Chapter 6: Seed Dispersal by Japanese Macaques

Tatsuya Otani

6.1 Introduction

Seed dispersal is a crucial process in recruitment of plant populations, as well as for pollen dispersal. The location of dispersed seeds affects the survival of seedlings and the spatial distribution pattern of plants. Plants employ various strategies for effective seed dispersal, and diaspores have unique structures that utilize biotic and/or abiotic factors such as fleshy arils for endozoochory, thorny hooks for epizoochory, and membrane wings for anemochory. Most studies on seed dispersal by mammals have concerned endozoochory, that is, when an animal eats the edible fleshy parts surrounding seeds and then disseminates intact seeds by defecating or spitting out the seeds, although a few studies have examined epizoochory (e.g., Mouissie et al. 2005). The viability or survival rate of seeds can be altered at each step of seed dispersal and recruitment process, starting from fruit foraging by animals, followed by seed passage through digestive tracts, seed deposition on the forest floor, germination, and finally seedling establishment (Schupp 1993). Numerous studies have reported that diverse primate species act as effective endozoochorous seed dispersers for tree species in tropical and subtropical forests (Balcomb and Chapman 2003; Russo et al. 2006). We have only one indigenous primate species, *Macaca fuscata*, in Japan, and previous studies have suggested that Japanese macaques are also effective agents of seed dispersal for tree species that compose the cool- and warm-temperate forests in Japan. In this chapter, I present findings from previous studies on seed dispersal by Japanese macaques.

T. Otani (✉)
Japan International Research Center for Agricultural Sciences (JIRCAS),
1-1 Ohwashi, Tsukuba, Ibaraki 305-8686, Japan
e-mail: tatsuyao@affrc.go.jp

N. Nakagawa et al. (eds.), *The Japanese Macaques,*
DOI 10.1007/978-4-431-53886-8_6, © Springer 2010

6.2 Fleshy-Fruited Species in Southern and Northern Japan

Species compositions of forest trees are widely different at the southern and northern ends of the Japanese macaques range in Japan. At the southern end, warm-temperate evergreen broad-leaved forests dominated by species of Lauraceae, Myrsinaceae, Moraceae, and Fagaceae cover the lowlands of Yakushima Island (Miyawaki 1980). At the other end, cool-temperate deciduous broad-leaved forests dominated by species of Fagaceae, Aceraceae, Betulaceae, and Pinaceae are found widely in the snowy region of northern Honshu Island (Miyawaki 1987). Soft and juicy parts of fruits, formed from various tissues such as aril, mesocarp, endocarp, and sepal, are considered as adaptations for endozoochory (Willson et al. 1989). The percentage of fleshy-fruited tree species of the total tree species found in a forest stand decreases with increase in latitude (Willson et al. 1989; Herrera 2002). In Japan, the percentage of fleshy-fruited woody species in evergreen broad-leaved forests in southern areas (mean, 71%) is higher than that in deciduous broad-leaved forests in northern areas (mean, 50%), and deciduous arbor species comprise a significantly lower number of fleshy-fruited species (37%) than other life forms such as evergreen arbors, evergreen and deciduous shrubs, and vines (53–68%; Otani 2005). These facts imply that animal seed dispersers can contribute to the recruitment process of more tree species in the southern part of Japan than in the northern part, and the potential importance of animal seed dispersers for fleshy-fruited plants in forests is greater in evergreen forests than in deciduous forests.

6.3 Plant Species Dispersed by Japanese Macaque Feces

Fecal analysis is a simple and reliable method for determining the type and frequency of seeds dispersed by animals. Tables 6.1 and 6.2 show the frequency of occurrence and number of seeds extracted from Japanese macaque feces collected at the western lowland of Yakushima Island and the northern part of Honshu Island, respectively. From the western lowland of Yakushima (30°20′N, 130°30′E), which is covered by primary and secondary broad-leaved evergreen forests, 34 species in 19 families including 31 fleshy-fruited species were reported to be dispersed by feces, and a fecal sample contained seeds of 2.8 ± 1.4 species on average (Table 6.1). Several hundred seeds were found in a fecal sample for the top four species: *Ficus superba* var. *japonica*, *Ficus thunbergii*, *Eurya emarginata*, and *Eurya japonica*. Hanya et al. (2003) also reported other seed species found in macaque feces in the lowland of Yakushima, such as *Ficus pumila*, *Euscaphis japonica*, and *Distylium racemosum*. At the two sites in the northern part of the Honshu Island, Kashima (37°42′N, 140°50′E) and Shimokita Peninsula (41°09′N, 140°47′E), seeds of 21 species in 16 families were extracted from fecal samples (Table 6.2). The number of seed species in a fecal sample averaged 2.4 ± 1.5 in Kashima and 1.9 ± 0.8 in Shimokita. Mean numbers of seeds per fecal sample exceeded 900 for tiny-seeded

Table 6.1 Frequency of occurrence and number of seeds in Japanese macaques' feces collected at the western coastal area of Yakushima Island

