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1 **Multi-annual variation in the diet composition and frugivory of the Japanese marten (*Martes***
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6 **2 *melampus*) in western Tokyo, central Japan**

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7 Running headline: multi-annual variation in diet of Japanese martens

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9

10 **Abstract** To examine multi-annual variations in the food habits of the Japanese marten (*Martes*
11 *melampus*), we analyzed the composition of marten feces in the Bonbori Forest Path in western Tokyo,
12 central Japan in two time periods a decade apart (1997–1998 and 2007–2008). The staple foods of
13 martens in both periods were fruits/seeds and animal materials (mainly insects and mammals). The
14 martens fed frequently on fruits/seeds and insects throughout the year in both periods, but the
15 consumption of mammals, birds, and arthropods/other animals showed seasonal variations. The
16 composition of fruits/seeds and the frequency of occurrence for each fruit-bearing species differed
17 between the two periods. These results suggest that both the foraging strategy and role of martens as a
18 seed dispersal agent changes yearly, presumably according to multi-annual variation in the availability of

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3 19 prey animals and/or fruits. We emphasize the importance of multi-annual studies both on food habits and
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6 20 to monitor food availability in the temperate region where the food environment changes among seasons
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9 21 as well as years.
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15 23 **Keywords** Dietary composition • Frequency of occurrence • *Martes melampus* • Multi-annual • Seed
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18 24 dispersal • Yearly variation
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24 26 **Introduction**

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27 27 Food habit analysis is a basic and important subject in studies on wildlife ecology. The food environment
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30 28 varies both temporally and spatially in accordance with variations in food availability (Herrera et al.
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33 29 1998; McShea 2000). In temperate regions, marked seasonal changes in plant phenology limit the fruiting
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36 30 period of frugivores (Hanya et al. 2013). Such variations in plant availability often affect the population
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39 31 size of prey animals, such as small rodents and sedentary birds, which in turn affect the food
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42 32 environments of omnivorous mammals (Helldin 1999; McShea 2000). As a result, both frugivorous and
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45 33 carnivorous mammals in temperate regions seem to change their food habits according to environmental
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48 34 conditions (O'Donoghue et al. 1998; Naves et al. 2006; Tsuji et al. 2006; Koike 2010), which implies that
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51 35 multi-annual information on the food habits of animals is needed to fully understand temporal variation in
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54 36 their feeding ecology.
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3 37 Mustelids (family Mustelidae) are small- to medium-sized mesopredators that have a wide
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6 38 distribution in the Northern Hemisphere (Buskirk et al. 1994). Martens, as generalist predators, switch to
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9 39 alternative prey when their principal foods are not readily available. Several multi-annual studies have
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12 40 shown that martens fed on rodents (voles and mice) during years when their availability was high, while
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16 41 the martens switched to feeding primarily on alternative diets, such as animal carcasses and fruits when
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19 42 the rodent availability was low (Pulliainen and Ollinmäki 1996; Ben-David et al. 1997). These examples
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22 43 imply that information about marten food habits based on short-term studies can lead to erroneous
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25 44 conclusions about their foraging strategies. Mustelids also feed on fruits (Rosalino and Santos-Reis
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28 45 2009), and therefore potentially disperse intact seeds that pass through their digestive tracts
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32 46 (endozoochory; Wilson 1993; Otani 2002). Thus, multi-annual variation in their food habits can also
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35 47 affect their roles as seed dispersal agents. Despite numerous studies on the food habits of mustelids, few
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38 48 have attempted multi-annual studies on variations in diet composition and its implications.

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41 49 In this study, we tried to address multi-annual variation in the food habits of wild Japanese martens
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44 50 (*Martes melampus*), an endemic mustelid species in Japan. We especially focused on multi-annual
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47 51 variation in their frugivory. Although several studies have examined the food habits of Japanese martens
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51 52 (Yamagishi 1990; Tatara and Doi 1994; Arai et al. 2003), no study except Arai et al. (2003) documented
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54 53 multi-annual variation. In western Tokyo, the food habits of Japanese marten were previously studied by
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57 54 Nakamura et al. (2001) in 1997–1998 (Period 1 hereafter), and thus we were able to examine
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3 55 multi-annual variation in diets by conducting a follow-up study in 2007–2008 (Period 2) and comparing
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6 56 the results between these two periods.
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10 58 **Materials and methods**

