Ecosystem impacts of folivory and frugivory by Japanese macaques in two temperate forests in Yakushima

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Abstract

Comparing animal consumption to plant primary production provides a means of assessing an animal's impact on the ecosystem and an evaluation of resource limitation. Here we compared annual fruit and leaf consumption by Japanese macaques (*Macaca fuscata*) relative to the annual production of these foods in the lowlands and highlands of Yakushima Island, Japan. We estimated consumption by macaques by the direct observation of macaques groups for one year in each habitat. We estimated leaf production as the sum of leaf litter fall (corrected for the effect of translocated organic and inorganic matter) and folivory by insects (assumed to be 10%) and by macaques. We estimated fruit production as the sum of fruit litter fall and consumption by birds (estimated by the seed fall) and macaques. The impact of macaque folivory at the community level was negligible relative to production (~0.04%) compared with folivory by insects (assumed to be 10%); however, for some species, macaque folivory reached up to 10.1% of production. Tree species on which macaques fed did not decline in abundance over 13 years, suggesting that their folivory did not influence tree species dynamics. For the three major fleshy fruited species in the highland site, macaques consumed a considerable portion of total fruit production (6-40%), rivaling the consumption by birds (32-75%). We conclude that at the community level, macaque folivory was negligible compared to the leaf production, but frugivory was not.

Keywords: primary production, primate, productivity, resource limitation, temperate forest

INTRODUCTION

Animals depend on plant production to sustain their populations, and animals can affect plants through pollination [Yumoto 1987], seed dispersal [Howe 1986] and predation on seeds, flowers and leaves [Adams et al. 2009; Sun et al. 2007]. The effects of plants on animals are usually understandable and well-studied [Chapman et al. 2010; Hanya et al. 2011], but the impact of animal consumption on plant primary production is scarcely quantified. Comparing animal consumption to plant production provides both a useful mean of assessing the ecosystem impact of animals and a way of evaluating if their populations are resource limited. There is substantial correlative evidence that animal populations are limited by plant productivity [Hanya et al. 2004; Hanya & Chapman 2013; Stevenson 2001] and direct tests of food limitation involving food removal or provisioning have also been conducted [Adler 1998; Moegenburg & Levey 2003]. However, an experimental approach is not feasible for animals ranging over a wide area or having a diverse diet, such as most primates [Hanya & Chapman 2013]. For some primates there is considerable controversy concerning whether they are limited by food resources or if such resources are superabundant. For example, Coelho et al. [1976] estimated that fruit production far exceeded the food intake for two primates and concluded the populations were not food limited. This study was criticized because it included only 2 months of data, and did not address nutritional requirements [Cant 1980]. Similarly, many researchers often assume that tree leaves are as superabundant for folivores, but there is increasing evidence that folivores compete over access to the best leaves and thus that these food item can be limiting [Koenig 2002; Snaith & Chapman 2007].

Large animals are often the most endangered species in an ecosystem [Corlett 2009; Primack 1995], thus, it is important to understand the ecosystem services they provide and to predict the impact of their disappearance. For example, extinction of large primates alters tree species composition as large-seeded plants, which depend on primate dispersers, are not dispersed [Chapman & Onderdonk 1998; Nuñez-Iturri & Howe 2007]. Some ecosystem services will be taken on by other animals with overlapping feeding niches [Peres & Dolman 2000], but it is difficult to predict which services will remain as the functional redundancy is affected by various factors [Rosenfeld 2002]. Therefore, it is necessary to assess the relative impact of various animals on forest productivity.

We aimed to compare the fruit and leaf biomass consumed by Japanese macaques (*Macaca fuscata*), folivorous insects and frugivorous birds, with the leaf and fruit production over 1 year on Yakushima, Japan. Our study sites included a warm- and a cool-temperate forest, which differ with respect to fruit production, macaque density, and diet [Hanya et al. 2003a; Hanya 2004; Hanya et al. 2004]. We also assessed the effect of macaques' folivory on forest tree species composition over 13 years.

METHODS

The research complied with protocols approved by the Primate Research Institute, Kyoto University and it adhered to the legal requirements of Japan and to the American Society of Primatologists Principles for the Ethical Treatment of Non Human Primates.

