RESEARCH ARTICLE

Endozoochorous Seed Dispersal by Japanese Macaques (*Macaca fuscata*): Effects of Temporal Variation in Ranging and Seed Characteristics on Seed Shadows

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Variation in seed shadows generated by frugivores is caused by daily, seasonal, and inter-annual variation in ranging, as well as inter-specific variability in gut passage times according to seed characteristics. We studied the extent to which seed weight, specific gravity, and daily (morning, afternoon, and evening) and inter-annual (2004 vs. 2005) variation in ranging affected seed shadows generated by wild Japanese macaques (*Macaca fuscata*) in northern Japan. The macaques ingested fleshy fruits of 11 species during the two year study period; *Viburnum dilatatum* (Caprifoliaceae: heavier seeds with higher specific gravity) and *Rosa multiflora* (Rosaceae: lighter seeds with lower specific gravity) were eaten frequently in both years. The travel distances of macaques after feeding on *V. dilatatum* and *R. multiflora* fruits were estimated by combining feeding locations and ranging patterns measured in the field with gut passage times of model seeds in captive animals. Median travel distances after fruit feeding were 431 (quantile range: 277–654) and 478 m (265–646), respectively, with a maximum of 1,261 m. Neither year nor time of day affected travel distances. The gut passage time of model *V. dilatatum* seeds was longer than that of model *R. multiflora* seed, but this did not affect dispersal distances. Seed shadows for both species over 2 years showed unimodal distribution (peak: 101–500 m) and more than 90%, 20%, and 3% of ingested seeds were estimated to be dispersed >100, >500, and >1000 m, respectively, the longest known distances among macaque species. *R. multiflora* seeds tended to be dispersed further in 2004 than 2005, but *V. dilatatum* seeds were not, implying that inter-annual variations in ranging pattern due to the distribution and abundance of nut fruiting could affect dispersal distance. Am. J. Primatol. 78:185–191, 2016.   © 2015 Wiley Periodicals, Inc.

INTRODUCTION

Seed shadows, the spatial distribution of seeds dispersed from an individual plant [Jordano & Schupp, 2002], have been generated for primates in many regions, and indicate that primates can transport seeds up to several hundreds of meters away from their feeding sites [Africa: Gautier-Hion et al., 1983; Madagascar: Moses & Semple, 2011; Asia: McConkey & Chivers, 2007; Terakawa et al., 2009; South America: Julliot, 1997; Stevenson, 2000], and that great apes sometimes dispersed seeds more than 1,000 m [Beaune et al., 2013; Tsuji et al., 2010a]. Depositing seeds across wide ranges enables the colonization of new sites by dispersing seeds far from the parent tree [Howe & Smallwood, 1982], and thus can contribute to maintaining plant populations and, ultimately, to forest structure [Chapman & Russo, 2007].

The dispersal distance should change in response to the abundance and distribution of both fruit-bearing plants and non-fruit items, combination of available species, nutritional requirements, and inter- and intra-group competition of the agents, all of which change temporally (daily, seasonal, and inter-annual). Seed characteristics also affect

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passage time; in tamarin monkeys (*Saguinus* spp.), the passage time of seeds with higher specific gravity was shorter [Garber, 1986], whereas the opposite was found for Japanese macaques (*Macaca fuscata*) [Tsuji et al., 2010b]. Thus, the type of fleshy fruits consumed might affect the dispersal distance. Despite the large number of studies on primate endozoochory, few researchers have addressed the effects of inter-annual variation in ranging and fruit-eating and of the characteristics of seeds on seed dispersal distances and seed shadows.

