consider how intra-specific competition  
30 with the Japanese red fox (*Vulpes vulpes japonica*) may shape marten feeding ecology.  
31 From 120 Japanese marten faecal samples, high elevation diet comprised (frequency of  
32 occurrence) 30.6-66.0 % mammals, 41.0-72.2 % insects and 10.6-46.2 % fruits,  
33 subject to seasonal variation, with a Shannon-Weaver index value of 2.77. These  
34 findings contrast substantially to seasonal marten diet reported in adjacent lowland  
35 regions (700-900 m), particularly in terms of fruit consumptions, showing the trophic  
36 adaptability of the Japanese marten. We also noted a substantial dietary overlap with  
37 the red fox (n = 26 scats) with a Shannon-Weaver index of 2.61, inferring little trophic  
38 niche mutual exclusion (trophic niche overlap: 0.95), although some specific seasonal  
39 prey selection differences were likely related to relative differences in body size  
40 between foxes and martens. This additional information on the feeding ecology of the  
41 Japanese marten enables a better assessment of the specific risks populations face in  
42 mountainous regions.

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5 44 **Key words:** diet, faecal analysis, *Martes melampus*, niche overlap, PCR amplification,  
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7 45 *Vulpes vulpes*.  
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## INTRODUCTION

In order to fully understand the ecology and life-history strategies of species, it is essential to examine foraging behaviour (Carr and Macdonald, 1986; Abrams, 1991; Geffen and Macdonald, 1993; Daan and Tinbergen, 1997), where the seasonal and spatial distribution of trophic resources can influence optimal foraging strategy, socio-spatial organization, and mating system (Gittleman, 1986; Roff et al., 2002; Macdonald and Johnson, 2015). Here we expand on knowledge of the feeding ecology of the Japanese marten (*Martes melampus*) (e.g., Tatara and Doi, 1994; Nakamura et al., 2001; Arai et al., 2003; Tsuji et al., 2014; Adachi et al., 2016), which inhabits a wide range of elevations from lowland up to alpine forests (e.g., Hoshino et al., 2014; see also Zhou et al., 2011a) on the three main Japanese islands of Honshu, Shikoku and Kyushu (Proulx et al., 2005).

Faecal analysis is typically used to survey the diet of carnivores because it is easy to obtain large sample sizes without harming individuals, unlike examining stomach contents (e.g., Litvaitis, 2000). However, prerequisite is that faeces can be attributed to the carnivore species depositing them without any ambiguity, or else misrepresentative conclusions may be drawn about their diet and foraging ecology. Marten faeces are commonly mis-identified due to their similar shape/texture to those of other sympatric carnivores. For example, Davison et al. (2002) report that 18 % of faeces visually

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5 66 identified by experts as ‘marten’ were actually from foxes. Similarly, Baines et al.  
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7 67 (2013) found that 23 % of marten/fox scats were misidentified by experienced  
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10 68 observers, also with a bias towards assigning marten scats as fox. These studies  
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13 69 illustrate how ability to discriminate the droppings of similar carnivores using visual  
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16 70 and olfactory characteristics can be ambiguous, leading to unreliability (e.g., Davison  
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18 71 et al., 2002; Birks et al., 2005). Because martens and foxes eat a similar, generalist,  
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21 72 omnivorous diet (e.g., Goszczynski, 1986; Storch et al., 1990), inter-specific  
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24 73 competition can arise, and so they can cross-influence each other’s trophic niche. It is  
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27 74 therefore crucial to establish the extent to which local diets overlap to include all of the  
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30 75 constraints influencing marten diet.

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32 76 Identifying the species depositing faeces using DNA techniques is increasingly  
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35 77 recognised as the most reliable and accurate method available (e.g., Kurose et al.,  
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38 78 2005), although costly. DNA diagnostic techniques have been applied to marten  
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41 79 species in other regions (for example, in Europe; see Balestrieri et al., 2010; Caryl et  
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44 80 al., 2012), and so here we undertook DNA diagnostics to test and calibrate the veracity  
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47 81 of visual and olfactory diagnostic approaches. This required us to develop genetic  
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50 82 markers specific to the Japanese marten (e.g., Foran et al., 1997; Farrell et al., 2000;  
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53 83 Kurose et al., 2005), trialling PCR amplification techniques. Using this approach, we  
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56 84 were able to assess the practical and financial trade-off between identifying faeces  
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59 85 directly, in situ, in the field, versus transporting samples to the laboratory for DNA  
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5 86 extraction and sequencing.  
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7 87 Building on accurate scat identification, we examine whether the principal food  
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10 88 types consumed by Japanese martens change with season in accord with changes in  
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13 89 availability of each food type (e.g., Zhou et al., 2011b). We then test whether niche  
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16 90 overlap indices with the Japanese red fox exert any trophic niche constraint on  
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19 91 Japanese marten diet; or if relative body-size differences cause these carnivores to  
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22 92 select different primary prey, resulting in trophic niche segregation. We also examine  
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25 93 whether Japanese marten diet differs between our high elevation study site (1,500 –  
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27 94 2,026 m) in the Mikuni mountain range (central Japan) and diets reported for lowland  
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30 95 (700 – 900 m) populations studied in these same mountains (Kanto Regional Forest  
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32 96 Office, 2012, 2013). Specifically, we posit that in upland areas martens will exhibit a  
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35 97 lower reliance on fruits, because fruits are less abundant and are available for a shorter  
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38 98 duration at higher elevation (see Kudo, 1993; Otani, 2002; Miyajima, 2007); noting  
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41 99 that martens can compensate for changes in food availability through adaptive foraging  
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43 100 (e.g., Zhou et al., 2011b).  
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## 47 102 MATERIALS AND METHODS