Species	Family	Life form	Frequency of occurrence	Number of seeds per feces (±SD)
Ficus superba var. *japonica*	Moraceae	Tree	0.52	456 ± 617
Ficus thunbergii	Moraceae	Vine	0.47	323 ± 374
Eurya emarginata	Theaceae	Shrub	0.32	277 ± 286
Eurya japonica	Theaceae	Shrub	0.26	284 ± 370
Actinidia rufa	Actinidiaceae	Vine	0.23	60 ± 69
Ficus erecta	Moraceae	Shrub	0.20	58 ± 76
Psychotria serpens	Rubiaceae	Vine	0.17	29 ± 32
Cleyera japonica	Theaceae	Shrub	0.11	51 ± 77
Elaeocarpus japonicus	Elaeaocarpaceae	Tree	0.05	8 ± 7
Vaccinium bracteatum	Ericaceae	Shrub	0.04	18 ± 13
Ficus nipponica	Moraceae	Vine	0.03	82 ± 43
Morinda umbellata	Rubiaceae	Vine	0.03	10 ± 10
Actinodaphne longifolia	Lauraceae	Tree	0.03	2 ± 1
Schefflera octophylla	Araliaceae	Tree	0.02	12 ± 1
Ampelopsis brevipedunculata	Vitaceae	Vine	0.02	11 ± 6
Vitis flexuosa	Vitaceae	Vine	0.02	7 ± 7
Callicarpa japonica	Verbenaceae	Shrub	0.02	2 ± 0
Ternstroemia gymnanthera	Theaceae	Tree	0.02	71 ± 70
Rubus grayanus	Rosaceae	Shrub	0.02	21 ± 12
Parthenocissus tricuspidata	Vitaceae	Vine	0.02	16 ± 10
Myrica rubra	Myricaceae	Tree	0.02	16 ± 11
Myrsine seguinii	Myrsinaceae	Shrub	0.02	11 ± 2
Ardisia sieboldii	Myrsinaceae	Tree	0.02	9 ± 8
Pittosporum tobira	Pittosporaceae	Shrub	0.02	3 ± 3
Psychotria rubra	Rubiaceae	Shrub	0.02	2
Diospyros morrisiana	Ebenaceae	Tree	0.02	1
Mallotus japonicus[a]	Euphorbiaceae	Tree	<0.01	188
Picrasma quassioides[a]	Simaroubaceae	Tree	<0.01	23
Dendropanax trifidus	Araliaceae	Tree	<0.01	17
Symplocos lucida	Symplocaceae	Tree	<0.01	11
Cinnamomum camphora	Lauraceae	Tree	<0.01	4
Citrus sp.	Rutaceae	Shrub	<0.01	2
Vitis ficifolia var. *lobata*	Vitaceae	Vine	<0.01	1
Unknown			<0.01	2

Species are arranged in decreasing order by frequency of occurrence. Number of seeds per feces was calculated on the basis of the mean fresh weight of a feces (15.3 gfw). Frequency of occurrence, proportion of number of feces including seeds to the total number of feces collected ($n = 132$)

[a] Not fleshy fruits

Source: Modified from Otani (2005)

Table 6.2 Frequency of occurrence and number of seeds in Japanese macaques' feces collected at two sites (Kashima and Shimokita) in northern Japan

Species	Family	Life form	Frequency of occurrence	Number of seeds per feces (±SD)	
				Kashima	Shimokita
Actinidia arguta	Actinidiaceae	Vine	0.55	156 ± 215	905 ± 1,029
Actinidia polygama	Actinidiaceae	Vine	0.28	992 ± 764	1,408 ± 1,299
Vitis coignetiae	Vitaceae	Vine	0.19	27 ± 25	20 ± 32
Akebia trifoliata	Lardizabalaceae	Vine	0.16	98 ± 71	2
Rubus phoenicolasius	Rosaceae	Shrub	0.14	2,522 ± 1,787	299 ± 328
Berchemia racemosa	Rhamnaceae	Vine	0.09	4 ± 3	108 ± 88
Schisandra repanda	Schisandraceae	Vine	0.09	3 ± 3	4 ± 2
Calliearpa japonica	Verbenaceae	Shrub	0.08	30 ± 31	29 ± 19
Broussonetia kazinoki	Moraceae	Shrub	0.07	142 ± 114	–
Morus australis	Moraceae	Shrub	0.05	39 ± 29	–
Rubus palmatus var. *coptophyllus*	Rosaceae	Shrub	0.05	470 ± 196	–
Polygonum filiforme[a]	Polygonaceae	Herb	0.03	9 ± 3	366 ± 298
Stachyurus praecox	Stachyuraceae	Shrub	0.03	8 ± 9	–
Acanthopanax sciadophylloides	Araliaceae	Tree	0.03	85 ± 49	–
Cornus kousa	Cornaceae	Tree	0.02	–	11 ± 9
Oryza sativa[a]	Gramineae	Herb	0.01	1 ± 1	–
Ilex macropoda	Aquifoliaceae	Tree	<0.01	174[b]	–
Viburnum dilatatum	Caprifoliaceae	Shrub	<0.01	–	3
Cornus brachypoda	Cornaceae	Shrub	<0.01	1	–
Celastrus orbiculatus	Celastraceae	Vine	<0.01	–	2
Prunus sp.	Rosaceae	Tree	<0.01	1	–