Study sites and subjects

We studied in highland (coniferous cool- temperate, 1000-1200 m a.s.l.) and lowland (evergreen broad-leaved warm-temperate, 0-200 m a.s.l.) forests separated by 7 km on the island of Yakushima (30°N, 131°E), Japan. We observed the feeding behavior of the HR group in the highland site and the NA and H groups in the lowland site. The annual home ranges of the HR, NA, and H groups were 2.7, 0.6, and 0.7 km^2, respectively. The home range of the HR group was a mosaic of primary and logged forest, but primary forest, where forest productivity was studied, comprised 83% of the total area. The home ranges of NA and H groups overlapped extensively and consisted of old secondary forest. Hanya [2004] and Hanya et al. [2007] provide further information about the study sites and subjects.

In these forests, biomass of sika deer (*Cervus nippon*) equals that of macaques [Agetsuma et al. 2003] and they influence forest dynamics [Koda et al. 2008]. However, we did not compare their impact because deer eat leaves from the ground, where the productivity cannot be estimated by litter trap. In addition, they eat a considerable amount of dead leaves [Agetsuma et al. 2011] they are thus often acting as decomposers. There are no other folivorous or frugivorous large mammals in the island. Marten (*Mustela itatsi*) and field mice (*Apodemus speciosus* and *A. argenteus*) may also eat fruits, but they were also not considered as they are terrestrial. Their biomass seems negligible compared with that of macaques because they are very small (~2 kg for martens and 20-60 g for mice) and very rare, considering the much lower photographic rate (1/10 of macaques) in camera trapping (Hanya et al., unpublished data).

Behavioral observations

We collected data between April 2000 and March 2001 for HR group in the highland site (510 hr) and between October 2003 and August 2004 for NA group in the lowland site (1080 hr). To supplement the September data lacking for the NA group, we also used the data of H group in September 1998. We collected behavioral data using focal animal sampling (duration of 1 hr) of seven adult females and six males for the highland group (mean±SD of observation time: 39±12 hr/individual), and five adult females for the NA group (216±75 hr/individual) and for five adult males in the H group (18±0.86 hr/individual). Data on the diet are available elsewhere [Hanya 2003; Hanya 2004; Hanya et al. 2007] (Appendix 1). We defined a feeding bout as starting when the animal put food into the mouth and stopping when 20 seconds had elapsed without the subject moving in the tree or manipulating food or when the animal left the tree or started eating other items. We recorded the number of food units that the animal ingested for as long as possible. One food unit was operationally defined depending on the particular item and plant species (e.g. one leaf, one fruit, one cluster of fruits).

Estimating food consumption

We estimated the dry weight intake of all stages of leaves (both mature and young leaves) and fruits (including seeds). We considered consumption as the removed biomass and included the weight of indigestible parts that were discarded before ingestion. For feeding bouts where the number of food units ingested could not be recorded, we estimated ingestion by multiplying the duration of the feeding bouts and the average feeding rate (#units/second) of all feeding bouts for that item of the species. To calculate this average, we discarded data when the duration of a feeding bout was less than 2 min unless this was the only datum available for the food species/item. This was because data of short duration were less reliable. Then, we multiplied the number of food units ingested (estimated or actually counted) during each feeding bout by its unit dry weight and summed the results for all feeding bouts of each focal observation. We multiplied the estimated dry weight intake per observation hour with the average day length of the month and the number of days in the month, to obtain the total estimated dry weight intake in the month. This could be justified as the distribution of observations was not biased to a particular time of the day or month: we made from dawn to dusk [Hanya 2004; Hanya et al. 2007] and equally distributed observation days in each month. We calculated total annual intake by summing the values of the 12 months. We summarized data of the unit weight and feeding rate in Appendix 2.

We estimated intake for age-sex classes that we did not observe assuming that macaque consumption was proportional to the 0.75 power of average body mass for the age/sex [Kleiber 1987] using body weight data from Watanabe [1975] (Appendix 3). For the highland site, data on adult males and females were available, so we estimated the average intake using the pooled data. For the lowland site, only the female data were available, so we estimated the male intake following the power rule. We used age-sex composition of the HR and NA groups to estimate the proportion of individuals of each age-sex class in the population. We used the data of these two particular groups, rather than the data on age-sex composition collected over a larger scale. This was because we needed to use data that were comparable with the behavioral and litter trap data, which were taken within the home range of these two particular groups. We calculated food consumption of each age-sex class at the population level by multiplying (1) the estimated food consumption of the class, (2) proportion of the class in the population and (3) the population density. We derived density from Yoshihiro et al. [1999] and Hanya et al. [2003b] (Appendix 3). We calculated food consumption at the population-level as the sum of all the age-sex classes. In the highland site, we also recorded the amount of leaves that macaques dropped during feeding. We estimated total amount of dropped leaves in that month by an adult individual by multiplying the amount of leaves (g) per observation time, average day length of the month and the number of days in the month. We estimated amount dropped at the population level over the year in the same way as we did for leaf intake.