Japanese macaques primarily feed on fleshy fruits and nuts throughout their range, especially in fall (September–November; reviewed in Tsuji, 2010, Tsuji et al., 2015), and defecate and spit out seeds of 12–35 plant species [Otani & Shibata, 2000; Tsuji, 2011, 2014; Tsuji et al., 2011] inside forests. Further, ingestion by macaques enhanced germination for seeds of several plant species [Otani & Shibata, 2000], although many seeds were masticated before ingestion [Otani, 2004; Tsuji et al., 2010b]. A recent study found that the topography of dispersed seeds matched the distribution of trees of target plants, which implies that the macaques contribute to the colonization and expansion of plant populations [Tsujino & Yumoto, 2009]. On Kinkazan Island, production of nuts, the staple diet of macaques in fall (September–November), showed clear inter-annual differences (e.g., energy production per hectare ($\times 10^3$ kcal/ha) between 2000 and 2005; range 12–1,043) [Tsuji et al., 2006]. This caused inter-annual variation in the degree of fruit feeding [Tsuji et al., 2006], ranging [Tsuji & Takatsuki, 2009], and the composition of seeds inside the feces [Tsuji, 2014]. Therefore, it is predicted that the inter-annual change of food affects the dispersal distance of seeds.

In this study, we generated a seed shadow by combining behavioral observations and feeding experiments on Japanese macaques for 2 years to evaluate the effects of inter-annual variation in ranging and seed characteristics on dispersal distances.

METHODS
Research Protocols

Our field research adhered to Japan's legal requirements. Our methodology in feeding experiments complied with protocols approved by the guidelines (Guide for the Care and Use of Laboratory Primates, Second Edition) of the Primate Research Institute, Kyoto University, Japan, and the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Study Site and Animals

Kinkazan Island (38.3°N, 141.6°E) is located 700 m from the Oshika Peninsula in northern Japan. The total area of the island is ca. 9.6 km^2, and the highest peak is 450 m a.s.l. Deciduous forests of *Fagus crenata* dominate the higher elevations (>150 m), whereas a mixture of deciduous forests of *Carpinus* spp. and coniferous forests of *Abies firma* cover the lower elevations (<150 m) on the island. Approximately 200–250 native Japanese macaques belonging to six troops inhabit the island [Tsuji & Takatsuki, 2012]. Our subject was Troop A, which has been habituated to observation at close proximity (<10 m) since 1982. During the study period (2004–2005) the troop's size varied from 29 to 39 individuals, and its home range size was ca. 3.3 km^2 [Tsuji & Takatsuki, 2009, 2012].

Ranging of the Macaques

We observed Troop A from late September to November, which corresponds to the season when many woody plants are fruiting [Tsuji, 2014], in both years (41 days in 2004 and 36 days in 2005). Total data collection time was 578 hr (304 hr in 2004 and 274 hr in 2005), which was composed of sets of observations for 2 or 3 consecutive days. We followed the troop from dawn to dusk, during which time we conducted focal animal observations. We observed focal animals (17 adult females [>5 years old] in 2004 and 14 females in 2005) for up to 6 hr, and followed one to three animals daily, conducting a total of 146 focal samplings during the study (72 focal samples in 2004 and 74 focal samples in 2005) [Tsuji & Takatsuki, 2012]. The mean ± SD length of a focal sample was 257 ± 70 min. We did not follow females in estrus in order to eliminate its effect on foraging behavior [Matsubara & Sprague, 2004]. When the focal animal was feeding on fleshy fruit for >5 min, we defined it as a fruit-feeding bout, and recorded the hour and plant species. The location of the feeding trees was also recorded by a handheld GPS. On Kinkazan Island, cheek pouch dispersal by the macaques [Tsujino & Yumoto, 2009; McConkey et al., 2014] was rarely observed [Tsuji et al., 2011]; therefore, we did not consider this type of dispersal in this study.

Ranging data were placed in a matrix relating the time between locations and distance traveled (corresponds to dispersal distance of seeds). The daily routes of macaques on Kinkazan Island are circuitous [Maruhashi et al., 1998; Nakagawa, 1989], and we predicted only a weak correlation between travel time and dispersal distance. We established 12 distance categories of 100 m in length (0–100 m to 1,101–1,200 m) depicting the proportions of macaque movements. Each dispersal distance represented movements during 4-hr time intervals (24 classes; 20–24 hr to 112–116 hr after feeding) obtained by connecting the feeding site and location at a given time. The time range represented the previously obtained minimum and maximum gut passage time

after feeding [Tsuji et al., 2010b, see below]. As continuous observation of the macaques was difficult, the number of recorded dispersal distances differed among time intervals.