Species are arranged in decreasing order by frequency of occurrence. Number of seeds per feces was calculated on the basis of mean volume of feces (13.9 ml)

Frequency of occurrence, proportion of number of feces including seeds to the total number of feces collected ($n = 182$)

[a] Not fleshy fruits

[b] Showing total number of seeds in a feces, because of the lack of data on feces volume

Source: After Otani (2003)

species of *Actinidia* and *Rubus* (1–2 mm in diameter). As for the life form of dispersed species, vines and shrubs dominate the species lists of Tables 6.1 and 6.2, with fewer tree species reported in Table 6.2 (4 species) than in Table 6.1 (13 species). The macaques in the northern Japanese sites used more disturbed and unforested lands than in Yakushima, because both the sites in northern Japan are covered by a mosaic of farmland, logged areas, conifer plantations, and secondary forests dominated by *Quercus serrata*, *Pinus densiflora*, and *Abies firma* in Kashima, and *Fagas crenata*, *Quercus crispula*, and *Thujopsis dolabrata* var. *hondai* in Shimokita; this might be one reason why so few species of trees are served by the macaques as endozoochorous seed dispersers.

Tsuji et al. (in preparation) found that seeds of at least 36 species in 22 families, including 20 fleshy-fruited species, were dispersed by macaque feces in Kinkazan Island, located off the Pacific shore of northern Japan. The forest in this island was relatively less disturbed by human activities. The top 5 major species in frequency of occurrence were *Viburnum dilatum*, *Rosa multiflora*, *Berchemia racemosa*, *Swida macrophylla*, and *Carpinus* sp., and the plant species list included 11 tree species, followed by six shrub and five vine species. These findings suggest that the macaques can act as seed dispersers for arbor species in undisturbed forests of northern Japan as for many species in the lowland of Yakushima.

6.4 Two Modes of Seed Dispersal

In addition to seed dispersal by their feces, Japanese macaques can disseminate seeds of fleshy fruits by spitting them out. They can store fruits in cheek pouches and then spit seeds out while moving or resting at remote sites away from foraged trees (Fig. 6.1). Yumoto et al. (1998) listed 19 species in 12 families, including three species of acorn, the seeds of which were dispersed by Yakushima macaques via cheek pouch. Except for the acorn species, all other species had relatively large-sized seeds ranging from 2.7 to 9.9 mm in diameter. Yumoto et al. (1998) reported that seeds of these fleshy-fruited species were also found in macaque feces but that larger-seeded species were less likely than smaller-seeded species to be found in feces. Although there is no report of seed spitting behavior in the northern areas, Tsuji et al. (in preparation) found relatively large fleshy-fruited seeds such as *Schisandra nigra*, *Cornus kousa*, *Diospyros lotus*, and *Prunus* sp. in fecal samples from Kinkazan. The seed size of these species (4.4–7.8 mm) is comparable to that of species dispersed via cheek pouch in Yakushima Island; therefore, these seeds may also be dispersed by spitting behavior of the macaques in northern Japan.

Seed handling of fleshy-fruited species by Yakushima macaques was classified into three groups, namely, swallowing, crunching, and spitting, and the morphological characteristics of the fleshy fruits were one of the determinants for the seed-handling techniques (Otani and Shibata 2000). Figure 6.2 shows the result of linear discriminant analysis for the relationship between the morphological characteristics of fruit and the seed-handling techniques of Yakushima macaques. It can be seen

Fig. 6.1 A young Yakushima macaques, *Macaca fuscata yakui*, with enlarged cheek pouch storing fruits. This behavior leads to seed dispersal by spitting out

that the swallowing and spitting groups are reflected in linear discriminant function 1 (LDF 1), which correlates positively with seed size, and crunching and other groups, that is, seed predation and seed dispersal, are reflected in LDF 2, which correlates positively with fruit size and flesh volume relative to total fruit volume. For example, *Vaccinium bracteatum* produces flesh-rich fruit with tiny seeds that are swallowed and then dispersed by feces. Other factors, such as seed hardness and plant secondary metabolites in seeds, also influence the foraging behavior and the seed-handling techniques of primates (Kinzey and Norconk 1993). Further research is required to fully understand the relationship between the characteristics of fleshy fruits and the seed-handling techniques of Yakushima macaques.