Litter trap

We established two vegetation plots within the home ranges of the groups and identified and measured all tree stems with a diameter at breast height (DBH) > 5 cm. Plot size was 50m * 50m in the highland site (0.09% of the home range of the HR group) and 100m * 50m in the lowland site (0.8% of the home range of the NA group). Aiba et al. [2007] and Hanya and Aiba [2010a] described details of the plots. These plots included both ridge and valley and phenological change recorded in these plots predicted the seasonal variation in the macaque diet [Hanya 2004; Hanya et al. 2007]. Therefore these plots seemed to be representative of the home range. We placed 25 and 20 litter traps (nylon mesh of <0.5 mm, 0.58 m^2 in size and 1-1.5 m above the ground) evenly distributed in highland and lowland site plots respectively. The minimum inter-trap distance was 10 m. We collected litter once a month, oven-dried it at 60 ºC for 96 hr and weighed and sorted items into broad-leaf, conifer needle, fruits, and others. Fruits included the whole or partial ripe fruits, unripe fruits and seeds separated from pulp. We sorted them by species and weighed them. We separated bird feces from 'others' in the highland plot.

Estimation of fruit and leaf production

We conducted the species-level analysis of leaf and fruit consumption for species that accounted for at least 1% of the annual feeding time in each area and when the fruit or leaf production of these species could be estimated by fruit fall or tree species composition in the plots. In addition to these species, we also examined fruit consumption of three fleshy-fruited species in the highland site (*Eurya japonica*, *Cleyera japonica*, and *Symplocos myrtaceae*), because we could also estimate bird consumption for these species.

Leaf production: We converted litter fall to kg/ha/year by dividing the total annual weight of litter by total litter trap area. We could estimate the weight of leaf litter for particular species from the data of relative basal area of the species because the relative basal area and leaf litter of each tree species was positively correlated ($r=0.81$, $p<0.0001$, $N=37$ species, data from the lowland plot for one year from December 2004). Therefore, when we estimated leaf fall for each species, we assumed that the leaf litter weight of a species was proportional to the species basal area relative to the total basal area in the plot.

In principle, annual leaf production is equal to annual leaf litter fall when the leaf biomass of the forest reaches equilibrium [Clark et al. 2001]. However, these two values are not necessarily the same because of (1) translocation of organic and inorganic matter from the abscised leaves and (2) herbivory. Mean leaf mass loss for temperate evergreen angiosperm leaves is 20.8% [Vergutz et al. 2012], so we divided the gross leaf litter fall by (1-0.208) to estimate the biomass of leaves before falling to the trap. Hereafter, we refer this value as 'corrected leaf fall'. We assumed the amount of insect herbivory as 10% of the leaf production, which is a mean value for temperate forests [Landsberg & Ohmart 1989] (3-17%). We calculated the leaf production as the sum of corrected leaf fall and consumption by macaques and insects, which are the only animals that eat leaves in the canopy layer on Yakushima.

Fruit production: We calculated the production of fruit for the highland site as the sum of fruit fall and consumption by macaques and birds. However, in the lowland site, data on bird consumption were lacking so macaque frugivory was compared only with the fruit fall. The current estimation in the highland was based on the data used also in Hanya [2005], who calculated only the total number of seeds removed by birds. However, in the current analysis, we present data for each species of plant. We confined the estimation of bird consumption to the three species (*E. japonica*, *C. japonica*, and *S. myrtaceae*) that constituted 92.5% of the fleshy fruit production in the highland site. These species have small seeds (<5 mm long) which were swallowed by macaques [Otani & Shibata 2000]. Thus, in the estimation, we could regard the pulpless seeds of these species dropped into the trap as having dispersed by birds [Kominami et al. 2003], along with the seeds found in bird feces. We did not find any macaque feces in the traps in the highland site. We confirmed that macaque feces were recognizable for at least one month after defecation by experimentally putting feces in a trap. We estimated the weight of fruits removed by birds using the data of (1) the number of seeds trapped, (2) the average number of seeds in one fruit for each species and (3) average weight of one fruit, of which data we collected by measuring >100 fruits for each species.