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### 52 104 Study area

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56 105 The study was conducted in the Joshinetsu-Kogen National Park near Mt. Sennokura  
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5 106 (36°48' N, 138°50' E), in the Mikuni Mountain range, which extends into the  
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8 107 Minami-Uonuma District (Niigata Prefecture). Surveys were conducted in the  
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10 108 sub-alpine habitat zone, at an elevation ranging over 1,500-2,026 m (Fig. 1). These  
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12 109 mountains receive weather systems off the Pacific Ocean and the Sea of Japan, leading  
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14 110 to substantial winter snowfall. From historic records obtained from the Yuzawa  
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16 111 meteorological observatory (13 km northeast of research area – elevation 340 m),  
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18 112 average temperature ranged from a minimum of -0.5 °C in January to a maximum of  
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20 113 24.7 °C in August (average of 1981-2010). Annual rainfall between 1981 and 2010  
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22 114 averaged 2,231 mm, with a maximum snow depth of 211 cm; higher up in this  
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24 115 sub-alpine study area, snow cover remained for around seven months, between  
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26 116 November and May, with a maximum depth of 350-500 cm. There were no residential  
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28 117 homes, businesses or agriculture within the study area, with the nearest town,  
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30 118 Minakami (Gunma Prefecture), lying approximately 15 km to the south-east.  
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40 119 The lowland broadleaf forests that comprise the study site were dominated by  
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42 120 Japanese beech (*Fagus crenata*) and Mongolian oak (*Quercus crispula*) (Hoshino et al.,  
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44 121 2014). Above 1,600 m this transitioned into sub-alpine mixed woods composed of  
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46 122 Maries' fir (*Abies mariesii*) and Erman's birch (*Betula ermanii*). Above ca. 1,800 m, in  
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48 123 the Pseudo-Alpine Zone (see Ohmori and Yanagimachi, 1991; Yasuda and Okitsu,  
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50 124 2007), there were shrub forests of Siberian dwarf pine (*Pinus pumila*), Japanese alpine  
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52 125 cherry (*Prunus nipponica*), as-well-as dwarf bamboos (Bambusoideae spp.), and other  
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5 126 high alpine vegetation. The ridge line of Mt. Tairappyo and Mt. Sennokura was a  
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7 127 wind-swept grassland that consisted of narcissus anemone (*Anemone narcissiflora*),  
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10 128 meadow buttercup (*Ranunculus acris* var. *nipponicus*), Japanese crowberry (*Empetrum*  
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13 129 *nigrum* var. *japonicum*), and Japanese mountain heath (*Phyllodoce nipponica*).  
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18 131 **Collection of faecal samples**  
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21 132 It was not possible to collect faecal samples during the winter (Nov – May) because  
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23 133 they became obscured by snow; furthermore, snow depth of up to 500 cm, over steep  
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26 134 terrain, made surveying unsafe and impractical. Consequently, faecal samples were  
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29 135 collected between July and October in 2011, with some further supplementary  
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32 136 collection from June to July in 2012. Samples were collected each month (three  
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34 137 consecutive sampling days/month) along a 10 km transect following an existing  
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37 138 mountain trekking route through the study area, which transcended habitat types  
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40 139 effectively through the full elevation range (Fig. 1).  
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43 140 Upon detection, the location of each faecal sample was logged using a hand-held  
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45 141 GPS device (Garmin). To enable subsequent DNA-based validation species depositing  
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47 142 faeces, all carnivore faecal samples were collected in plastic hermetic containers,  
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50 143 preserved in 95% ethanol immediately and transported to the laboratory.  
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5 145 **Assigning faeces to species in the field using visual and olfactory criteria**  
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7 146 In situ, in the field, we assigned marten and fox faeces to species using diagnostic  
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10 147 criteria: diameter – marten faeces are smaller (ca. 8-13 mm; see Tsuji et al., 2011a, b)  
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12 148 than those of fox (> ca.15 mm; see also Hisano et al., 2016); shape; odour – marten  
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14 149 scats smell characteristically sweet (see Hisano et al., 2016) while those of fox smell  
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16 150 musky and foul (see Vine et al., 2009). Corroborative support was established from  
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18 151 nearby tracks and, in exceptional cases, the presence of marten hair (following the  
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21 152 general methods of Zhou et al., 2011b). Note; we did assign any faeces to other  
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23 153 carnivores known to be sympatric in this region: masked palm civet (*Paguma larata*),  
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25 154 ermine (*Mustela erminea*), Japanese weasel (*Mustela itatsi*), Raccoon dog (*Nyctereutes*  
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27 155 *procyonoides*), Japanese badger (*Meles anakuma*), domestic cat (*Felis catus*) and  
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29 156 domestic dog (*Canis familiaris*); all of which can easily be distinguished from marten  
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31 157 faeces by their appearance (e.g., colour, shape and size), texture smell, or use of  
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33 158 latrines (see Zhou et al., 2008a). Although faeces of the Japanese weasel are  
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35 159 morphologically similar to those of marten, they are smaller: 4.3 mm-7.2 mm (Tsuji et  
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37 160 al., 2011a, b), and so we ensured we did not include weasel scats by not collecting  
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39 161 faeces of less than 8.0 mm diameter.  
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53 163 **DNA-based validation of species depositing faeces**  
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56 164 We applied a genetic technique to approximately half of the total number of faecal  
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5 165 samples collected, to test and verify whether our field-diagnostic criteria had identified  
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7 166 Japanese marten faeces accurately and reliably. That is, we sought to prove definitely  
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10 167 that we had not mistakenly assigned any other superficially similar looking scats from  
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13 168 the eight sympatric carnivore species among our putative set of marten scats. Total  
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16 169 DNA was extracted from ca. 300 mg of each faecal sample using the QIAamp DNA  
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19 170 Stool Mini Kit (Qiagen) according to the manufacturer's instructions, and then 1.0 µl  
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21 171 of the extract was used for PCR amplification. We trialled two methods of PCR  
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24 172 amplification, general single PCR and multiplex PCR of partial sequences from the  
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27 173 mitochondrial DNA (mtDNA) control region, which is the most variable part of  
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30 174 mtDNA. We sourced mtDNA control region sequences from the DNA Data Bank of  
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32 175 Japan (DDBJ), and aligned them to design PCR primers for: Japanese weasel  
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34 176 (accession number of DDBJ: AB007327), Japanese marten (AB525722), Japanese  
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37 177 badger (AJ563700), masked palm civet (EU910478), raccoon dog (EU642434), ermine  
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40 178 (AB061213), red fox (AB292741), domestic dog (AB007398) and domestic cat  
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43 179 (AJ441318 and EU864495). Species-specific sequences were selected to design the  
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46 180 PCR primers, especially as to match the 3' end of the species' sequence (Table 1). In  
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49 181 addition, we identified conservative sequences among these species, enabling us to  
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51 182 design a universal reverse primer (UprR in Table 1). Target animals were then  
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54 183 distinguished by the molecular sizes of the PCR products. The Multiplex PCR method  
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57 184 was able to discriminate definitively between all sympatric carnivore species by using  
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5 185 the target-animal-specific primers as designed above. Two primers (spCat and spFox)  
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8 186 for domestic cat and red fox, respectively, were referenced Nonaka et al. (2009). We  
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10 187 used the Multiplex PCR Kit (Qiagen) on each primer set (primer set 1: for Japanese  
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13 188 weasel, Japanese marten, masked palm civet and domestic cat; primer set 2: for  
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16 189 Japanese badger, red fox, raccoon dog and domestic dog). The general single PCR was  
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18 190 designed to identify specifically ermine DNA, using primer set ER-F1/R1, following  
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21 191 Shimatani et al. (2008); this was used when no reactions occurred for the other species  
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24 192 in the multiplex PCR program.

