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Estimated Seed Shadow Generated by Japanese Martens (*Martes melampus*): Comparison with Forest-Dwelling Animals in Japan

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To evaluate the seed shadow generated by wild Japanese martens (*Martes melampus*), we combined data on their ranging behavior from the northern foot of Mt. Fuji, central Japan (seven males and three females) with data on gut passage time obtained from martens in Toyama Municipal Family Park Zoo (three males and one female). The movement distances varied, and mean distances for 0–1, 2–3, and 4–5 h intervals were 152.4, 734.7, and 1,162.4 m, respectively, with no significant sex difference. The mean gut passage time of ingested seeds was 7.4 h (range: 0.6–51.7 h), and two-thirds were defecated within 12 h. Seeds of fleshy fruits was frequently transported to 501–1,000 m, and 20% of ingested seeds were transported > 1,000 m from feeding sites. We found positive correlations between body size and home range of the animals in Japan and their seed dispersal distances. We conclude that Japanese martens are medium-range dispersers that can transport seeds from the source to open habitats conducive for germination and/or growth, partly due to scent marking behaviors.

Key words: endozoochory, home range, Japan, mustelid, seed shadow

INTRODUCTION

Many plant species depend on animals to disperse their seeds; some provide fresh fruits for animals that consume these fruits and defecate the seeds at locations far from feeding sites (endozoochory). Characteristics of dispersal vary among agents; animal behavioral, physiological, and post-defecation processes affect the survival and growth of dispersed seeds (González-Varo et al., 2013). Effective dispersal agents should defecate intact seeds, move long distances relative to gut passage times, deposit seeds in ways that reduce inter-seed competition, and defecate in habitats that increase seed fitness (Hickey et al., 1999).

Recent studies have revealed that non-flying animals, especially omnivorous mammals, can disperse seeds if they possess the key attributes of having large body masses and large home ranges because their primary diets (such as small animals) occur at relatively low density (McNab, 1963). They move longer daily distances than that by birds, and deposit intact seeds (Herrera, 1989; Wilson, 1993; Hickey et al., 1999; Rosalino and Santos-Reis, 2009). They possess a larger mouth, and can eat more kinds of fleshy fruits than sympatric frugivorous birds (Wheelwright, 1985). In particular, the Order Carnivora includes many facultative frugivores (Hickey et al., 1999). Their large spatial movement

ability implies that seeds inside fruits could be dispersed over a wider area, which could make fruit-eating carnivores effective dispersal agents in temperate forest ecosystems.

Japanese martens (*Martes melampus*) inhabit temperate regions in which fruit productivity is low, and primarily eat vertebrate prey, but also feed on fleshy fruits (as shown by the range of frequency of fruit in fecal samples: 24.5–63.2% ($n = 262$) in Yamanashi (Nakamura, 2001a); 36.2–61.2% ($n = 168$) in Tokyo (Nakamura, 2001b), and 41.6–56.9% ($n = 1,236$) in Tsushima Island (Tatara and Doi, 1994), especially those of lianas such as *Vitis* spp., *Actinidia* spp., and *Akebia* spp., mainly in the fall (reviewed in Koike and Masaki, 2008). Within their home range, martens avoid forest edges composed of shrubs and herbaceous plants (such as roadsides), in the spring and summer (Nakamura, 2001a), but prefer them in the fall and winter (Yamanashi Prefecture, 2009). Martens often defecate in such open habitats (Yasumoto and Takatsuki, 2015), perhaps as a scent marking behavior (Clapperton, 1989; Gorman, 1990), and many intact seeds of various plant species are transported via defecation (endozoochory) (Otani, 2002; Koike et al., 2008; Tsuji et al., 2011b). Thus, Japanese martens conduct directional dispersal (Howe and Smallwood, 1982; Nakashima et al., 2010; Yasumoto and Takatsuki, 2015) via foraging.

To evaluate the contribution of the Japanese marten to the dispersal of fleshy-fruit-bearing plants, especially lianas in temperate forests, we modeled how far martens dispersed the seeds of fleshy fruits, about which little information is currently available. We then compared the seed shadow generated by the martens with those of other forest-

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dwelling animals in Japan (such as bears, other mustelids, canids, monkeys, and birds) to evaluate the uniqueness of the martens' seed dispersal in the temperate forests of Japan.