Long-term changes of forest composition

To assess the impact of macaque folivory on forest tree species dynamics, we established a 2.4 ha vegetation plot (4% of the home range of the NA group) in 1990 in the lowland site. The plot consisted of 10 line transects (5 m wide, 30-150 m long) set every 100 m within the entire home range of the NA and the H groups. We recorded the species and the DBH of all trees >5 cm DBH in 1990 and 2003. In the highland site, for the analysis of forest composition dynamics, we used the plot of 0.25 ha that we set to collect litter. We established this plot in 1999 and resampled in 2012. We examined changes in density between the two periods using a G-test for species with more than 9 stems in one of the years. We tested a null hypothesis which assumed no difference in the proportion of decreasing species between food and non-food species. We examined 47 lowland (5 food and 42 non-food species) and 10 highland species (3 food and 7 non-food species).

RESULTS

Folivory

In both the lowland and highland sites, the impact of macaque folivory at the community level was negligible relative to leaf production or assumed folivory by insects. The leaf biomass consumed by macaques was only 0.037% and 0.39% of the estimated total leaf production in the lowland and highland sites, respectively (Table 1). These values increased if we considered only food species, but it still remained low (0.21% in the lowland site and 0.90% in the highland site). At the species level, however, macaque leaf consumption reached 5.7% of the estimated leaf production in the lowland site (*Daphniphyllum teijsmannii*) and 10.1% in the highland site (*Symplocos prunifolia*). For other species, macaques consumed between 0.93% and 2.14% of the leaves produced. In the highland site, we estimated the biomass of dropped leaves as 3.93 kg/km^2/year, which was 0.21% of the consumed leaves.

There was no evidence that macaque food trees died at a greater rate than non-food trees over the 13 years of monitoring (Table 2). In the lowland site, the proportion of decreasing species was not different between the food and non-food species (G=0.50; p=0.48). None of the species decreased in abundance at the highland site.

Frugivory

In contrast to leaves, macaques consumed a considerable portion of the total fruit production. For the three fleshy-fruited species in the highland site, for which we quantified both bird and macaque consumption, macaque consumption was 3.2-39% of the total fruit production depending on plant species, whereas birds consumed between 32 and 75% of the fruit production (Table 3b). Macaques and birds together consumed more than two-thirds of the fruit production for all the species. In the lowland site, fruit consumption by macaques constituted 8.8%, 10.1%, and 68.8% of fruit fall for all species, food species, and the most frequently eaten species, respectively (Table 3a). Although there were 12 fruiting species that constituted more than 1% of the annual feeding time (sum of the duration of the feeding bouts) for the lowland site macaques, fruits of only one of them appeared in the litter trap.

DISCUSSION

Impact of folivory and its effect on long-term forest dynamics

Our data suggested that at the community level the amount of leaves consumed by Japanese macaques in Yakushima was negligible compared with the leaf production. Total leaf consumption by macaques constituted less than 0.4% of the total leaf production. However, for some species, the impact of macaque folivory reached 10% in the highland site, which was comparable to the community-level impact of insect folivory known for various types of forests (3-17%) [Landsberg & Ohmart 1989]. Because some tree species can survive even if they lose all their leaves by browsing [Rooke & Bergstrom 2007], we need further study to confirm the effect of folivory on plant longevity, growth, and/or reproduction.

Species whose leaves were eaten by macaques did not decrease in abundance over 13 years. However, it is still possible that some species are negatively affected by overgrazing by macaques. For example, *Daphniphyllum teijsmannii*, which was the most extensively eaten species in the lowland site, decreased in number from 182 to 133 (G= 7.65, p=0.0057). However, this species is not shade-tolerant [Aiba et al. 2001] thus the decrease was likely caused by the lack of forest disturbance.