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26 193 For both techniques, an aliquot of 9.0  $\mu\text{l}$  of the PCR reaction product was mixed  
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29 194 with 1.0  $\mu\text{l}$  of loading buffer. Multiplex PCR products were electrophoresed on a 4 %  
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32 195 agarose gel and single PCR products on a 2 % agarose gel. These PCR products were  
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35 196 then stained with ethidium bromide and visualised under an ultraviolet illuminator.

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### 38 39 198 **Dietary analysis**

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42 199 Following the methods of Jędrzejewska and Jędrzejewski (1998; modified by Zhou et  
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45 200 al., 2011b), faecal samples assigned as marten or fox were first washed through a  
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48 201 0.5mm mesh metal sieve, to remove larger digested remains, such as hair, bones, teeth,  
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51 202 feathers, scales, exoskeleton, elytra, fruits cuticles, and seeds. These dietary remains  
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54 203 were identified to prey category type using morphological criteria (Zhou et al., 2008a)  
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56 204 under stereoscopic optical microscopy, with reference to collections of specimens  
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5 205 (seeds, insects, reptiles and amphibians) from the study area. Mammal hairs were  
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7 206 identified based on the features of the medulla, using the chart provided by Murai et al.  
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10 207 (2011). The characteristic shape of spines and ribs allowed us to discriminate between  
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12 208 amphibians and reptiles unambiguously (see Murai et al., 2011). Faecal contents were  
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15 209 identified to at least the taxonomic level of Order, except for fish, birds and molluscs.  
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18 210 In order to establish the percentage dry weight of each sample, and thus to calculate  
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20 211 relative proportions of each dietary item with minimum weight of >1 mg, samples  
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22 212 were dried for 24 hours at 80 °C using a circulation drier. Insects were identified to the  
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24 213 level of taxonomic Order, with one entire insect assigned as the minimal contribution  
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26 214 to the percentage dry weight. Food items were assigned to 10 categories: mammals,  
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28 215 birds, reptiles, amphibians, insects, molluscs, fruits, fish, artificial materials and other  
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30 216 plant material (that is, the “items” comprised “categories”). We used these methods in  
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32 217 order to compare our findings with similarly-derived data from reports from lowland  
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34 218 population in the same area (Kanto Regional Forest Office, 2012, 2013), as well as  
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36 219 other literature on marten and red fox feeding ecology (e.g., Prigioni et al., 2008; Zhou  
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38 220 et al., 2011a, b).

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40 221 Marten diet composition was then calculated according to three indices: (1) The  
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42 222 frequency of occurrence [FO (%): (the number of occurrences of each food item/ the  
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44 223 total number of faecal items) × 100]; (2) The relative frequency of occurrence [RFO  
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46 224 (%): (the number of occurrences of each food item/ the total number of food items  
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225 occurring)  $\times 100$ ]; and (3) The proportion of dry matter [PDM (%): (dry weight of  
226 each faecal item/dry weight of each separate faecal deposit)  $\times 100$ ].

227 The six month-study period was divided into three functional seasons: ‘Summer  
228 2011’ (July–August 2011), ‘Autumn 2011’ (September–October 2011), and  
229 ‘Early-summer 2012’ (June–July 2012). To assess whether marten diet differed  
230 between these seasons, Fisher’s exact test of independence was applied to FO and RFO  
231 data. If a significant ( $\alpha = 0.05$ ), seasonal difference was detected, we then conducted  
232 *post-hoc* pairwise Fisher’s exact tests with Bonferroni correction to determine in which  
233 season martens consumed food categories more/less frequently (see also Tsuji et al.,  
234 2014). In addition, FO and RFO for each food category were pooled across seasons  
235 and Fisher’s exact test of independence was applied to compare of marten and fox diet.

236 The Shannon-Weaver Index ( $H'$ ) was also used to quantify the diversity of food  
237 types consumed:

$$H' = \sum_{i=1}^S P_i \ln P_i$$

238 where  $S$  represents the number of food categories and  $P_i$  represents the ratio of the  
239 category  $i$  against total number of food categories. The RFO was used to investigate  
240 the trophic niche overlap ( $R_O$ ) between species for which samples were obtained:

$$R_O = \frac{\sum_i (x_i + y_i) \log(x_i + y_i) - \sum_i x_i \log x_i - \sum_i y_i \log y_i}{(x + y) \log(x + y) - x \log x - y \log y}$$

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243 where  $x$  and  $y$  represent the sum of occurrence of each food category for each

244 carnivore, and  $x_i$  and  $y_i$  give the  $i$ -th numbers of food items that occurred. We also

245 contrast our data against dietary data reported by lowland studies (Kanto Regional

246 Forest Office, 2012, 2013). All statistical analyses were conducted using R 3.2.4 (R

247 Development Core Team, 2016).

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## RESULTS

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### 251 The identification of faecal samples; species verification using DNA analysis

252 A total of 165 faecal samples was collected, aiming only to select marten and fox scats

253 in the field. Seventy-eight of these were subjected to the DNA identification technique

254 and 87 examined using only visual / olfactory identification criteria (due to costs and

255 limited project resources). Among this total sample, a proportion of faeces were broken

256 ( $n = 23$ ) / semi-broken ( $n = 22$ ), and we used these predominantly for the genetic

257 technique ( $n = 20$  and 15, respectively) (Table 2), where the integrity of samples would

258 make no difference.

259 From the genetic technique, 70 (89.7%) samples yielded PCR products with

260 expected molecular sizes, indicating reliability (Table 2). No PCR products were

261 obtained from the other eight samples. Of these 70 samples, 54 samples were

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5 262 confirmed genetically to come from the Japanese marten, whereas 15 samples were  
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7 263 identified as red fox. The remaining single sample was ambiguous, showing PCR  
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10 264 amplifications for both the Japanese marten and red fox, and was excluded. We thus  
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13 265 verified that we had fulfilled our intention to collect only marten and fox scats from  
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16 266 the field, and had not inadvertently collected scats from the other sympatric carnivores.

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18 267 From this, we established that our non-genetic visual identification criteria were  
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21 268 97.1 % relative to PCR diagnostics, but only when applied to the 34 intact/un-broken  
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24 269 faeces among the subset of 78 samples used to calibrate techniques. The reliability of  
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27 270 visual identification decreased to 60.0 % ( $n = 15$ ) for semi-broken faeces and 45.0 %  
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29 271 ( $n = 20$ ) for broken faeces. Consequently, we excluded those 10 samples that were not  
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32 272 fully intact from our sub-sample examined only visually, and added the remaining  
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35 273 intact 77 in this subset to the 69 species assignments assured by PCR (Table 2). This  
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37 274 enabled us to extend > 95 % confidence across 146 samples.