MATERIALS AND METHODS

Study area

We conducted a field survey in the forests of the northern base of Mt. Fuji, central Japan. Mt. Fuji (3,776 m a.s.l.) is a dormant volcano with a typical pyramidal shape. Northern Mt. Fuji (35°N, 138°E) is a special area with high variation in elevation (800–3,776 m within a distance of 18 km) (Jiang et al., 2005). The soil of the area originated mainly from lava and volcanic ash, and is low in fertility and high in water permeability. In the area below 2,000 m, the range of mean annual temperature is 5–11°C, ranging from –5°C in January to 16°C in July. Annual precipitation ranges from 1,845 to 3,000 mm and snow is usually available for about 120 days per year from late December to early April. The cumulative snow depth ranges between 40–80 cm, depending on the topography and vegetation, from early January to mid-March (Jiang et al., 2005). The dominant woody plant species in the montane and alpine zones are *Fagus crenata*, *Abies homolepis*, *Betula platyphylla*, and *Abies veitchii*. In the shrub layer, the floristic composition is simple and the seedlings of the tree species are important components (Jiang et al., 2005). The vegetation begins vegetative growth in early May and senesces in mid-October. Planted forests, such as those of the larch (*Larix kaempferi*), Japanese red pine (*Pinus densiflora*), and Nikko fir (*Abies homolepis*), are distributed in the elevation range of 800–1,800 m.

Marten home ranges

Adult martens were live-trapped using cage traps (bait: fried chicken or chicken bone). Captured martens were immobilized with an intramuscular injection of ketamine hydrochloride (dose: 20 mg/kg). We determined the sex and measured the body size of each individual. We then attached a 40 g radio collar (< 5% of body weight) to the marten and released it at the capture site. Our methodology adhered to the guidelines of the Japan Mammalogical Society and related laws of Japan.

We radio-tracked 11 adult martens (eight males, three females) between October 2003 and November 2008. We lost one male immediately after it was released, so location data were obtained from the remaining 10 animals. Martens were repeatedly located during tracking sessions that lasted 1–24 h. We plotted each location on maps and recorded locations as UTM coordinates. For each marten we calculated the straight-line distance between all sequential pairs of locations separated by less than 12 h, not considering movement around geographic barriers. Average home range sizes of the male ($n = 6$) and female ($n = 2$) martens was 2.86 km² (range: 0.54 to 5.38) and 2.12 (0.37 and 3.86) km², respectively (Yamanashi Prefecture, 2009).

Ranging data were placed in a matrix relating the time between locations and distance moved. Martens normally limit their movements to home ranges (Powell, 1994), and we predicted only a weak correlation between movement time and distance moved. We created 12 distributions depicting the proportions of marten movements in each distance category. Each distribution represented movements from a movement time interval (12 interval classes; 0–1 h to 11–12 h) between locations. Total time intervals did not have equal sample sizes, so each movement distribution reflected the number of movements in a given distance category divided by the total number of movements for that time category.

Seed passage times

We conducted a series of feeding experiments at Toyama Municipal Family Park Zoo, central Japan, in 2010 and 2011, and

obtained gut passage times for Japanese martens (Tsuji et al., 2011a, 2015). Four adult animals (three males and one female, body weight: 1.0–1.8 kg) were held in indoor individual cages (length 1.80 m × width 1.8 m × height 2.8 m). We fed martens dead chicks and fruit once a day (fresh weight 230–300 g). Since we could not use wild plants, we put model seeds (commercial plant seeds) into the stomach of the chicks. All chicks and fruits were eaten immediately after feeding, after that, the behavior of the martens was continuously recorded by security cameras set on the roof of the cages, from which we estimated the time of defecation. We collected all feces, washed them under fresh water, and picked out the seeds. We then created a distribution of seed passage times based on the proportion of passed seeds in each time category. We conducted four experiments with seeds of different sizes, and we found that the seed size had no effect on gut passage time (Tsuji et al., 2011a). This has also been found for other carnivores (Varela and Bucher, 2006; López-Bao and González-Varo, 2011). We therefore did not consider the characteristics of seeds in this study.