6.5 Seed Destruction by Japanese Macaques

Seeds of fleshy fruits must be ingested and defecated intact by the macaques for successful seed dispersal. However, seeds of flesh-poor fruits (e.g., *Rhaphiolepis indica* var. *umbellata*; Fig. 6.2) can also be targets of foraging. Cracked and fragmented seeds of *Akebia trifoliata*, *B. racemosa*, and *Prunus* sp. were found in the feces of macaques from northern Japan along with intact seeds (Otani 2003). Thus, Japanese macaques act as seed predators as well as endozoochorous seed dispersers. It is difficult to assess the effect of fruit foraging and seed passage through digestive tracts on survival proportion of ingested seeds under field conditions. A fruit-feeding experiment was conducted with four captive Japanese macaques that were given known number of *E. emarginata* fruits, which is typically a endozoochorous fruit, to estimate the accurate proportion of seeds defecated

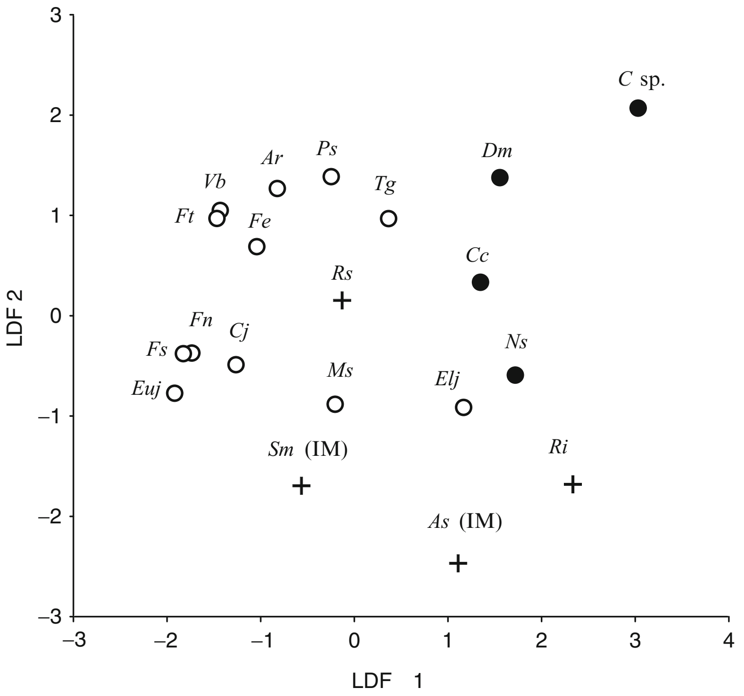

Fig. 6.2 The results of linear discriminant analysis for the relationships between the characteristics of fleshy fruits and the seed-handling techniques of Yakushima macaques. The seed-handling techniques were classified into three categories: swallowing (*open circle*), crunching (*cross*), and spitting (*solid circle*). The abbreviated names of analyzed species are as follows: *Ft*, *Ficus thunbergii*; *Fs*, *Ficus superba* var. *japonica*; *Fn*, *Ficus nipponica*; *Ar*, *Actinidia rufa*; *Euj*, *Eurya japonica*; *Fe*, *Ficus erecta*; *Vb*, *Vaccinium bracteatum*; *Cj*, *Clereya japonica*; *Ps*, *Psychotria serpens*; *Sm* (IM), immature fruits of *Swida macrophylla*; *Tg*, *Ternstroemia gymnanthera*; *Rs*, *Rhus succedanea*; *Ms*, *Myrsine seguinii*; *Dm*, *Diospyros morrisiana*; *C* sp., *Citrus* sp.; *Cc*, *Cinnamomum camphora*; *Elj*, *Elaeocarpus japonicus*; *As* (IM), immature fruits of *Ardisia sieboldii*; *Ns*, *Neolitsea sericea*; and *Ri*, *Rhaphiolepis indica* var. *umbellata.* (Redrawn from Otani and Shibata 2000, with kind permission of Springer)

intact to the total number of seeds ingested. The experiment gave the surprising result that only 4.4% of ingested seeds could pass intact through the macaque gut (Otani 2004). This severe destruction of seeds probably occurred during mastication, because the bite forces of the macaques are overwhelmingly higher (~200 N; Hill et al. 1995) than the pressure resistance of the seeds (9.5 N; Otani 2004), and the macaques do not have mechanical digestive tracts such as the gizzard in birds. The results of another feeding experiment using the fleshy fruits of five species – *Actinidia rufa*, *F. superba* var. *japonica*, *Eurya japonica*, *Eurya emarginata*, and *Vaccinium bracteatum* – showed relatively higher percentages of defecated intact seeds (mean, 23.1%; range, 0–71.2%; Otani, unpublished data) than that of Otani (2004). Seed destruction during foraging behavior by the macaques contrasts significantly with the almost 100% seed passage through frugivorous birds (Yagihashi et al. 1998;

Schabacker and Curio 2000). Seed destruction during foraging behavior can be a major factor in decreasing the effectiveness of seed dispersal by Japanese macaques, and this factor should be examined for other primates and fleshy-fruited plants.

6.6 Distance of Seed Dispersal away from Parent Trees

Direction of animal movement away from a fruiting parent tree and distance between a parent tree and seed deposition site have a direct influence on the spatial distribution of seedlings germinated from dispersed seeds. As for seed dispersal via the cheek pouches of Japanese macaques, we can estimate the distance of seed dispersal by closely observing feeding and ranging behavior, assuming that all the spat-out seeds come from the last fruit foraging site or parent tree. Yumoto et al. (1998) and Tsujino and Yumoto (2009) showed the distribution of seed dispersal distance for four fleshy-fruited species with relatively large-sized seeds. For example, seeds of *Persea thunbergii* were carried an average 19.7 m and the maximum distance was 105 m, although more than 80% of seeds were deposited within 30 m from parent trees (Yumoto et al. 1998). Tsujino and Yumoto (2009) also reported a mean seed dispersal distance of several tens of meters (16.7, 26.1, 32.4, and 41.8 m for *Myrica rubra*, *P. thunbergii*, *Litsea acuminata*, and *Neolitsea sericea*, respectively), and illustrated the highly skewed distribution of seed dispersal distance (Fig. 6.3).