In contrast to our results, Chapman et al. [2013] reported that in Kibale National Park, Uganda, there was a tendency for tree species that were eaten by two species of colobus monkeys to decrease in abundance but no such tendency was found for the species that colobus did not eat. The difference between Yakushima and Kibale is likely due to difference in primate biomass. Primate biomass in Kibale (2759 kg/km^2) [Chapman et al. 1999] is 6.77 and 24.2 times larger than that in the lowland and highland sites of Yakushima respectively and folivorous colobines make up the greatest portion (75%) of that biomass [Chapman et al. 1999]. Total litter fall (including leaves, branch, and reproductive parts) in Yakushima was 565,000 kg/km^2/year in the lowland site and 473,000 kg/ km^2/year in the highland site. This represented 71% and 59% of the average documented for 12 tropical forests (average = 966,200 kg/ km^2/year, maximum: 1,235,000 kg/ km^2/year) [Hanya & Aiba 2010b]. Therefore, if we suppose that leaf production in Kibale is average for a tropical forest, leaf production in Kibale is calculated only as 1.41 times larger than that in the lowland site and 1.69 times of that in the highland site of Yakushima. Supposing further that the amount of leaf consumption is proportional to primate biomass; leaf consumption/production ratio in Kibale is 4.80 (6.77/1.41) times larger than in lowland site and 17.1 (24.2/1.41) times larger than in the highland site of Yakushima. Given that 75% of the primate biomass in Kibale is folivorous colobines, this is likely to be a conservative estimate. That is, if Japanese macaques in Yakushima consume ca. 10% of produced leaves for some species, more folivorous Kibale primates would impose more serious damage to many species. In addition, latitudinal variations in leaf turn-over cycle [Reich et al. 1996] may affect the different impact of folivory in Yakushima (temperate) and Kibale (tropical). More detailed data on leaf production and consumption by Kibale primates are needed to confirm our estimates. In any case, however, comparisons of Yakushima and Kibale suggest that the threshold value of primate biomass above which primate folivory has a critical impact on the forest lies somewhere between Yakushima and Kibale.

Impact of frugivory

Of the three fleshy-fruited species evaluated at the highland site, Japanese macaques were the most important fruit consumer for one (*E. japonica*), consuming approximately 40% of production. As for the two other species, bird consumption was 11-23 times larger than that of macaques. These two groups of frugivores consumed up to two thirds of the fruit production. Although one third of the fruits were not eaten, we think that fruits may nevertheless be a limited resource. According to our data on the seasonality of fruit fall, a majority (91%) of the uneaten fruits of these species dropped before the macaques and birds stop feeding on them (by November) and it appeared that finding fruits was difficult. When frugivores stopped feeding on these fruits, there were only very few fruits remaining. In addition, considering the degree of inter-annual variability in diet, frugivores could have depleted the uneaten fruit biomass. Hanya [2005] showed that the fruit consumption by macaques and birds in 1999 reached 1.66 times higher than in 2000. Tsuji et al. [2006] reported even higher inter-annual variation in the amount of fruits consumed by wild Japanese macaques in Kinkazan, northern Japan.

The impact of macaque frugivory at the community level remains to be further investigated, but we can expect that it would be larger than the case of folivory, but smaller than the case of intensively-fed *E. japonica* fruits. This is because macaques consumed only 10% of the fruit fall for all the food species. In addition, most (65%) of the fruit fall for the species eaten by macaques comprised two gravity-dispersed species (*Distylium racemosum* and *Camellia japonica*) [Hanya & Aiba 2010a], which were unlikely to be eaten by birds (Hanya, per. obs). Macaques might be seed predators for these species.

We cannot fully assess the impact of the frugivory by Japanese macaques in the lowland site because there are no data on bird consumption there. For several reasons, however, it is likely that the tendency would be the same in the lowland site as in the highland sites. First, most (58%) of the fruit fall of food species for macaques in the lowland site was acorns [Hanya & Aiba 2010a], which most birds in Yakushima do not consume. Second, at the species level, macaques are likely important fruit consumers for some species. For example, fruits of *Litsea acuminata* consumed by macaques reached 68% of the fruit fall, which is a similar level to that of *E. japonica* in the highland site. Fruits of *L. acuminata* are among the largest in Yakushima and only a few bird species can swallow the seeds [Noma & Yumoto 1997]. In addition, it has already been clarified that fruit consumption by macaques in the lowland site Yakushima is much larger (>32 times) than that by birds for two fleshy-fruited species (*Ficus superba* and *Myrica rubra*) [Otani 2001; Terakawa et al. 2008]. Third, 11 out of 12 major food fruit species for Japanese macaques were ‘rare’ species whose fruit abundance cannot be accurately estimated by litter traps. Since they are rare, the fruit production of these species is likely to be lower than the common species, such as *L. acuminata*. Therefore, the ratio of macaque frugivory to fruit production would be higher for these species than *L. acuminata*.