Seed shadow modeling

We followed the method described in Hickey et al. (1999) to calculate the seed shadow generated by Japanese martens. First, we combined data on ranging obtained from wild animals and gut passage times obtained from captive animals. To model the seed shadow, the proportions were then rescaled to accommodate distance classes of different widths. We fitted the scale to that of Hickey et al. (1999) for interspecific comparison.

For the seed passage data, let S_{ik} be the proportion of seeds passed in time class t of experiment k for marten i . Let

$$\bar{S}_t = \frac{1}{4} \sum_{k=1}^4 S_{tik},$$

be the mean (across four experiments) proportion of seeds passed by marten i in time class t ; and

$$\bar{S}_t = \frac{1}{4} \sum_{i=1}^4 \bar{S}_{ti},$$

is the mean (across four martens) proportion of seeds passed in time class t .

For the movement data, let m_{tdj} be the number of movement observations in time class t , distance class d , for marten j ;

$$m_t = \sum_{j=1}^{10} m_{tdj},$$

be the total (over means) number of observations in time class t , distance class d ;

$$m_t = \sum_{d=1}^{12} \sum_{j=1}^{10} m_{tdj},$$

be the total (over distance classes and martens) number of observations in time class t ; and

$$d_{td} = \frac{m_{td}}{m_t},$$

be the proportion of movement observations in time class t that are in distance class d (the proportions add to 1 over the distance classes). The proportion of seeds that were dropped in distance class d from their presumed place of origin is then estimated by

$$p_d = \sum_{t=1}^{12} \bar{S}_t d_{td}.$$

In order to test for differences in movement distance between sexes, which have been found in other carnivore species (Nakashima and Sukor, 2010; Koike et al., 2011), we conducted a generalized linear mixed model (GLMM) with distance as the dependent variable and sex as the explanatory variable. We set the interval of the location as the offset term, and defined that error

structure of the dependent variable as following a normal distribution. We performed the GLMM using the “glmmPQL” function in library (MASS) of statistical software R ver. 2.15.2 (R Development Core Team, 2012).

RESULTS

Movement patterns

During the study period, we obtained 401 location points from 11 individuals, from which we obtained 320 movement distances from 10 individuals over time intervals of 1–12 h. The majority of the distances were < 1500 m regardless of the time intervals (Fig. 1). For 0–1 h and 1–2 h between locations (92 and 117 distances, respectively), 0–100 m was the most common distance moved, and > 95% of movement distances were < 1,000 m (Fig. 1). For 2–3 h between locations (53 distances), 251–500 m was the most common (34.0%). For 4–5 h between locations (21 distances), martens moved a median of 501 m and moved 0 m, 1,501–2,000 m, and 2,501–3,000 m in similar (ca 10%) proportions. We did not include data on time intervals of 5–12 h for following analyses due to the small sample size (24 distances in total). We found no significant effect of sex on the movement distances (GLMM: $t = -1.26$, $P = 0.248$), and therefore we pooled the movement distances of both sexes in the following analyses.

Seed passage rates

Individuals exhibited highly variable passage times among days (0.6–3.0 h for 1 marten to pass its first feces containing seeds). For the four martens, seeds passed in a median and modal time of 6–7 h, and two-thirds of seeds were defecated within 12 h (Fig. 2). Between 10 and 21 h, equal proportions of seeds (< 4%) passed in the time inter-