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40 275 From these 146, we attributed 120 faeces to marten, and these were then used in  
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43 276 dietary analyses (21 from July 2011, 15 from August 2011, 21 from September 2011,  
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46 277 16 from October 2011, 27 from June 2012 and 20 from July 2012). The remaining 26  
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48 278 samples were attributed to fox (eight from July 2011, four from September 2011, three  
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51 279 from October 2011, nine from June 2012 and two from July 2012; Table 3).

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281 **Seasonal change in marten diet**

282 The FO of food items detected from marten faeces is provided in Table 3, and Fig. 2  
283 illustrates the seasonal change in the RFO and the PDM. Martens consumed mammals,  
284 birds, reptiles, amphibians, insects, molluscs, fruits and other plants (i.e., eight  
285 categories); representing species observed in the environment while conducting  
286 surveys.

287 Mammal species comprised the main component of marten diet throughout the  
288 study (FO: 50.0 %, range 13.3-75.0 %; RFO: 23.6 %, range 6.9-36.6 %), although  
289 varying in extent. Mammal species consumed predominantly included rodents, such as  
290 *Apodemus* spp., Cricetidae spp., and Japanese hare (*Lepus brachyurus*). Additionally,  
291 Japanese serow (*Capricornis crispus*) occurred twice in the diet and wild boar (*Sus*  
292 *scrofa*) just once; presumably being eaten opportunistically, when the carcasses of  
293 dead animals were encountered (too large to be predated by martens) (Table 3). The  
294 FO of mammals differed significantly among seasons (Fisher's exact test for  
295 independence:  $\chi^2 = 10.3$ ,  $df = 2$ ,  $P = 0.006$ ), and was significantly lower in Summer  
296 2011 (30.6 %; *post-hoc* pairwise Fisher's exact tests:  $P = 0.006$  with Bonferroni  
297 correction) than Early-summer 2012 (66.0 %; Table 3). The PDM of these food  
298 categories showed a similar tendency to the FO (Fig. 2).

299 Birds comprised 15.6 % (FO, range 7.7-22.2 %) and 7.4 % (RFO, range  
300 3.8-11.1 %) of the Japanese marten's diet; feathers indicated the majority of these birds

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5 301 were mature adults, not chicks, although eggs (evidenced by thick and hard shell  
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7 302 fragments, compared with reptiles) were also eaten. Both the FO and RFO consumed  
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10 303 by birds did not show any significant differences among seasons.  
11

12  
13 304 Reptiles consumed included lizards (Scincidae spp.) (FO: 9.0 %; range  
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15 305 1.4-12.7 %) and snakes (Serpentes spp.) (FO: 2.5 %, range 0.0-6.4 %), which showed  
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17  
18 306 no significant seasonal variation. Amphibians were detected in faeces in every season  
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21 307 (FO: 24.6 %, range 13.8-30.8 %) with no significant seasonal difference. Additionally,  
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24 308 one snail (Gastropoda sp.) was also eaten (FO: 0.8 %; Table 3).  
25

26 309 Insect species consumed were principally Coleoptera spp. (FO: 23.8 %, range  
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29 310 13.9-48.9 %), Orthoptera spp. (FO: 9.8 %, range 4.3-15.4 %) and Hymenoptera spp.  
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32 311 (FO: 18.9 %, range 5.1-47.2 %; Table 3). The FO of insects differed significantly  
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34 312 among seasons (Fisher's exact test for independence:  $\chi^2 = 7.6$ ,  $df = 2$ ,  $P = 0.022$ ), and  
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36  
37 313 these were consumed significantly more frequently in Summer 2011 (FO: 72.2 %) than  
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40 314 Autumn 2011 (FO: 41.0 %; *post-hoc* pairwise Fisher's exact tests:  $P = 0.030$  with  
41  
42 315 Bonferroni correction). Similar to FO, the PDM of insect prey also showed clear  
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45 316 differences between these two seasons (Fig. 2).  
46

47 317 In terms of plant material, we detected a variety of seeds in marten faeces,  
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49  
50 318 indicating that they consumed intact fruits, and a few fragments of other incidental  
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53 319 plant material (categorised as other plants). Both the FO and RFO of fruits differed  
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56 320 significantly among seasons (Fisher's exact test for independence:  $\chi^2 = 13.6$ ,  $df = 2$ ,  $P$   
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5 321 = 0.001 for FO;  $\chi^2 = 14.1$ ,  $df = 2$ ,  $P < 0.001$  for RFO), and significantly less quantities  
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7 322 of fruit were consumed in Early-summer 2012 (FO: 10.6 %, RFO: 4.7 %, with  
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10 323 remarkable little fruit consumption in June 2012 ( $n = 1/27$ , FO: 3.7 %, RFO: 1.5 %))  
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12 324 compared to Autumn 2011 (FO: 46.2 %, RFO: 23.1 %; *post-hoc* pairwise Fisher's  
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15 325 exact tests with Bonferroni correction:  $P = 0.001$  for FO;  $P < 0.001$  for RFO). The  
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18 326 PDM for fruit followed the same trend as FO and RFO.

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21 327 Focusing on month-to-month changes in the types of fruit species consumed,  
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23 328 martens took advantage of whatever fruits were available in specific months, and no  
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26 329 fruit species occurred over more than two consecutive months. Cherry (*Prunus* spp.)  
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29 330 was eaten in July 2011 (FO: 28.6 %); bilberry (*Vaccinium* spp.) was eaten in August  
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31  
32 331 2011 (FO: 13.3 %) and in July 2012 (FO: 15.0 %); hardy kiwi (*Actinidia arguta*) and  
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35 332 Korean whitebeam (*Sorbus alnifolia*) fruits were eaten from September (FO: 19.0 %  
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38 333 and 4.8 %, respectively) to October 2011 (FO: 16.7 %, 22.2 %, respectively); and  
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40 334 mountain ash (*Sorbus commixta*) was eaten in October 2011 (11.1 %).

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#### 44 45 336 **Dietary comparison between the marten and the sympatric fox**