In contrast to seed dispersal by spitting out, direct measurement of the distance of seed dispersal by feces has been a near-impossible task, because we cannot trace seeds once they are swallowed by animals. However, a recent development in molecular biology has made it possible to identify the maternal origin of dispersed seeds in fecal samples. Parent trees of seeds in animal feces can be identified by comparing the genotypes between fruiting trees and dispersed seeds (Godoy and Jordano 2001). Terakawa et al. (2009) analyzed the microsatellite loci of *M. rubra*

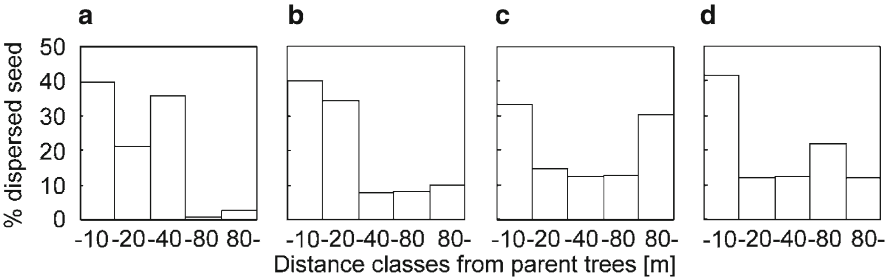

Fig. 6.3 Percentages of seeds dispersed via cheek pouches of Yakushima macaques at different distances for *Myrica rubra* (**a**), *Persea thunbergii* (**b**), *Neolitsea sericea* (**c**), and *Litsea acuminata* (**d**). (Redrawn from Tsujino and Yumoto 2009, with kind permission of Dr. Tsujino and Wiley-Blackwell)

endocarps dispersed by Yakushima macaques and reported that a fecal sample contained, on average, seeds from three different parent trees, and seed dispersal distance ranged from 20.4 to 634.0 m, with an average of 270.0 m (Fig. 6.4). This is the first estimate of distance of seed dispersal via macaque feces and allows us to discuss the limitations on distance of seed dispersal by Yakushima macaques.

The traveling speed of the macaque groups in the western part of Yakushima was assessed at 2.19 m/min (Maruhashi et al. 1998), and the mean seed retention time in digestive tracts was estimated as 39.1 h by using captive Japanese macaques (Otani 2004). Assuming that the day length is 12.28 h (Agetsuma and Nakagawa 1998) and the macaques are active exclusively in daytime; seeds ingested by the macaques could be transported up to 3,227 m, which is overwhelmingly farther than the seed dispersal distance estimated by Terakawa et al. (2009). In addition, Tsuji et al. (2010) reported that the maximum retention time of seeds and plastic markers in the gut of captive Japanese macaques reached 52–114 h, indicating a potential of extremely longer seed transportation by the macaques. Although the macaques do not travel linearly on the ground, the relative short distance of seed dispersal by feces inferred from the ranging behavior of the Yakushima macaque groups and the small home range (0.29–0.9 km^2, Maruhashi et al. 1998; Hanya et al. 2006) limited the expansion of seed deposition sites. Moreover, Japanese macaques shift their foraging site depending on annual and seasonal fluctuations in fruit resources (Agetsuma and Noma 1995; Tsuji and Takatsuki 2008). This observation means that a macaque group tends to use only certain parts of its home range during the foraging period of a major fruit season, implying shorter distances of seed dispersal. In fact, Tsujino and Yumoto (2009) showed that seeds of *M. rubra* and *P. thunbergii*, which grew abundantly on a ridge site, were dispersed primarily

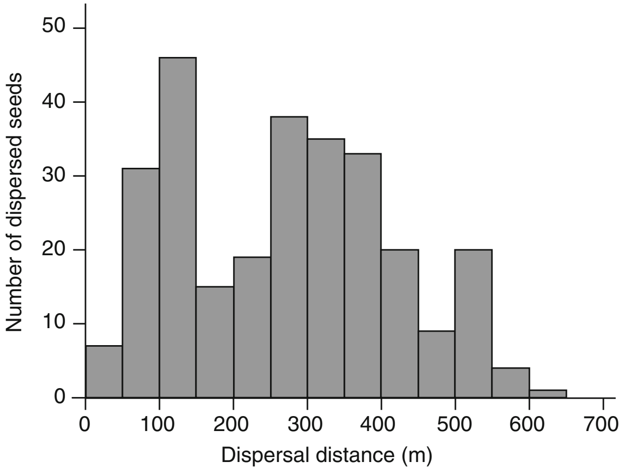

Fig. 6.4 Number of *Myrica rubra* seeds dispersed by Yakushima macaque feces at different distances. (Redrawn from Terakawa et al. 2009 with kind permission of Dr. Terakawa and Springer)

at the ridge site by spitting behavior; in contrast, seeds of valley growing trees such as *L. acuminata* were deposited at the valley site. These results suggest that the aggregated distribution of parent trees in a specific topography leads to a smaller range of seed deposition, and the location of parent trees is itself a limiting factor for seed deposition.