Seed Passage Times

We conducted a series of feeding experiments (eight trials/animal) at the Primate Research Institute, Kyoto University, and obtained the gut passage times of seeds [Tsuji et al., 2010b] for five adult females (body weight: 6.7–10.5 kg, in good health and not pregnant). Each animal was placed in an individual cage (width: 760 mm, length: 900 mm, height: 850 mm) in an air-conditioned (20°C) experimental room for the experiments. Due to the management policy of the institute, we could not provide seeds of fleshy fruits. Instead, we put commercial seeds whose weight and specific gravity were similar to those of target seeds into banana chunks and fed them to the macaques with monkey chow (100 g in flesh weight: a usual diet). The banana chunks with seeds were eaten immediately after feeding. We collected all feces from the floor of the cage every 2 hr, washed them under fresh water, and picked out the seeds, from which we created a distribution of seed passage times based on the proportion of passed seeds in each time category. The number of seeds provided, intact rate (obtained by dividing the total number of intact seeds by the total number of seeds), and recovery rates are shown in Tsuji et al. [2010b].

Seed Shadow Modeling

We followed the method reported by Hickey et al. [1999] to calculate seed shadows generated by macaques by combining data on their travel distances, obtained from behavioral observation and gut passage times obtained from captive animals. For the seed passage data, let S_{ti} be the proportion of seeds passed in time class t (after feeding, h) of a given feeding experiment for macaque i, and

$$\bar{s}_t = \frac{1}{5}\sum_{i=1}^{5}\bar{s}_{ti},$$

is the mean (across five animals) proportion of seeds passed in time class t.

For movement data, let m_{td} be the number of travel distances in time class t, travel distance class d;

$$m_t = \sum_{d=1}^{12}m_{td},$$

be the total (over distance classes) 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 proportion of seeds that were dropped in distance class d from their presumed place of origin is then estimated by

$$p_d = \sum_{t=1}^{24}\bar{s}_t d_{td}.$$

Statistical Analysis

In order to test the effects of the year (2004 and 2005) and daily time of fruit-feeding bouts (morning: 06:00–10:00, afternoon: 10:00–14:00, evening: 14:00–18:00) on the travel distances, we used generalized linear mixed models (GLMM) with travel distance as a dependent variable (defined as having an error structure following the gamma distribution) and year, daytime hours, and their interaction as the explanatory variables. We treated each fruit-feeding bout as a random factor to avoid pseudoreplication. We set the gut passage time after the fruit feeding as an offset term. We performed two-sample Kolmogorov–Smirnov tests in order to compare the shape of seed shadows between the plant species over 2 years or between years for each plant species. We performed statistical analyses with the statistical software R ver 2.15.2 [R Development Core Team, 2012] and set the statistical significance (α) to be 0.05.

RESULTS

Fruit-Feeding Events and Travel Distances

During the study period, we recorded a total of 145 fruit-feeding bouts with 11 fleshy fruit species (four high trees (>5 m in tree height), three shrubs, three vines, and one hemi-parasite species) over 2 years, from which we obtained 1,133 travel distances between 20 and 116 hr after feeding. The numbers of fruit-feeding bouts for *Viburnum dilatatum* (Caprifoliaceae: 16 bouts and 86 travel distances in 2004, 20 bouts and 216 travel distances in 2005) and for *Rosa multiflora* (Rosaceae: 41 bouts and 351 travel distances in 2004, 10 bouts and 98 travel distances in 2005) were much greater than those for other fleshy fruit-bearing plants. Therefore, we generated seed shadows for these two shrub species.