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47 337 No fox faeces were found in August 2011, and so we limit inter-specific comparison to  
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50 338 exclude August 2011. The red fox had a broadly similar diet to the marten; the trophic  
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53 339 niche overlap index ( $R_O$ ) between the two species was 0.95 and the trophic diversity  
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56 340 indices ( $H'$ ) of marten and fox was similar (2.77 and 2.61) when pooled across seasons.  
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5 341 However, substantial inter-specific differences in the compositions of their diets were  
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7 342 evident. Consumption of mammals differed significantly between the two species  
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10 343 (Fisher's exact test for independence:  $\chi^2 = 9.8$ ,  $df = 1$ ,  $P = 0.001$  for FO). In particular,  
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12 344 foxes consumed hares (FO: 46.2 %, RFO: 16.2 %) significantly more frequently than  
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15 345 did martens (FO: 17.8 %, RFO: 8.4 %; Fisher's exact test for independence:  $\chi^2 = 9.4$ ,  
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17 346  $df = 1$ ,  $P = 0.004$  for FO;  $\chi^2 = 6.1$ ,  $df = 1$ ,  $P = 0.020$  for RFO). In terms of fruit  
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19 347 consumption, the FO for foxes (50.0 %) was significantly greater than for martens  
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21 348 (27.1 %) (Fisher's exact test for independence:  $\chi^2 = 5.1$ ,  $df = 1$ ,  $P = 0.034$ ). Unlike  
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23 349 martens, foxes did not feed on amphibians (Fisher's exact test for independence for  
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26 350 RFO:  $\chi^2 = 7.9$ ,  $df = 1$ ,  $P = 0.002$  for FO;  $\chi^2 = 7.8$ ,  $df = 1$ ,  $P = 0.002$ ), but did eat fish  
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28 351 (FO: 3.8 %) and artificial materials (scavenged human refuse) (FO: 19.2 %;  $\chi^2 = 21.4$ ,  
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30 352  $df = 1$ ,  $P < 0.001$  for FO;  $\chi^2 = 18.6$ ,  $df = 1$ ,  $P < 0.001$  for RFO)), which martens did  
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33 353 not.

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39 354 Figure 3 contrasts the RFO and the PDM of the food items eaten by martens  
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41 355 (excluding data from August 2011) and foxes. RFO and the PDM results generally  
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43 356 accorded with FO patterns, although RFO tended to weight insect prey more heavily  
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45 357 than PDM for both species, whereas PDM weighted mammals more heavily for foxes  
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48 358 and reptiles for martens (Fig. 3).  
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## 55 56 360 **DISCUSSION**

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362 **The application of genetic techniques to verify field diagnostic faeces**

363 **identification**

364 Our genetic PCR techniques and newly designed primers worked well for identifying  
365 the species depositing faeces unambiguously (see also Caryl et al., 2012). Several  
366 authors have questioned the reliability and veracity of relying visual and olfactory  
367 criteria (reviewed by Heinemeyer et al., 2008; for Japanese carnivores see Kaneko et  
368 al., 2009) and Heinemeyer et al. (2008) recommends that samples should be always be  
369 confirmed by DNA analysis. Nevertheless, the PCR technique we used proved that our  
370 visual and olfactory diagnostic techniques, when applied to fresh, odouriferous faeces  
371 in good condition, were > 95% reliable for identifying marten and fox faeces, against a  
372 back-ground of the seven other potential carnivore species that could have caused  
373 confusion. This refutes concerns on the ability to identify marten (and other small  
374 carnivore) scats correctly (e.g., Davison et al., 2002; Birks et al., 2005; Baines et al.,  
375 2013) and supports Caryl et al. (2012), who also describe that trained field surveyors  
376 can distinguish the faeces of pine martens from those of red foxes correctly (obtaining  
377 an identification success > 90 %). In part, we attribute the high reliability of  
378 identification in our study to the additional diagnostic value derived from considering  
379 the in-situ position of faeces in the field, combined with the use of scent (for example,  
380 marten scats smell sweet (Hisano et al., 2016), whereas fox droppings smell foul (Vine

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5 381 et al., 2009)). We acknowledge, however, that the reliability of visual identification  
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8 382 declined to around 50:50 (random chance) when scats were broken. Additionally,  
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10 383 samples are misidentified more often when target species are less abundant (Davison et  
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13 384 al., 2002; Prugh and Ritland, 2005; Kelly et al., 2012). In our study area, the Japanese  
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16 385 marten and red fox were the carnivores that occurred most commonly, further  
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18 386 facilitating identification accuracy. Consequently, we were enabled to undertake our  
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21 387 study of marten diet, and look at trophic interactions with the red fox, with confidence,  
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24 388 restricted to fresh/intact faecal samples.  
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#### 27 28 29 390 **Food habits and dietary switching of Japanese martens in sub-alpine habitat**

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31 391 Zhou et al. (2011a) reviewed the food habits of the genus *Martes* and found that they  
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34 392 exhibit a preference for small mammals, invertebrates, and fruits. Our study took place  
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37 393 at high elevation, where the productive summer season is short, and fruiting and peak  
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40 394 insect abundance occur later in the summer than in lowland areas. Nevertheless, we  
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43 395 found these same categories to be the most important; resonating with other studies  
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46 396 from Japan (e.g., Tatara and Doi, 1994; Otani, 2002; Tsuji et al., 2014; Adachi et al.,  
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48 397 2016).  
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50 398 While snow-cover and extreme mountain weather prevented us from collecting  
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53 399 faeces in the winter, we can be certain that during winter months no fruit was available  
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56 400 for martens, and any insect and amphibian/reptile prey would be hibernating and thus  
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5 401 difficult to acquire. This supports strong ecological inference that martens must feed  
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7 402 almost exclusively on active small mammal (rodent/leporid) and bird prey throughout  
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10 403 the winter.

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13 404 Snowpack (up to 500 cm) does not melt until June in our elevated study area,  
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15 405 which substantially retards leafing/fruitlet phenology. As a consequence, even by  
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18 406 Early-summer 2012, we observed that with little fruits availability early in the year  
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21 407 (FO: 10.6 %, PDM: 4.3 %) martens consumed predominantly mammals (FO: 66.0 %,  
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23 408 PDM: 46.1 %). Our data show that this consumption of mammalian prey also persisted  
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26 409 through the summer season (FO: 30.6 %); however, similar to the dietary habits of  
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29 410 yellow-throated martens (*M. flavigula*) in central China (Zhou et al., 2011b), we found  
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32 411 that the Japanese martens switched to rely more substantially upon fruits and insects as  
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34 412 they became available during the productive summer months. Although we did not  
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37 413 collect formal data on environmental food availability, the specific time of ripening of  
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40 414 local fruits was apparent to data recorders working in the field. This was reflected in  
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43 415 the diet of the martens in our study, as they switched the fruit species they exploited  
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46 416 most in accord with changes in fruit species availability (see Zhou et al., 2011b).