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16 59 Our study was conducted at the Bonbori Forest Path (36° N, 139° E) between Hachioji City and Akiruno
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19 60 City, approximately 50 km west of the central part of Tokyo. The path is about 10 km long and about 5 m
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22 61 wide, and it is almost entirely asphalt-paved (Tsuji *et al.* 2011a). Mean annual precipitation and
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25 62 temperature at Hachioji, the nearest weather station to the study site, during Period 1 were 2358 mm and
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28 63 14.8°C, respectively, while in Period 2, they were 2074 mm and 14.6°C, respectively (Japan
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32 64 Meteorological Agency, <http://www.jma.go.jp/jma/index.html>). The area is mostly covered with forest
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35 65 vegetation dominated by deciduous broad-leaved secondary forests on slopes as well as planted
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38 66 coniferous forests of *Cryptomeria japonica* and *Chamaecyparis obtusa* in valleys (Nakamura *et al.* 2001;
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41 67 Tsuji *et al.* 2011a).

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44 68 We surveyed the forest path at least once a month from July 2007 to July 2008 (23 surveys in total),
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47 69 and collected marten feces along/on it. When we found feces in one large pile, we treated it as one sample
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51 70 if the color was the same or as independent samples if the color differed. We could easily distinguish
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54 71 marten feces from that of sympatric mammals, such as Japanese macaques (*Macaca fuscata*) and red fox
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57 72 (*Vulpes vulpes*) by its shape. We could also distinguish marten feces from that of sympatric mustelids,
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3 73 Japanese weasels (*Mustela itatsi*), by its size (mean \pm SD width: 10.1 ± 1.5 mm for martens and 6.5 ± 1.1
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6 74 mm for weasels; Tsuji *et al.* 2011b). When we collected feces, we removed stones and leaves that were
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9 75 present on the surface.
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12 76 In the laboratory, defrosted feces were washed through a 0.5-mm mesh sieve, and remnants on the
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16 77 sieve were identified under a microscope. Based on Nakamura *et al.* (2001), we classified the contents
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19 78 into the following eight categories: mammals (including rodents and insectivores), birds,
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22 79 reptiles/amphibians, insects, arthropods/other animals, fruits/seeds, other plant parts (including leaves,
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25 80 stems, and roots), and others/unidentified items. To examine multi-annual variation in the contribution of
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29 81 fruits, fruits/seeds were sorted to the level of species or genus. Fruits/seeds identification followed
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32 82 Nakayama *et al.* (2000) and our own references. The percent frequency of occurrence in feces ($\%FO =$
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35 83 number of fecal samples containing a specific food item/total number of fecal samples) was used to show
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38 84 seasonal and year-round food habits, as well as multi-annual variation.
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41 85 We separated the study period into four seasons: spring (March–May), summer (June–August), fall
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44 86 (September–November), and winter (December–February). To test effect of season on the $\%FO$ of the
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47 87 given food item in each period, we used chi-square tests for independence. If significant seasonal
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51 88 difference was obtained, we conducted *post-hoc* Bonferroni tests to address when the martens fed on the
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54 89 item more frequently. To test the effect of study period on the $\%FO$ of a given food item in a given
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57 90 season, we used chi-square tests for independence. In these analysis, α was set at 0.05 except for the
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3 91 Bonferroni tests in which we adjusted the significance levels (α) to 0.013 (for 4 seasons) and 0.017 (for 3
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6 92 seasons) to avoid type I error. Data analyses in this study were performed using the statistical software R
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15 95 **Results**

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18 96 During Period 2, we collected 381 fecal samples, among which we analyzed 257 samples ($N = 33$ in
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22 97 spring, 20 in summer, 26 in fall, and 178 in winter). In total, 594 identifiable food items were found in the
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25 98 257 fecal samples, which corresponded to an average of 2.32 food categories per fecal sample (SD =
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28 99 0.83, range: 1–5). Fruits/seeds (annual %FO: 94.9), mammals (annual %FO: 69.6), insects (annual %FO:
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31 100 51.0), and other plant parts (annual %FO: 61.5) were the staple food items during Period 2 (Table 1).
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35 101 Birds, reptiles/amphibians, arthropods/other animals, and fungi were supplementary sources, whose
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38 102 annual %FOs were less than 5%.

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41 103 As to seasonal change, the %FO of mammals in Period 2 was significantly higher in spring and
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44 104 summer than winter ($p < 0.017$). The %FO of birds in Period 2 was significantly higher in spring than
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47 105 winter ($p < 0.013$). The %FO of arthropods/other animals in Period 1 was significantly higher in spring
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51 106 than other seasons ($p < 0.013$), while %FO of arthropods/other animals in Period 2 was significantly
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54 107 higher in summer than winter ($p < 0.013$) (Table 1).