For both species, the majority of the travel distances after feeding were within 500 m regardless of the time interval class (median [quantile range]: 431 m [277–654] for *V. dilatatum*, 478 m [265–646] for *R. multiflora*; Fig. 1). Year (GLMM, $t_{25} = 1.18$, $P = 0.249$ for *V. dilatatum*, $t_{39} = 0.26$, $P = 0.793$ for *R.*
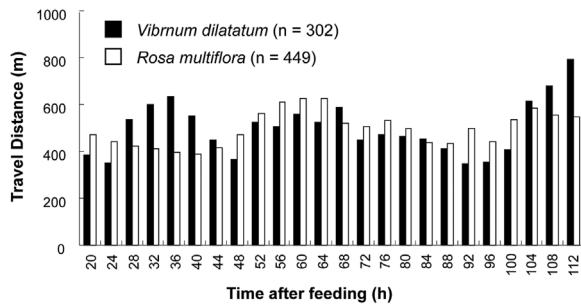
Fig. 1. Mean travel distance (m) of wild Japanese macaques after feeding on *Viburnum dilatatum* and *Rosa multiflora* fruits, in 4-hr time intervals (range: 20–116 hr), on Kinkazan Island, northern Japan.

multiflora), daytime hours ($t_{25} = 1.75$, $P = 0.093$ for *V. dilatatum*, $t_{39} = 0.58$, $P = 0.567$ for *R. multiflora*), and their interaction ($t_{25} = -1.75$, $P = 0.093$ for *V. dilatatum*, $t_{39} = -0.58$, $P = 0.567$ for *R. multiflora*) did not affect the travel distances.

Seed Passage Rates

As noted above, we could not use wild fruits for experiments. We instead used spinach (*Spinacia oleracea*) seeds (weight: 11.35 mg, specific gravity: 0.65 mg/mm^3) as a surrogate for *V. dilatatum* seeds (weight: 7.90 mg, specific gravity: 0.68 mg/mm^3), and potherb mustard (*Brassica* sp.) seeds (weight: 1.74 mg, specific gravity: 0.95 mg/mm^3) as a surrogate for *R. multiflora* seeds (weight: 2.82 mg, specific gravity: 0.85 mg/mm^3, Tsuji et al. [2010b]). Dosed number of spinach and potherb mustard seeds were 25 and 230, respectively. We, hereafter, refer to the model seeds as "*V. dilatatum*" and "*R. multiflora*." The macaques exhibited relatively narrow variation in gut passage times (20–24 hr after feeding for one macaque to pass its first feces containing seeds for both species). The mean retention times (time when half of the seeds were defecated) of *V. dilatatum* and *R. multiflora* seeds were 44–48 and 24–28 hr after feeding, respectively (Fig. 2). Almost all intact seeds for each species were defecated within 100 hr after the feeding.

Seed Shadow Generated by the Macaques

Seed shadows obtained by combining travel distance and seed passage rates showed that macaques transported seeds over a wide range of distances: for *V. dilatatum*, 92.3%, 23.4%, and 3.3% of defecated seeds were estimated to be dispersed >100, >500, and >1,000 m, respectively. Corresponding values for *R. multiflora* were 94.7%, 38.7%, and 4.3%, respectively (Fig. 3). The macaques transported *V. dilatatum* seeds with a modal distance of 301–500 m. The range of the modal distance of *R. multiflora* (101–500 m) was wider
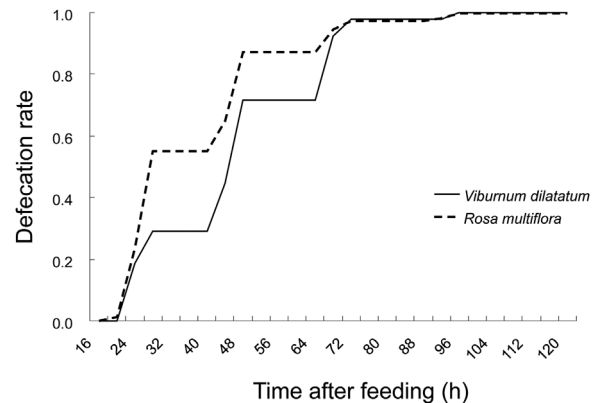