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48 In accord with our predictions, we found that martens in our study area  
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50 418 consistently consumed less fruit throughout the study period (RFO: 14.0 % (July  
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53 419 2011); 13.7 % (August 2011); 19.5 % (September 2011); 27.0 % (October 2011);  
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56 420 1.5 % (June 2012); 5.9 % (July 2012)) than the Kanto Regional Forest Office (2012,  
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5 421 2013) reported for lowland sites (36°40'N, 138°59'E) in the same region (RFO: ca.  
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7 422 50 % (July 2011); ca. 30 % (August 2011); ca. 70 % (September 2011); ca. 70 %  
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10 423 (October 2011); ca. 15 % (June 2012); ca. 24 % (July 2012); although the data  
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12 424 summarised in these reports was not presented in a format permitting robust statistical  
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14 425 comparison. Furthermore, although martens consumed 17 fruit varieties in the foothills  
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16 426 (478 faecal samples; Kanto Regional Forest Office, 2012, 2013) only 12 fruit species  
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18 427 (120 faecal samples) were consumed at higher elevation. This is similar to the 11 fruit  
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20 428 species from 141 faecal samples reported by Otani (2002) in a similar sub-alpine area  
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22 429 in northern Japan. This accord with habitat differences in relation to elevation, where  
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24 430 lowland broad-leaved forests (with a diversity of fruiting trees) transition into  
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26 431 coniferous woodlands (with less fruiting trees) (Hoshino et al., 2014). We observed a  
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28 432 substantial decrease in fruiting tree species with increasing elevation in our study area  
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30 433 (see also Miyajima, 2007) due, in part, to the shorter period of primary productivity in  
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32 434 highland mountain habitats (see Okitsu, 1984; Otani, 2002). Because of this, martens  
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34 435 'compensated' by eating more non-fruit food categories (see also Hisano et al., 2016).  
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36 436 For example, in the mid-summer, they exploited insects to a greater extent (particularly  
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38 437 in August; FO: 93.3 %), as populations of each increased, due to annual breeding  
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40 438 cycles, presumably enhancing the availability of these food types. These findings  
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42 439 imply that these martens foraged fairly optimally, in accord with the marginal value of  
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44 440 the food categories they consumed (sensu, Charnov, 1976).  
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5 441 In terms of ecosystem function, by consuming fruit Japanese martens play a role  
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8 442 in seed dispersal in both temperate (Tsuji et al., 2011a) and sub-alpine forests (Otani  
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10 443 2002) in Japan; as do other *Martes* species in other regions (e.g., Schaumann and  
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12 444 Heinken, 2002; Zhou et al., 2008b; Zhou et al., 2013). Due to differences in fruit  
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15 445 consumption between lowland and upland areas, martens are likely to have a more  
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18 446 important seed dispersal function at lower elevation, acting more as a carnivore /  
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21 447 insectivore higher in the mountains (see Tsuji et al., 2011a).  
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26 449 **The effect of competition with foxes on marten diet**  
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29 450 Even though martens and foxes showed quite high dietary niche overlap indices (0.95),  
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31 451 there were some notable differences in food selection by the two species. Because  
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33 452 foxes are larger (4.0-7.0 kg versus 1.0-1.5 kg; Komiya, 2002; Ohdachi et al., 2009) and  
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35 453 faster across the ground than more arboreal martens, they seemed better able to predate  
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37 454 upon hares, which comprised 46.2 % (FO) of their annual diet (compared with just  
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39 455 17.8 % in marten diet). This may be crucial to resource partitioning between the  
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41 456 otherwise similar diets of foxes and martens in this region, permitting coexistence, but  
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43 457 potentially restricting the extent to which martens can utilise the rodent prey available.  
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45 458 Kondo (1980) found similar diet partitioning between martens and foxes in western  
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47 459 Japan, and foxes in Italy (Prigioni et al., 2008), Spain (Padial et al., 2002) and Poland  
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49 460 (Goszczynski, 1986) also consumed more hares than did stone/pine martens (*M.*  
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5 461 *foina/martes*). While smaller martens tend to show narrower mammalian prey niches  
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8 462 than do larger foxes (e.g., Russell and Storch, 2004), they are able to climb trees to  
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10 463 access fruit before it falls (see also Tsuji et al., 2011a).

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13 464 Notably, we detected no fox faeces in our study area in August 2011. In this month,  
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16 465 no rodents occurred in marten faeces and martens consumed hares less frequently (FO:  
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18 466 13.3 %) compared to the previous (FO: 23.8 %) and following months (FO: 19.0 %).  
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21 467 Martens appeared to compensate for this lack of mammalian prey by consuming more  
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24 468 insects, for which FO in August was the highest across the study period (93.3 %).  
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27 469 Foxes, however, are not this flexible and are more reliant upon mammalian prey. We  
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29  
30 470 thus speculate that foxes may have vacated the study area through August and headed  
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33 471 down to lower elevations (larger foxes tend to have more extensive home-range than  
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36 472 martens; e.g., Gittleman et al., 1982; Lindstedt et al., 1986); also explaining how they  
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39 473 accessed human refuse in their diet, which is not present in the environment, and thus  
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42 474 not consumed by martens, at higher elevation (see also Kondo, 1980; Ueuma et al.,  
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45 475 2005).  
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## 48 **Conclusions**

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51 478 By establishing that visual/olfactory scat identification criteria were 97.1% effective  
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54 479 compared with genetic techniques, our study demonstrates that Japanese marten scats  
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57 480 can be identified accurately in the field by trained surveyors provided they are in good  
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5 481 condition and fresh enough to have a characteristic odour. This is especially important  
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8 482 with respect to distinguishing marten scats from similar red fox scats; faeces of other  
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10 483 sympatric carnivores can be distinguished much more easily and reliably. This is  
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13 484 reassuring for ecological surveyors, to include academic, ecological consultants,  
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16 485 government wildlife officers, because DNA diagnostic techniques are relatively  
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19 486 expensive and beyond the scope of many surveys (see Masuda et al., 2009).

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21 487 Based on this reliable identification of faeces, we discovered that despite elevated  
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24 488 habitat, martens seemed to thrive in our study site. Faeces were abundant throughout  
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27 489 the summer, and dietary switching appeared to function to maintain an optimal,  
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30 490 predominance of the currently highest energy-ranked prey in the martens' diet (i.e.,  
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32 491 ratio of energy gained to costs incurred by prey acquisition; Charnov et al., 1976). We  
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35 492 propose that the apparent ability of martens to avoid reliance upon sub-optimal prey  
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38 493 types suggests that they are not in marginal habitat, compared to lowland populations  
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40 494 (see Powell, 1979, 1981).

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43 495 Knowledge of the ecology of the Japanese marten is lacking but important; as  
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46 496 evidenced by the unanticipated predation of martens on a highly vulnerable population  
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49 497 of Japanese ibis (*Nipponia nippon*) in Sado Island, when martens were introduced (The  
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51 498 Asahi Shimbun, 2010). These diet data are informative for parameterising future  
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54 499 habitat suitability models for Japanese marten reintroductions (e.g., Schulz, 1992; Watt  
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56 500 et al., 1996) and for assessing the possible ecosystem risks posed. For example, the  
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5 501 commercial management of forests, altering tree species composition and age structure  
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8 502 (Sano, 1997) has consequences for marten feeding ecology that must be better  
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10 503 understood in order to assess the risks marten populations face in mountainous regions.  
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## FIGURE LEGENDS AND TABLE CAPTIONS

**Table 1.** Multiplex PCR primers for species identification and molecular characteristics.

<sup>a</sup> Expected size of amplification products when PCR was performed with a corresponding forward primer and UprR.