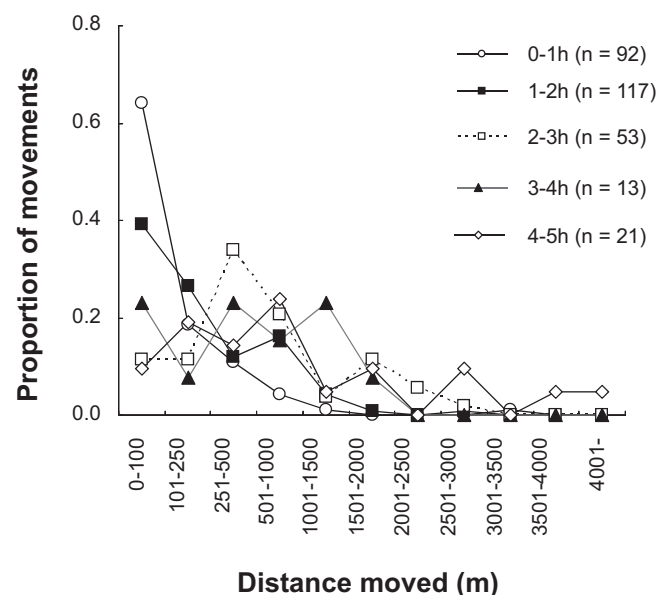


Fig. 1. Distribution of movement distances of radio-collared Japanese martens over 1-h time intervals in the northern foot of Mt. Fuji, central Japan, 2003–2006. Sample sizes were 0–1 h, 92 distances; 1–2 h, 117 distances; 2–3 h, 53 distances; 3–4 h, 13 distances; and 4–5 h, 21 distances. Time intervals >5 h were not shown due to the small number of distances ($n = 24$).

vals, and we therefore used only data within 12 h in the following analyses.

Seed shadow

Our models combining data on movement distance and seed passage rates showed that martens dispersed seeds over a wide range of distances; 83.6% and 53.3% of seeds were estimated to be dispersed > 100 m and > 500 m, respectively (Fig. 3). The model estimated that martens transport seeds a modal distance of 501–1,000 m, and the mean dispersal distance was 767.9 m. The percentages of seeds dispersed > 1,000 m and > 2,000 m were 26.2% and 3.6%, respectively (Fig. 3).

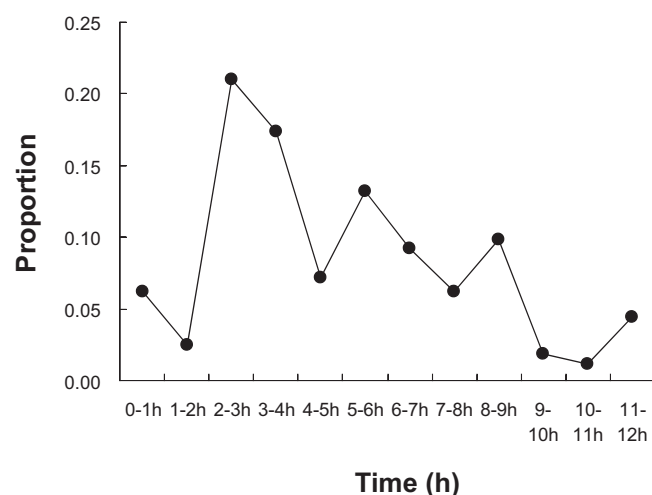


Fig. 2. Distribution of gut passage times for seeds ingested by Japanese martens fed on a diet of chicks and fruits in Toyama Municipal Family Park Zoo, central Japan, 2010–2011. Gut passage times were averaged for four adult martens (three males and one female).

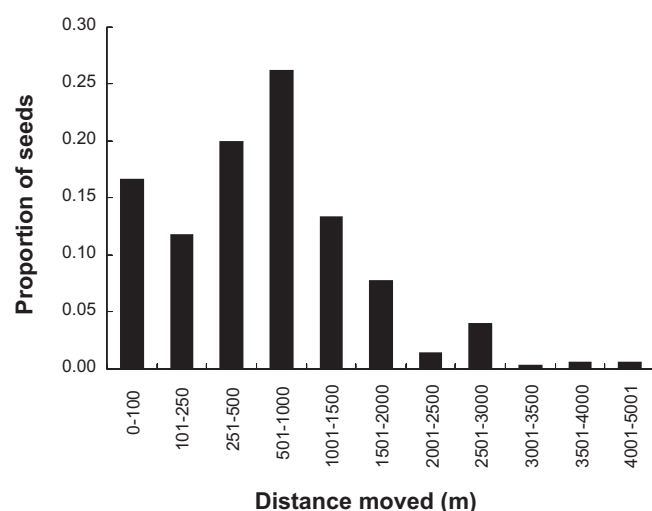


Fig. 3. The seed shadow generated by wild Japanese martens in the northern foot of Mt. Fuji, central Japan. Results were generated by a model that considered the gut passage times of four martens fed on a diet of chicks and fruits (2010–2011), and movement data for 10 radio-tracked martens (2003–2006).