Fig. 2. Distribution of gut passage time for spinach seeds (as representative of *Viburnum dilatatum* seeds, black line) and potherb mustard seeds (as representative of *Rosa multiflora* seeds, dashed line) ingested by captive Japanese macaques in the Primate Research Institute, Kyoto University. Defecation rates are averages for five female macaques. See Tsuji et al. [2010b] for details.
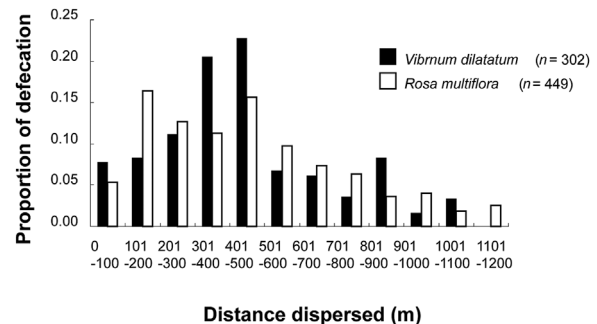

Fig. 3. The seed shadows for *Viburnum dilatatum* (filled bars) and *Rosa multiflora* (open bars) generated by Japanese macaques on Kinkazan Island, northern Japan. Data obtained in 2004–2005 were pooled. Results were generated by a model that considered the gut passage times of five macaques and ranging data for the observed habituated troop. There was no significant difference between species (Kolmogorov–Smirnov test, $D = 0.307$, $P = 0.570$).

than that of *V. dilatatum* (Fig. 3), but there was no significant difference in the shape of the seed shadows between species (two-sample Kolmogorov–Smirnov test, $D = 0.31$, $P = 0.570$). No inter-annual difference in the shape of the seed shadow for *V. dilatatum* was detected ($D = 0.45$, $P = 0.206$); the median (quartile range) of the dispersal distance was 467 m (323–624) in 2004 and 425 m (270–666) in 2015. On the other hand, the shape of the seed shadow for *R. multiflora* differed between the two years ($D = 0.54$, $P = 0.046$); the median of the dispersal distance was 486 m (281–672) in 2004 and 420 m (254–539) in 2005.

DISCUSSION

Regardless of the time after feeding, most dispersal distances from feeding sites were less than 500 m, and inter-annual and inter-specific

differences were not detected. The gut passage time of ingested seeds ranged 20–112 hr. This value was much longer than those of New World monkeys (3.3–6.8 hr, Chapman & Russo [2007]) and prosimians (2.3–7.5 hr, Edwards & Ullrey [1999]), and comparable to those of great apes [Lambert, 1997], though in future we should reconsider how other items consumed at same time influence the seed passage times. The home range area of Japanese macaques can reach several square kilometers [Takasaki, 1981; Tsuji, 2010], within which they range with circuitous movement [Nakagawa, 1989; Maruhashi et al., 1998]. Therefore, detecting a proportional relationship between the passage time and travel distance of the macaques [Otani, 2005] would be difficult.

The seed shadows generated for two shrub species (*Viburnum dilatatum* and *Rosa multiflora*) ranged between 0 and 1,200 m with a unimodal distribution and a peak within 100 and 500 m. The home range size of the subject troop is ca. 3.3 km^2 [Tsuji & Takatsuki, 2012], which corresponds to a circle with a radius of ca. 1 km. This implies that the macaques can disperse seeds everywhere within their home range via endozoochory. It is noteworthy that seeds of both *V. dilatatum* and *R. multiflora* tended to be dispersed longer distances in 2004 (and that the latter showed a significant difference in distance). A plausible reason is interannual variation in home range use. The ranging patterns of the macaques were affected by the fruiting of nut species, which are a staple diet of the macaques in fall: the macaques moved long distances to visit scattered *Torreya nucifera* trees bearing nuts in 2004, whereas the moving distance of the macaques became shorter in 2005 because abundant *Fagus crenata* trees fruited heavily in this year and the macaques consumed them that year [Tsuji et al., 2006; Tsuji & Takatsuki, 2009]. As fleshy fruit feeding occurs between nut feeding in the same day, distances between nut-feeding sites can cause these inter-annual differences in dispersal distance.