Yumoto et al. (1998) pointed out that approximately half of *P. thunbergii* seeds removed from parent trees were deposited by spitting on sunny places including road surfaces, when Yakushima macaques rested there. Although a road surface is an unsuitable site for plant recruitment, this fact appears to support the directed dispersal hypothesis that an effective seed disperser deposits seeds on favorable sites for seedling establishment. In the deciduous forests of northern Japan, the home range size of a macaque group is considerably wider (2.3–39.7 km^2: Izumiyama et al. 2003; Hanya et al. 2006) than that in the lowlands of Yakushima; thus, seed dispersal distance seems to be longer, yet topography-oriented seed deposition may occur, and a long seed dispersal distance may contribute to enrichment of degraded sites in the northern Japan, because some macaque groups travel over a mosaic of natural and logged forests. If directed dispersal to sunny places or open sites would occur in northern Japan, forest rehabilitation by macaque seed dispersal may enhance degraded sites such as logged forests and abandoned farmlands.

6.7 Effects of Macaque Ingestion on Germination

Compared with seeds not ingested by animals, dispersed seeds often exhibit different germination behaviors, such as an increased number of germinated seeds and a shorter period needed for germination (Traveset 1998). Yumoto et al. (1998) found that seeds of three species, *N. sericea*, *P. thunbergii*, and *M. rubra*, that were dispersed by spitting behavior of Yakushima macaques, showed relatively greater germination percentage than seeds collected from trees and defleshed manually, whereas there was no difference between dispersed and nondispersed seeds for *Syzigium buxifolium*. The effects of spitting on germination are not positive for all tree species; this is also applicable in the case of seed dispersal by feces. Otani and Shibata (2000) reported that positive, negative, and neutral effects were observed for seeds defecated by Yakushima macaques, compared with uningested seeds. Unfortunately, these studies of germination traits contained an oversight in experimental design. To compare germination behavior between dispersed and nondispersed seeds, the same seed source must be used for both groups. For example, during a field observation for foraging behavior of the macaques, we can notice that they may choose well-developed and mature fruits that may contain vigorous seeds. If this is true, when a researcher collects control fruits for a germination test from trees that have been foraged by macaques, seed characteristics such as maturity may differ between dispersed and nondispersed seeds.

There is an example of a carefully designed germination test to examine the effects of seed ingestion by macaques. Otani (2004) examined the effects of seed ingestion on germination by using captive Japanese macaques and *E. emarginata* fruits. He found that seeds passed through the macaque gut did not show better germination comparing with that of uningested seeds (Fig. 6.5a,b), although acid- and hot water-bathed seeds showed higher germination percentages than control seeds. The stimulation by gastric acid and body temperature during the gut passage may increase the germination percentage; however, it is inferred that seed ingestion by the macaques also has some negative effects on germination. Otani (2004) also reported that artificially defleshed seeds exhibited higher germination percentages than seeds in intact fruits (Fig. 6.5c,d), implying that the exocarp and the flesh surrounding seeds act as a mechanical or chemical deterrent to germination. These findings suggest that germination enhancement of *E. emarginata* occurs as a