DISCUSSION

The mean dispersal distance of seeds by Japanese martens in the northern foot of Mt. Fuji was ca. 770 m, with a maximum of > 2,000 m. The home ranges of Japanese martens in Nagano (3.6 km², Kawauchi et al., 2003) and Tsushima Island (0.6–0.7 km², Tataru, 1994) were similar to those in our study site (0.8–2.5 km², Nakamura, 2001a; Yamanashi Prefecture, 2009), and thus, the seed dispersal distance found in this study should also be relevant to the other study sites. The dispersal distance of the Japanese martens fell in the range of distances of other *Martes* species (ca. 500 m on average for American martens, *M. americana* (Hickey et al., 1999), 408 m on average for European pine martens *M. martes* (González-Varo et al., 2013), and ca. 650–700 m for European stone martens *M. foina* (Jordano et al., 2007)). The range of dispersal distances of Japanese martens is similar to other *Martes* species. However, the dispersal density inside home ranges might differ among species, in response to decreases in fruit abundance from south to north (Otani, 2005; Moles et al., 2009). *Martes* species in boreal regions become more carnivorous (Zalewski, 2004; Zhou et al., 2011) and their daily movements and home ranges became larger (Zalewski et al., 2004). Thus, Japanese martens inhabiting temperate regions might disperse ingested seeds within the home range more densely than do boreal *Martes* species.

Among forest-dwelling animals in Japan, what role do Japanese martens play as dispersal agents? We summarized the body weight, home range size, and dispersal distance of seeds by forest-dwelling animals in Japan (Table 1). The modeled dispersal distances of fruit seeds ingested

by Japanese martens was shorter than that of Japanese black bears (*Ursus thibetanus*) (2.5 km, Koike et al., 2011), but longer than those of ermines (*Mustela erminea*) (10–80 m, Sone, 2006), Japanese macaques (*Macaca fuscata*) (301–500 m, Terakawa et al., 2009; Tsuji and Morimoto, 2016), raccoon dogs (*Nyctereutes procyonoides*) (115–411 m, Sakamoto and Takatsuki, 2015), and frugivorous birds (< 100 m, Sakakibara, 1989; Fukui, 1996) (Table 1). Both the home range size (0.8–2.5 km², Nakamura, 2001a; Yamanashi Prefecture, 2009) and body size (0.8–1.8 kg, Ohdachi et al., 2009) of Japanese martens are intermediate among forest-dwelling animals in Japan (Table 1). Since the relations between body size and home range size and dispersal distance tended to be positive, martens presumably help to transport seeds of fleshy fruits intermediate distances from their feeding sites. Differences in the range of dispersal distances among species and positive correlations between dispersal distance and body size have been reported in European temperate forests (Jordano et al., 2007; González-Varo et al., 2013). In Japan, the relative percentage of fleshy fruits is lower than in tropical regions (Otani, 2005; Moles et al., 2009), and diverse frugivores share fleshy fruits. For example, *Vitis* spp., *Akebia* spp., and *Actinidia* spp. fruits are eaten not only by martens, but also by Japanese black bears, Japanese macaques, Japanese badgers (*Meles anakuma*), and raccoon dogs (Koike et al., 2008; Tsuji et al., 2010). Therefore, for fleshy-fruit-bearing species in temperate forests, having multiple frugivorous species with different dispersal ranges may help increase their survival rate and reproductive success by dispersing seeds widely at a lower density.

In this study, we detected no sex differences in move-

Table 1. Inter-specific variation in characteristics of body size, home range size, and seed dispersal characteristics of forest-dwelling animals on the main island of Japan.