<sup>b</sup> The maximum number of mismatched base pairs within target animal sequences.

<sup>c</sup> The number of consecutive base pairs which are conserved at the 3' end of the sequence within target animals.

**Table 2.** The numbers of Japanese marten and red fox faeces collected in the field and diagnosed by DNA and visual/olfactory diagnosis.

\* Comprised with intact (n = 34), semi-broken (n = 15) and broken (n = 20) faeces.

**Table 3.** The frequency of occurrence (FO; %) of food items occurring in the faeces of Japanese martens from a sub-alpine area in central Japan between July – October 2011 and June and July 2012.



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6 **Fig. 1.** The study area in central Japan. The dashed line shows the boundary between  
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9 Gunma and Niigata prefectures, and the solid-bold line represents the faecal sampling  
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11 route (based on the topographical map produced by the Geospatial Information  
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13 Authority of Japan: <http://www.gsi.go.jp/ENGLISH/index.html>). Contours show 100 m  
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15 intervals.  
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23 **Fig. 2.** Seasonal changes in (a) the relative frequency of occurrence (RFO) and (b)  
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25 proportion of dry matter (PDM) of food categories consumed by Japanese martens in a  
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27 sub-alpine area of central Japan between 2011 and 2012.  
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35 **Fig. 3.** Comparison of food categories consumed by Japanese martens and red foxes in  
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37 a sub-alpine area of central Japan between 2011 and 2012: (a) the relative frequency of  
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39 occurrence (RFO), and (b) the proportion of dry matter (PDM). Data for contrasting  
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41 marten and fox diet for August 2011 were excluded because no fox faeces were found in  
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Table 1. Multiplex PCR primers for species identification and molecular characteristics.

Target species	Primer name	Primer sequence (5'-3')	Number of base-pair	$T_m$ value (°C)	Size of PCR products <sup>a</sup>	Maximum number of mismatches <sup>b</sup>	Conservation at 3' end <sup>c</sup>
Japanese marten	spMtn2	5'-TTCCTCTCCCCATGACTTAAT-3'	21	54.6	203	1	6
Japanese weasel	spJwl	5'-CAACATTTAATGTGCTTGCCC-3'	21	54.6	173	1	19
Masked palm civet	spMpc	5'-TATATCGTGCATTATACCATTCA-3'	23	51.5	92	2	3
Raccoon dog	spRdg2	5'-GCCATGTCGGCACGTCCAC-3'	19	62.5	201	1	6
Japanese badger	spBgr	5'-AGCATTTTCTCAGCACACATT-3'	21	52.3	157	0	21
Domestic dog	spDog2	5'-AATGCATATCACTTAGTCCAAT-3'	22	51.1	59	1	9
Universal	UprR	5'-GCCTCGAGAAACCATCAATC-3'	20	56.3			

<sup>a</sup> Expected size of amplification products when PCR was performed with a corresponding forward primer and UprR.

<sup>b</sup> The maximum number of mismatched base pairs within target animal sequences.

<sup>c</sup> The number of consecutive base pairs which are conserved at the 3' end of the sequence within target animals.

Table 2. The numbers of Japanese marten and red fox faeces collected in the field and diagnosed by DNA and visual/olfactory diagnoses.

	Collected/diagnosed	Included for dietary analysis	Excluded from dietary analysis
DNA diagnostic techniques	78	Succeeded: 69*	Failed: 9
Visual/olfactory diagnostic techniques	87	Intact: 77	Broken/semi-broken: 10
Total	165	146	19

\* Comprised with intact ( $n = 34$ ), semi-broken ( $n = 15$ ) and broken ( $n = 20$ ) faeces.

Table 3. The frequency of occurrence (FO; %) of food items occurring in the faeces of Japanese martens from a sub-alpine area in central Japan between July – October 2011 and June and July 2012.

Food items	Japanese marten				Red fox
	Summer 2011	Autumn 2011	Early-summer 2012	All seasons	All seasons
	(Jul-Aug 2011)	(Sept-Oct 2011)	(Jun-Jul 2012)		
	<i>n</i> = 36	<i>n</i> = 37	<i>n</i> = 47	<i>n</i> = 120	<i>n</i> = 26
<b>Mammals</b>	<b>30.6</b>	<b>48.7</b>	<b>66.0</b>	<b>50.0</b>	<b>84.6</b>
Lagomorpha					
<i>Lepus brachyurus</i>	19.4	17.9	14.9	17.2	46.2
Artiodactyla					
<i>Capricornis crispus</i>	2.8	-	-	0.8	-
<i>Sus scrofa</i>	2.8	2.6	-	1.6	-
Rodentia					
<i>Apodemus</i> spp.	2.8	15.4	29.8	16.4	23.1
Cricetidae spp.	2.8	10.3	6.4	7.4	7.7
<i>Sciurus lis</i>	-		2.1	0.8	-
<i>Petaurista leucogenys</i>	-	2.6	-	0.8	3.8
Insectivora					
<i>Sorex shinto</i>	-	-	2.1	0.8	-
Soricidae spp.	-	-	-	-	-
<i>Urotrichus talpoides</i>	2.8	-	10.6	4.9	3.8
Unidentified	-	2.6	2.1	1.6	3.8
<b>Birds</b>	<b>22.2</b>	<b>7.7</b>	<b>17.0</b>	<b>15.6</b>	<b>11.5</b>
Unidentified adults	19.4	7.7	17.0	14.8	11.5

Unidentified eggs	5.6	-	-	1.6	-
<b>Reptiles</b>	<b>2.8</b>	<b>10.2</b>	<b>19.1</b>	<b>11.5</b>	<b>11.5</b>
Lacertilia spp.	2.8	10.2	12.8	9.0	3.8
Serpentes spp.	-	-	6.4	2.5	7.7
<b>Amphibians</b>					
Anura spp.	<b>13.4</b>	<b>30.8</b>	<b>27.7</b>	<b>24.6</b>	-
<b>Fish</b>					
Unidentified	-	-	-	-	<b>3.8</b>
<b>Insects</b>	<b>72.2</b>	<b>41.0</b>	<b>59.6</b>	<b>57.4</b>	<b>57.7</b>
Coleoptera spp.	13.9	2.6	48.9	23.8	34.6
Orthoptera spp.	11.1	15.4	4.3	9.8	30.8
Hymenoptera spp.	47.2	5.1	8.5	18.9	23.1
Diptera spp.	2.8	-	-	0.8	-
Hemiptera spp.	5.6	2.6	2.1	3.3	7.7
Unidentified larvae	2.8	-	4.3	2.5	-
Unidentified imagoes	13.9	18.0	-	9.8	3.8
<b>Mollusca</b>					
Pulmonata spp.	-	-	<b>2.1</b>	<b>0.8</b>	-
<b>Fruits</b>	<b>27.8</b>	<b>46.2</b>	<b>10.6</b>	<b>27.0</b>	<b>50.0</b>
Actinidiaceae	-	-	-	-	-
<i>Actinidia arguta</i>	-	17.9	-	5.7	26.9
<i>Actinidia polygama</i>	2.8	-	-	0.8	-
<i>Actinidia kolomikta</i>	-	-	-	-	3.8
Rosaceae					