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57 108 Significant effects of study period on %FO were detected for mammals in the annual mean ($\chi^2 =$
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3 109 4.7, $df = 1$, $p = 0.031$), for birds in winter ($\chi^2 = 11.8$, $df = 1$, $p < 0.001$), reptiles and amphibians in the
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6 110 annual mean ($\chi^2 = 3.9$, $df = 1$, $p = 0.049$), arthropods/other animals in the annual mean ($\chi^2 = 11.1$, $df = 1$, p
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9 111 < 0.001), and other plant parts in each season (spring: $\chi^2 = 16.3$, $df = 1$, $p < 0.001$; summer: $\chi^2 = 20.0$, $df =$
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12 112 1 , $p < 0.001$; fall: $\chi^2 = 11.4$, $df = 1$, $p < 0.001$; winter: $\chi^2 = 9.3$, $df = 1$, $p = 0.002$; the annual mean: $\chi^2 =$
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15 113 65.1 , $df = 1$, $p < 0.001$). However, no significant difference in %FO was observed for insects and
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19 114 fruits/seeds among the study periods ($p > 0.05$ for each; Table 1).

22 115 Throughout the study periods, at least 19 species of fruits/seeds were found in the feces. Some
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25 116 fruits appeared in feces during only one period (Table 1): in spring, *Rubus* spp. and *Aspidistra elatior*
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28 117 fruits appeared only in Period 1, while *Actinidia arguta*, *Stachyurus praecox*, *Morus bombycis*, *Hovenia*
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31 118 *dulcis*, *Pyrus pyrifolia*, *Celtis sinensis*, *Aphananthe aspera*, and *Physalis alkekengi* appeared only in
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35 119 Period 2; in summer, *Rubus* spp., *A. arguta*, and *Broussonetia kazinoki* appeared only in Period 1, while
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38 120 *M. bombycis* appeared only in Period 2; in fall, *Rubus* sp., *H. dulcis*, and *Cinnamomum camphora*
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41 121 appeared only in Period 1, while *C. sinensis*, *Viburnum dilatatum*, *Cocculus orbiculatus*, and *Sorbus* sp.
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44 122 appeared only in Period 2; in winter, *Cardiospermum halicacabum*, *Mollugo verticillata*, and *Prunus* sp.
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47 123 appeared only in Period 1, while *S. praecox*, *H. dulcis*, *P. pyrifolia*, *C. sinensis*, *Prunus jamasakura*,
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51 124 *Actinidia polygama*, and *Vitex* spp. appeared only in Period 2 (Table 1).

54 125 Variation in %FO was also observed in several fruits between the two periods. In fall, the %FO of *A.*
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57 126 *arguta* was significantly higher during Period 2 ($\chi^2 = 3.9$, $df = 1$, $p = 0.049$). In winter, the %FOs of

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3 127 *Rubus* spp. ($\chi^2 = 4.7$, $df = 1$, $p = 0.030$) and *Diospyros kaki* ($\chi^2 = 51.2$, $df = 1$, $p < 0.001$) were
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6 128 significantly higher in Period 1, while the %FO of *A. arguta* ($\chi^2 = 10.1$, $df = 1$, $p = 0.002$) was higher in
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9 129 Period 2. On an annual basis, the %FOs of *Rubus* spp. ($\chi^2 = 14.9$, $df = 1$, $p < 0.001$), *D. kaki* ($\chi^2 = 11.2$, df
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12 130 = 1, $p = 0.001$), *Akebia quinata* ($\chi^2 = 14.1$, $df = 1$, $p < 0.001$), and *P. jamasakura* ($\chi^2 = 15.7$, $df = 1$, $p <$
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16 131 0.001) were significantly higher in Period 1, while those of *A. arguta* ($\chi^2 = 45.5$, $df = 1$, $p < 0.001$) and *S.*
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19 132 *praecox* ($\chi^2 = 8.5$, $df = 1$, $p = 0.003$) were significantly higher in Period 2 (Table 1).
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134 **Discussion**

135 Japanese martens in the Bonbori Forest Path fed mainly on animal materials and fruits during both study
136 periods. Their omnivorous diets were similar to what has been reported at other sites (Yamagishi 1990;
137 Tataka and Doi 1994; Arai *et al.* 2003). In terms of seasonal changes in food habits, the martens fed
138 frequently on fruits/seeds and insects throughout the year in both periods, while other categories, like
139 mammals, showed seasonal variation.