Species	Japanese marten	Ermin ^c	Raccoon dog	Asiatic black bear	Japanese macaque	Brown-eyed bulbul	Varied tit
	<i>Martes melampus</i>	<i>Mustela erminea</i>	<i>Nyctereutes procyonoides</i>	<i>Ursus thibetanus</i>	<i>Macaca fuscata</i>	<i>Hypsypetes amaurotis</i>	<i>Parus varius</i>
Order	Carnivora	Carnivora	Carnivora	Carnivora	Primates	Passeriformes	Passeriformes
Adult body weight ^a	♂ : 1.3–1.8 ♀ : 0.8–1.2	♂ : 0.20 ♀ : 0.16	4.1±0.9	♂ : 40–84 ♀ : 28.5–43.5	♂ : 8.5–13.5 ♀ : 6.3–11.7	0.06–0.075	0.02
Society	Solitary	Solitary	Solitary or Pair	Solitary	Group	Group	Group
Home range (km ²)	♂ : 0.8–2.5 ^a ♀ : 0.5–2.0	♂ : 0.40–0.83 ^b ♀ : 0.18–0.50	0.1–6.0 ^b	♂ : 226.8–284.6 ^b ♀ : 161.8–247.8	0.3–26.7 ^b	0.026	0.11 ^g
Space	Terrestrial/arboreal	Terrestrial	Terrestrial	Terrestrial/arboreal	Terrestrial/arboreal	Arboreal	Arboreal
Dispersal distance (m)							
Mean (peak)	770	10–80	115–411	1250	301–500	?	< 50
Range	0–5001	0–1800	0–462	250–22000	0–1200	0–300	0–210
Passage time (h)							
Mean	9.7	?	?	18.5–19.1	37–54 ^d	< 1 h	?
Range	0.6–51.8	?	?	3.2–44.3	22–109	?	?
Source of dispersal distance	This study	Sone (2006)	Sakamoto and Takatsuki (2015)	Koike et al. (2011)	Terakawa (2009), Tsuji and Morimoto (2016)	Fukui (1995, 1996)	Sakakibara (1989)

^aHosoda and Tataru (1996)

^bOhdachi et al. (2009)

^cThere is a possibility that feces of the martens are included.

^dTsuji et al. (2010)

ment distances and gut passage times. Previous studies have reported that the home ranges of adult male martens are 2–3 times larger than those of females (Hosoda and Tataru, 1996; Nakamura, 2001a; Yamanashi Prefecture, 2009), but our finding that daytime movement within the home range was the same implied that male martens would disperse the seeds of fleshy fruits more widely with lower density. However, it is possible that the small female sample size led to the present result, and we should reconsider this issue after increasing our sample size from females.

The specific home range use of the martens can be a unique aspect of their seed dispersal. Japanese martens in northern foot of Mt. Fuji preferred open habitat such as forest edges (Yamanashi Prefecture, 2009), perhaps due to scent marking (Clapperton, 1989; Gorman, 1990). For many plants, especially liana species, such open habitat seems advantageous to germination and growth, and the scent marking of the martens implies that they actively transport the seeds of fleshy fruits to suitable places, that is, directional dispersal (Howe and Smallwood, 1982; Yasumoto and Takatsuki, 2015). It has been reported that such directional dispersal is important to colonization or habitat expansion for several plant species (Tsuji and Yumoto, 2009; Nakashima et al., 2010). In Japan, evidence of directional dispersal has been reported only from Japanese macaques, which disperse seeds of *Myrica rubra* to locations suitable for germination (Tsuji and Yumoto, 2009). Further systematic study may confirm directional dispersal for Japanese martens.

We estimated dispersal distance based only on a 1-year data set of martens' home range use, so we should be careful about generalizing our findings. Dietary habits of frugivores change inter-annually (Jędrzejewski, 1993; Ben-David et al., 1997; Zhou et al., 2008; Tsuji et al., 2014), which is mainly attributed to long-term variation in diet abundance. In the cases of red foxes (*Vulpes vulpes*) and European badgers (*Meles meles*), for example, these species shifted their diet from rodents to fleshy fruits when the availability of the former decreased (Perea et al., 2012). Asiatic black bears, red foxes, and European pine martens showed inter-annual differences in dispersal distance (Koike et al., 2011; González-Varo et al., 2013), and the number of seeds per fecal sample and ingestion ratio also changed inter-annually (Perea et al., 2012). From a broader perspective, inter-annual variation in the food environment affects the food preference of animals belonging to dispersal guilds, and affects the dispersal density and relative contribution of each member (González-Varo et al., 2013). Thus, long-term variation in the dispersal characteristics and inter-specific comparisons in performance should be conducted to generalize the relative importance of martens in endozoochory.

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