We evaluated the gut passage times for two types of model seeds with comparable seed characteristics in terms of seed weight and specific gravity; spinach seeds (as representative of *V. dilatatum* seeds), having greater weight and higher specific gravity, took longer for defecation than potherb mustard seeds (as representative of *R. multiflora*), with lower weight and lower specific gravity. The different gut passage times of the species, however, did not affect seed dispersal distance and shape of the seed shadow. Therefore, the seed dispersal distances of *V. dilatatum* and *R. multiflora* (and perhaps of other species) would be determined not by the digestive physiology of the macaques, but by the distribution and abundance of staple diets within the home range, and corresponding feeding behavior.

In the habitats of *Macaca*, the number of plant species [Otani, 2005] and fruit production [Moles et al., 2009] decrease at higher latitudes, whereas seasonality in fruit production increases [Hanya et al., 2013]. As a result, macaques at higher latitudes spend less time and show higher seasonality in fruit feeding [Tsuji et al., 2013], and inter-troop competition over fruits is much weaker [Saito et al., 1998], which contribute to increasing the time spent searching for fruit and to enlarging their home range size [Takasaki, 1981]. Thus, macaques at higher latitudes should transport seeds longer distances via defecation. This prediction is supported by an inter-site comparison: the endozoochorous seed dispersal distance of Japanese macaques on Kinkazan Island (northern Japan, 38°N; median: 431–478 m, maximum: 1,261 m) was much greater than that of the same species on Yakushima Island (southern Japan, 30°N; mean: 270.0 m, range: 20.4–634.0 m) [Terakawa et al., 2009], that of rhesus macaques (*M. mulatta*) in Buxa Tiger Reserve (northern India, 26°N; mean: 64.1–299 m, maximum: 774 m) [Sengupta et al., 2014], and that of Taiwanese macaques (*M. cyclopis*) in Kenting (southern Taiwan, 21°N; mean: 258.7 m, range: 56.0–662.5 m) [Liu et al., 2012]. Thus, Japanese macaques inhabiting a cool temperate region likely create the largest dispersal distances via defecation. Temperate regions lack large frugivorous birds such as hornbills and fruit pigeons [Corlett, 2009], and mammals should be important agents for long-distance dispersal [Jordano et al., 2007]. To evaluate the relative importance of macaques as seed dispersers, we should evaluate the dispersal distance and dispersal density of sympatric frugivores, such as birds and omnivorous mammals, to compare with those of macaques.

In this study, we did not consider the characteristics of defecation sites. Recent studies have shown that defecation sites matched microhabitats where target plant seeds prefer to germinate and grow [Tsujino & Yumoto, 2009, but see also Nakashima et al., 2010], that is, the macaques might perform topography-specific seed dispersal. Even if there is no inter-annual difference in the dispersal distances, transportation to a specific micro-habitat in 1 year might contribute more to the colonization and/or expansion of populations for several species than in other years. To evaluate this prediction, we should examine the relationship between the distribution of parent trees in each age-class and the pattern of seed dispersal by the macaques in each year.

By accumulating data on the dispersal distance of macaques from various primate species and study sites, we can make generalizations about the determinants of the dispersal distance and/or their phylogenic differences. Further, we can address several questions regarding dispersal, such as distance- and density-dependent seed mortality, which is critical for evaluating seed dispersal

effectiveness among species in the same site and/or within species in different sites. These findings can contribute to better understanding the ecological role of primates as seed dispersal agents.

ACKNOWLEDGMENTS

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