140 We found variation in dietary composition between the two study periods: the annual %FOs of
141 mammals, reptiles/amphibians, and arthropods/other animals were higher, while those of some berry
142 species were lower in Period 1 than in Period 2. Since climatic conditions were similar between the two
143 periods (see Materials and methods), the results strongly suggest three possibilities: fruit production
144 varied annually, prey animal abundance varied annually, or both fruit production and prey animal

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3 145 abundance varied annually. The availability of prey animals (Saito *et al.* 1998, 2007) and fruit production
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6 146 (Komiya *et al.* 1991; Suzuki *et al.* 2005) are known to vary annually in Japan. Thus, the martens at our
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9 147 study site seem to adjust their dependence on animal materials in accordance with the availability of prey
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12 148 animals and/or fruits, as do other mustelids (Buskirk *et al.* 1994; Pulliainen and Ollinmäki 1996; Zhou *et*
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16 149 *al.* 2011; Caryl *et al.* 2012). In this study we could not quantify the food availability, and our
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19 150 interpretation of the multi-yearly variation in the dietary composition is speculative. Collecting such
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22 151 information would be useful to investigate how dietary preferences change with availability of their staple
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25 152 foods.

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28 153 We also found considerable variation in fruit occupation in the fecal composition between the two
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31 154 study periods. A similar phenomenon was noted by Otani (2002) when studying martens in northern
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35 155 Japan: he found differences in fruit composition among samples during a 2-year study; e.g., seeds of
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38 156 *Taxus cuspidata* var. *nana* and *Prunus nipponica* were only found in feces in 1 year. These results can be
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41 157 attributed to yearly variation in fruit production. In our study, for example, the availability of *A. arguta*
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44 158 and *S. praecox* from fall to the next spring should have been greater in Period 2, while the availability of
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47 159 *Rubus* sp. in all seasons except for fall, *D. kaki* and *A. quinata* in fall, and *Prunus japonica* in summer
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51 160 should have been greater in Period 1. This implies that the role of Japanese martens as seed dispersal
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54 161 agents would also vary annually according to fruit availability.

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57 162 The annual %FO of other plant parts, mainly leaves, was higher in Period 2. Because we removed
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3 163 leaves that were attached to the surface of fecal samples at collection, detected leaves were likely to be
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6 164 food-originated. Folivory by Japanese martens has been reported at other study sites (e.g., Shiratsuki et al.
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9 165 1973; Yamagishi 1990). Whether folivory is a “side effect” of capturing insects on leaves or a separate
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12 166 feeding strategy of the martens is not clear. The amount of leaves in feces, however, was very low
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15 167 (Yamagishi 1990), and the relative importance of leaves for martens seems lower than that of fruits and
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19 168 animal matter.

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22 169 We demonstrated that multi-annual studies are required to fully understand temporal variation in
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25 170 marten diet. Furthermore, monitoring the availability of plant and prey animals is necessary to explain
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28 171 multi-annual variation in the foraging behaviors performed by martens (e.g., Pulliainen and Ollinmäki
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31 172 1996; Ben-David et al. 1997; Caryl et al. 2012) and to confirm their role as a seed dispersal agent (Otani
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34 173 2002; Tsuji et al. 2011a). Accumulating such fundamental data from multiple time points and localities
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37 174 would be useful to meta-analyses investigating large-scale drivers of prey availability and diet.

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Table 1. Seasonal change in food habits of Japanese martens in Boubori Forest Path, western Tokyo, central Japan based on fecal analyses and expressed as frequency of occurrence (%FO) from the feces.