<i>Rubus</i> spp.	-	2.6	-	0.8	3.8
<i>Prunus</i> spp.	16.7	-	-	4.9	7.7
<i>Sorbus alnifolia</i>	-	12.8	-	4.1	-
<i>Sorbus commixta</i>	-	5.1	-	1.6	-
Vitiaceae					
<i>Vitis coignetiae</i>	-	7.7	-	2.5	-
Cornaceae					
<i>Swida controversa</i>	-	2.6	-	0.8	15.4
<i>Benthamidia japonica</i>	-	-	-	-	3.8
Ericaceae					
<i>Gaultheria adenostrix</i>	-	-	2.1	0.8	7.7
<i>Vaccinium</i> spp.	5.6	-	6.4	4.1	-
Caprifoliaceae					
<i>Viburnum furcatum</i>	-	5.1	1.6	1.6	-
Poaceae spp.	-	-	0.9	0.8	-
Unidentified	2.8	-	-	0.8	3.8
<hr/>					
<b>Other plants</b>					
Twigs or grasses	<b>30.6</b>	<b>15.4</b>	<b>29.8</b>	<b>25.4</b>	<b>42.3</b>
<hr/>					
<b>Artificial materials</b>					
Plastic envelope or raw garbage	-	-	-	-	<b>19.2</b>
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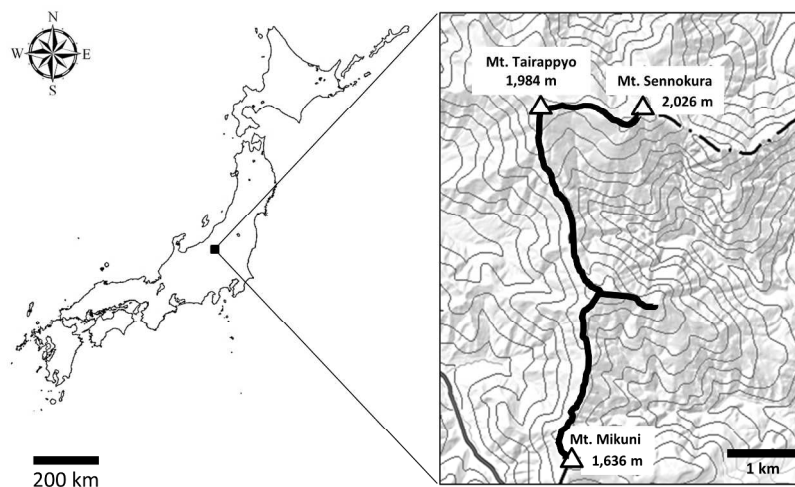


Fig.1. The study area in central Japan. The dashed line shows the boundary between Gunma and Niigata prefectures, and the solid-bold line represents the faecal sampling route (based on the topographical map produced by the Geospatial Information Authority of Japan: <http://www.gsi.go.jp/ENGLISH/index.html>). Contours show 100 m intervals.

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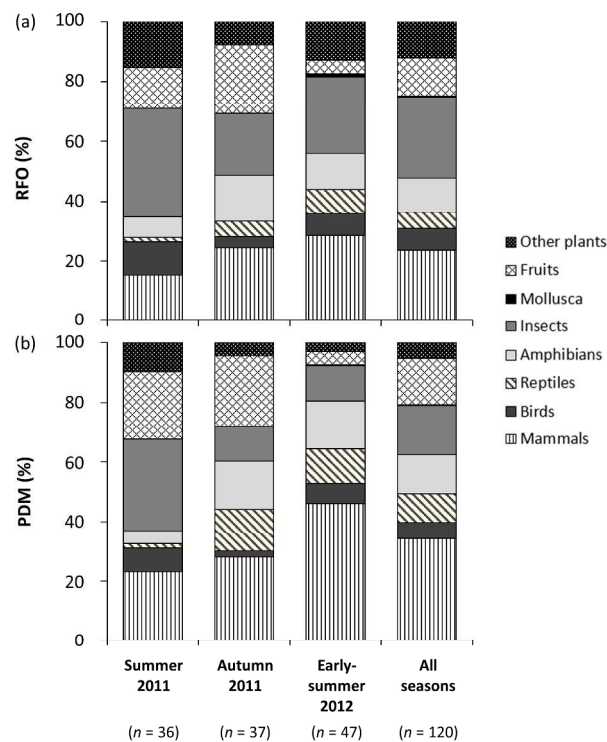


Fig.2. Seasonal changes in (a) the relative frequency of occurrence (RFO) and (b) proportion of dry matter (PDM) of food categories consumed by Japanese martens in a sub-alpine area of central Japan between 2011 and 2012.

254x190mm (300 x 300 DPI)



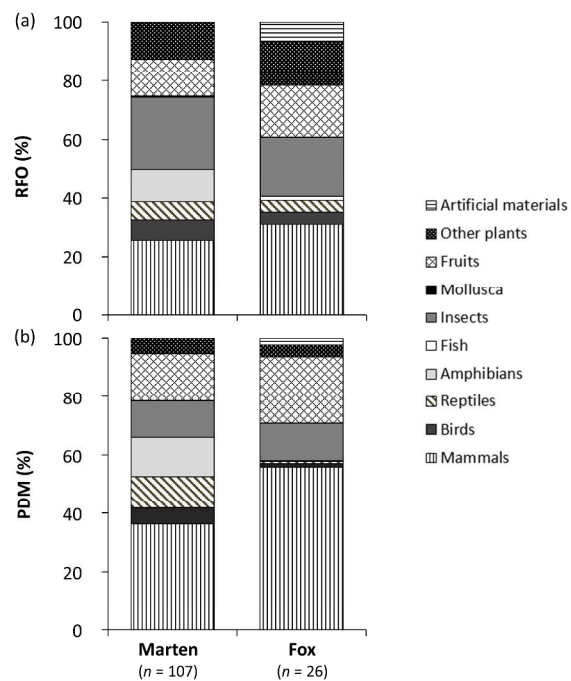


Fig.3. Comparison of food categories consumed by Japanese martens and red foxes in a sub-alpine area of central Japan between 2011 and 2012: (a) the relative frequency of occurrence (RFO), and (b) the proportion of dry matter (PDM). Data for contrasting marten and fox diet for August 2011 were excluded because no fox faeces were found in this month.

254x190mm (300 x 300 DPI)