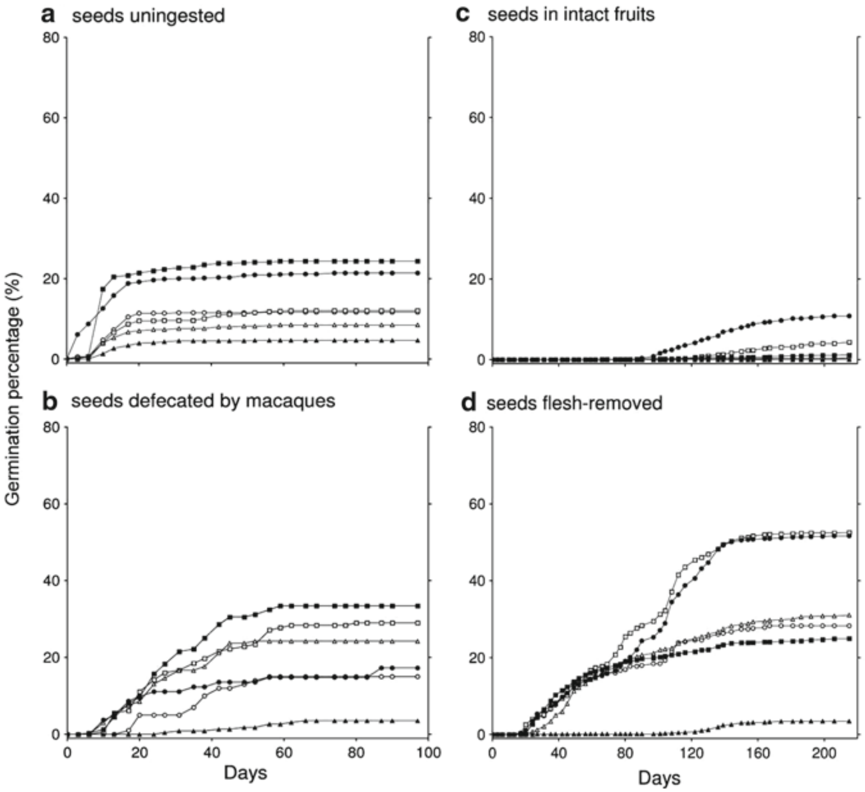

Fig. 6.5 Germination processes of *E. emarginata* seeds collected from six individual trees: uningested seeds (defleshed seeds) (**a**), seeds defecated by captive macaques (**b**), seeds in intact fruits (**c**), and defleshed seeds (**d**). Comparisons should be made for **a** vs. **b**, and **c** vs. **d**, because seeds of **a** and **d** underwent different treatments. Different symbols correspond to each individual tree. (Redrawn from Otani 2004, with kind permission of Springer)

consequence of flesh removal by foraging, not as a result of gut passage. These results were reported for only one tree species, so more work is needed on other fleshy-fruited species to understand any alterations in germination traits induced by the macaques.

6.8 Seed Dispersal and Local Extinction of the Macaque

In evergreen and deciduous forests in Japan, frugivorous birds (e.g., the brown-eared bulbul, *Hypsipetes amaurotis*; the copper pheasant, *Syrmaticus soemmerringii*; the pale thrush, *Turdus pallidus*) and some carnivores (e.g., marten, *Martes melampus*; raccoon dog, *Nyctereutes procyonoides*; Asiatic black bear, *Ursus thibetanus*) also play roles as seed dispersers of fleshy-fruited plants (Otani 2002; Kominami et al. 2003; Koike et al. 2008). Terakawa et al. (2008) pointed out that compared with the common frugivorous bird, the brown-eared bulbul, Yakushima macaques consume approximately 35 times more *M. rubra* fruits in lowland areas of Yakushima (893 fruits/macaque/day vs. 25.1 fruits/bird/day), and the amount of fruit eaten by brown-eared bulbuls did not increase (24.0 fruits/bird/day) even under macaque-free conditions on Tanegashima Island, which is located near Yakushima, where the macaques were extinct in recent times less than 90 years ago. Such a small amount of fruit ingested by bulbuls is probably because of the relatively heavy weight and large size of the *M. rubra* fruits (1.44 g fresh weight, 13.2 mm in diameter; Yumoto et al. 1998). This evidence indicates that bulbuls cannot compensate for the reduction in fruit removal and *M. rubra* seed dispersal in forests without macaques. The Japanese macaque appears to be a reliable seed disperser for arbor trees with large-sized fruits and seeds, although animal contributions to tree recruitment should be compared among more species including birds, macaques, and carnivores.

6.9 Future Directions

We still lack general information related to seed dispersal by the macaques in northern Japan, such as seed spitting, seed destruction in the gut, and germination behavior of dispersed seeds. Further research is required to obtain quantified data on seed survivorship through the processes of seed dispersal to fully understand the macaque's contribution to tree recruitment. Comparison of the survival process of seedlings from dispersed and nondispersed seeds should be conducted in both northern and southern Japan. Molecular biological techniques should be applied for more fleshy-fruited species to measure seed dispersal distance directly in evergreen and deciduous forests, where the home range size of a macaque group is widely different. This work may provide a starting point for a discussion on limiting factors of dispersal distance and the macaque's contribution on rehabilitation of degraded forests.

Acknowledgments I am grateful to Dr. Y Tsuji for kindly showing unpublished data on seed species dispersed by Japanese macaques in Kinkazan Island. I also thank three editors for their helpful comments on the draft.

References

Agetsuma N, Nakagawa N (1998) Effects of habitat differences on feeding behaviors of Japanese monkeys: comparison between Yakushima and Kinkazan. Primates 39:275–289

Agetsuma N, Noma N (1995) Rapid shifting of foraging pattern by Yakushima macaques (*Macaca fuscata yakui*) in response to heavy fruiting of *Myrica rubra*. Int J Primatol 16:247–260

Balcomb SR, Chapman CA (2003) Bridging the gap: influence of seed deposition on seedling recruitment in a primate-tree interaction. Ecol Monogr 73:625–642

Godoy JA, Jordano P (2001) Seed dispersal by animals: exact identification of source trees with endocarp DNA microsatellites. Mol Ecol 10:2275–2283

Hanya G, Noma N, Agetsuma N (2003) Altitudinal and seasonal variations in the diet of Japanese macaques in Yakushima. Primates 44:51–59

Hanya G, Kiyono M, Yamada A, Suzuki K, Furukawa M, Yoshida Y, Chijiiwa A (2006) Not only annual food abundance but also fallback food quality determines the Japanese macaque density: evidence from seasonal variations in home range size. Primates 47:275–278