Food Item	Spring (March-May)		Summer (June-August)		Fall (September-November)		Winter (December-February)		Annual		Seasonal Change	
	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2	Period 1	Period 2
	N = 40	N = 33	N = 49	N = 20	N = 48	N = 26	N = 31	N = 178	N = 168	N = 257		
Animal materials	85.0	72.7 NS	71.4	90.0 NS	66.7	46.2 NS	45.2	50.6 NS	92.9	69.6 NS	NS	NS
Mammals	42.5	36.4 NS	28.6	30.0 NS	—	—	12.9	6.2 NS	20.8	11.3 *	*** (Sp = Su = Wi)	*** (Su > Wi, Sp > Wi)
Birds	12.5	15.2 NS	2.0	10.0 NS	2.1	3.8 NS	16.1	1.1	6.5	3.9 NS	* (Sp = Su = Fa = Wi)	** (Sp > Wi)
Reptiles/amphibians	10.0	—	—	—	6.3	—	—	1.1	4.2	0.8 *	NS	NS
Insects	37.5	48.5 NS	51.0	80.0 NS	64.6	42.3 NS	32.3	49.4 NS	48.8	51.0 NS	NS	NS
Arthropods/other animals	37.5	3.0 NS	6.1	20.0 NS	2.1	—	3.2	1.1 NS	11.9	2.7	*** (Sp > Su, Sp > Fa, Sp > Wi)	*** (Su > Wi)
Plants	55.0	97.0 NS	65.3	95.0 NS	97.9	100.0 NS	96.8	100.0 NS	80.0	100.0 NS	NS	NS
Fruits and seeds	52.5	84.8 NS	63.3	70.0 NS	97.9	96.2 NS	96.8	99.4 NS	77.4	94.9 NS	NS	NS
<i>Rubus</i> spp.	17.5	—	14.3	—	2.1	—	12.9	2.2 *	11.3	1.6	***	***
<i>Diospyros kaki</i>	7.5	3.0 NS	—	—	2.1	11.5 NS	83.9	6.2	17.9	5.8	***	***
<i>Akebia quinata</i>	2.5	3.0	—	—	60.4	38.5 NS	3.2	1.7 NS	19.0	5.4	***	***
<i>Aspidistra elatior</i>	2.5	—	—	—	—	—	—	—	0.6	—	—	—
<i>Acrinidia arguta</i>	—	39.4	8.2	—	33.3	80.8 *	19.4	81.5 **	15.5	69.6	***	***
<i>Stachyurus praecox</i>	—	39.4	—	—	14.6	3.8 NS	—	12.9	4.2	14.4	**	**
<i>Morus bombycis</i>	—	15.2	—	45.0	—	—	—	—	—	—	—	5.4
<i>Hovenia dulcis</i>	—	6.1	—	—	4.2	—	—	0.6	1.2	1.2	NS	NS
<i>Pyrus pyrifolia</i>	—	6.1	—	—	—	—	—	1.1	—	1.6	—	—
<i>Celtis sinensis</i>	—	3.0	—	—	—	3.8	—	3.4	—	3.1	—	—
<i>Aphananthe aspera</i>	—	3.0	—	—	—	—	—	—	—	0.4	—	—
<i>Physalis alkekengi</i>	—	3.0	—	—	—	—	—	—	—	0.4	—	—
<i>Prunus jamasokura</i>	—	—	36.7	10.0 NS	—	—	—	0.6	10.7	1.2	***	***
<i>Broussonetia kazinoki</i>	—	—	6.1	—	—	—	—	—	1.8	—	—	—
<i>Acrinidia polygama</i>	—	—	—	—	6.3	3.8 NS	—	1.1	1.8	1.2	NS	NS
<i>Cinnamomum camphora</i>	—	—	—	—	2.1	—	—	—	0.6	—	—	—
<i>Viburnum dilatatum</i>	—	—	—	—	—	3.8	—	—	—	0.4	—	—
<i>Cocculus orbiculatus</i>	—	—	—	—	—	3.8	—	—	—	0.4	—	—
<i>Sorbus</i> sp.	—	—	—	—	—	3.8	—	—	—	0.4	—	—
<i>Cardiospermum halicacabum</i>	—	—	—	—	—	—	3.2	—	0.6	—	—	—
<i>Mollugo verticillata</i>	—	—	—	—	—	—	3.2	—	0.6	—	—	—
<i>Prunus</i> spp.	—	—	—	—	—	—	3.2	—	0.6	—	—	—
<i>Vitis</i> spp.	—	—	—	—	—	—	—	1.7	—	1.2	—	—
Nuts	10.0	—	—	—	2.1	—	—	—	3.0	—	—	—
Poaceae	—	3.0	—	—	—	—	—	1.7	—	1.6	—	—
Polygonaceae	—	3.0	—	—	—	—	—	—	—	0.4	—	—
Other seeds	25.0	—	—	—	2.1	—	6.5	—	7.7	—	—	—
Other plants	5.0	75.8 ***	4.1	85.0 ***	4.2	50.0 ***	9.7	57.9 **	5.4	61.5 ***	NS	NS
Fungi	2.5	6.1 NS	—	—	—	—	—	2.3	0.6	2.5	NS	NS
Others (unidentified materials)	5.0	6.1 NS	2.0	5.0 NS	6.3	—	—	2.3	3.6	2.5	NS	NS

Effects of study periods on the %FO are also shown for each season (performed by chi-square tests for independence). ***, $p < 0.001$, **, $p < 0.01$, *, $p < 0.05$, NS: not significant ($p > 0.05$)

Results of multiple comparison (Bonferroni tests in which significant levels (α) are adjusted to 0.013 (4 comparisons) and 0.017 (3 comparisons)) are shown in parenthesis

Period 1: 1997-1998 (from Nakamura et al 2001)

Period 2: 2007-2008

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244 The English in this document has been checked by at least two professional editors,

245 both native speakers of English. For a certificate, please see:

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