Herrera CM (2002) Seed dispersal by vertebrates. In: Herrera CM, Pellmyr O (eds) Plant–animal interactions: an evolutionary approach. Blackwell, Oxford, pp 185–208

Hill DA, Lucas PW, Cheng PY (1995) Bite forces used by Japanese macaques (*Macaca fuscata yakui*) on Yakushima Island, Japan to open aphid-induced galls on *Distylium racemosum* (Hamamelidaceae). J Zool 237:57–63

Izumiyama S, Mochizuki T, Shiraishi T (2003) Troop size, home range area and seasonal range use of the Japanese macaque in the Northern Japan Alps. Ecol Res 18:465–474

Kinzey WG, Norconk MA (1993) Physical and chemical properties of fruit and seeds eaten by *Pithecia* and *Chiropotes* in Surinam and Venezuela. Int J Primatol 14:207–227

Koike S, Morimoto H, Goto Y, Kizakai C, Yamazaki K (2008) Frugivory of carnivores and seed dispersal of fleshy fruits in cool-temperate deciduous forests. J For Res 13:215–222

Kominami Y, Sato T, Takeshita K, Manabe T, Endo A, Noma N (2003) Classification of bird-dispersed plants by fruiting phenology, fruit size, and growth form in a primary lucidophyllous forest: an analysis, with implications for the conservation of fruit–bird interactions. Ornithol Sci 2:3–23

Maruhashi T, Saito T, Agetsuma N (1998) Home range structure and inter-group competition for land of Japanese macaques in evergreen and deciduous forests. Primates 39:291–301

Miyawaki A (1980) Vegetation of Japan, Yakushima. Shibundo, Tokyo (in Japanese)

Miyawaki A (1987) Vegetation of Japan, Tohoku. Shibundo, Tokyo (in Japanese)

Mouissie AM, Lengkeek W, van Diggelen R (2005) Estimating adhesive seed-dispersal distances: field experiments and correlated random walks. Funct Ecol 19:478–486

Otani T (2002) Seed dispersal by Japanese marten *Martes melampus* in the subalpine shrubland of northern Japan. Ecol Res 17:29–38

Otani T (2003) Seed dispersal and predation of fleshy-fruited plants by Japanese macaques in the cool temperate zone of northern Japan. Mammal Study 28:153–156

Otani T (2004) Effects of macaque ingestion on seed destruction and germination of a fleshy-fruited tree, *Eurya emarginata*. Ecol Res 19:495–501

Otani T (2005) Characteristics of middle-size mammals as a seed disperser of fleshy-plants. Nagoya Univ For Sci Res 24:7–43 (in Japanese with English summary)

Otani T, Shibata E (2000) Seed dispersal and predation by Yakushima macaques, *Macaca fuscata yakui*, in a warm temperate forest of Yakushima Island, southern Japan. Ecol Res 15:133–144

Russo SE, Portnoy S, Augspurger CK (2006) Incorporating animal behavior into seed dispersal models: implications for seed shadows. Ecol 87:3160–3174

Schabacker J, Curio E (2000) Fruit characteristics as determinants of gut passage in bulbul (*Hypsipetes philippinus*). Ecotropica 6:157–168

Schupp E (1993) Quantity, quality and effectiveness of seed dispersal by animals. Vegetatio 107(108):15–29

Terakawa M, Matsui K, Hamada T, Noma N, Yumoto T (2008) Reduced seed dispersal effectiveness in the large-seeded tree *Myrica rubra* in the absence of the Japanese macaque on Tanegashima Island, Japan. Jpn J Conserv Ecol 13:161–167 (in Japanese with English summary)

Terakawa M, Isagi Y, Matsui K, Yumoto T (2009) Microsatellite analysis of the maternal origin of *Myrica rubra* seeds in the feces of Japanese macaques. Ecol Res 24:663–670

Traveset A (1998) Effect of seed passage through vertebrate frugivores' guts on germination: a review. Perspect Plant Ecol Evol Syst 1(2):151–190

Tsuji Y, Takatsuki S (2008) Effects of yearly change in nut fruiting on autumn home-range use by *Macaca fuscata* on Kinkazan Island, northern Japan. Int J Primatol 30:169–181

Tsuji Y, Morimoto M, Matsubayashi K (2010) Effects of the physical characteristics of seeds on gastrointestinal passage time in captive Japanese macaques. J Zool 280:171–176

Tsujino R, Yumoto T (2009) Topography-specific seed dispersal by Japanese macaques in a lowland forest on Yakushima Island, Japan. J Anim Ecol 78:119–125

Willson MF, Irvine AK, Walsh NG (1989) Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. Biotropica 21:133–147

Yagihashi T, Hayashida M, Miyamoto T (1998) Effects of bird ingestion on seed germination of *Sorbus commixta*. Oecologia (Berl) 114:209–212

Yumoto T, Noma N, Maruhashi T (1998) Cheek-pouch dispersal of seeds by Japanese monkeys (*Macaca fuscata yakui*) on Yakushima island, Japan. Primates 39:325–338