It is already known that the Japanese macaques in Yakushima provide effective seed dispersal services with respect to the quality, such as dispersal distance and topography [Noma & Yumoto 1997; Otani & Shibata 2000; Terakawa et al. 2009; Tsujino & Yumoto 2009; Yumoto et al. 1998]. Seed dispersal effectiveness could be evaluated as the product of quantity and quality of seed dispersal [Schupp et al. 2010]. Our results suggest the quantitative importance of seed dispersal by macaques and thus suggest they play an important role in forest regeneration through seed dispersal.

Robustness of the results

Our results remain preliminary as they are based on several assumptions. Here we discuss the possible biases in the estimations and the robustness of our findings. We hope our preliminary analysis will stimulate future research in this rarely studied but important area of primate ecology.

First, although our dietary data were based on detailed observation of feeding behavior, food intake at the population level was estimated based on many assumptions. Error may have occurred when we (1) estimated food intake of one age-sex class from the data of different classes, (2) estimated age-sex composition of the population, and (3) calculated population-level intake from the population density. As for the first assumption, Hanya [2003] has confirmed that variation in the mass of food ingested by wild Japanese macaques of different age classes are roughly consistent with our assumption. We believe the second assumption did not cause serious error, as we used the age-sex composition of the subject groups, which was the most likely composition of the macaques using the area within the home ranges of the subject groups. As for the third assumption, the density data seemed correct because they agreed with the the long-term record of the distribution of identified groups [Yoshihiro et al. 1999; Hanya et al. 2003]. Error could have occurred if there was heterogeneity in density within the study site and the home range of the study group was situated where density was particularly high or low, although it seemed unlikely that this was the case given the distribution of groups in the study area.

Second, data on productivity were derived from plots of only 0.25 ha or 0.5 ha. This area was much smaller than the home ranges of the study groups, and may not reflect productivity across the entire home range area. We note, however, that productivity measured in plots within the same altitudinal zones of Yakushima differed at most by a factor of two [Aiba et al. 2007]. This difference is much smaller than the difference in leaf productivity and macaque consumption. Therefore, the qualitative conclusion of our analysis – that macaque folivory is negligible – is not likely to be affected by plot size. However, the conclusion at the population level needs further examination, as certain plant species may show a non-random in the monkeys' home range. Focal tree observation might be a better approach to assess consumption and productivity for rare species.

Third, the small plot size in the highland site constrained the analysis of tree species dynamics. Therefore, our evaluation of forest dynamics in the highland site is preliminary. However, given that none of the species decreased in abundance, it is unlikely that larger plot sizes would produce contrary findings. We cannot discard the possibility that macaques can have significant negative impact on rare species which did not appear in the vegetation plot. Various plots are established in different altitudinal zones of Yakushima [Aiba et al. 2007], so meta-analysis of tree species dynamics with respect to macaque folivory will be feasible in the future. The plot size in the lowland site was rather large (2.4 ha) and cover the entire home range, so the results from here seemed reliable.

Finally, there were no data from the NA group for one month, so we filled in missing values with data from another year and another group. Considering the large seasonal variation in the diet in Yakushima [Hanya 2004; Hill], we believe this is a better solution than calculating the intake in this month as an average of the other 11 months. Because the home ranges of the two groups overlapped extensively, we assumed that dietary differences were minimal. Main foods in this month were fruits of figs and *Rhus succedanea*, both of which exhibit small supra-annual variations in fruiting intensity. Therefore, large supra-annual variations in the diet in this month also seem unlikely. In addition, the actual over- or underestimation related to using the data of other year/group should be small because it constitutes only one of the twelve months.

In conclusion, macaque folivory was negligible compared to leaf production at the community level because macaque consumption constituted only ~0.04% of the leaf production and macaque food species did not decrease over 13 years. However, the impact of macaque frugivory has more important consequences for the plants consumed.

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Legend to the figure

Fig. 1. Map of Yakushima showing lowland and highland study sites. Contours are drawn every 300 m.

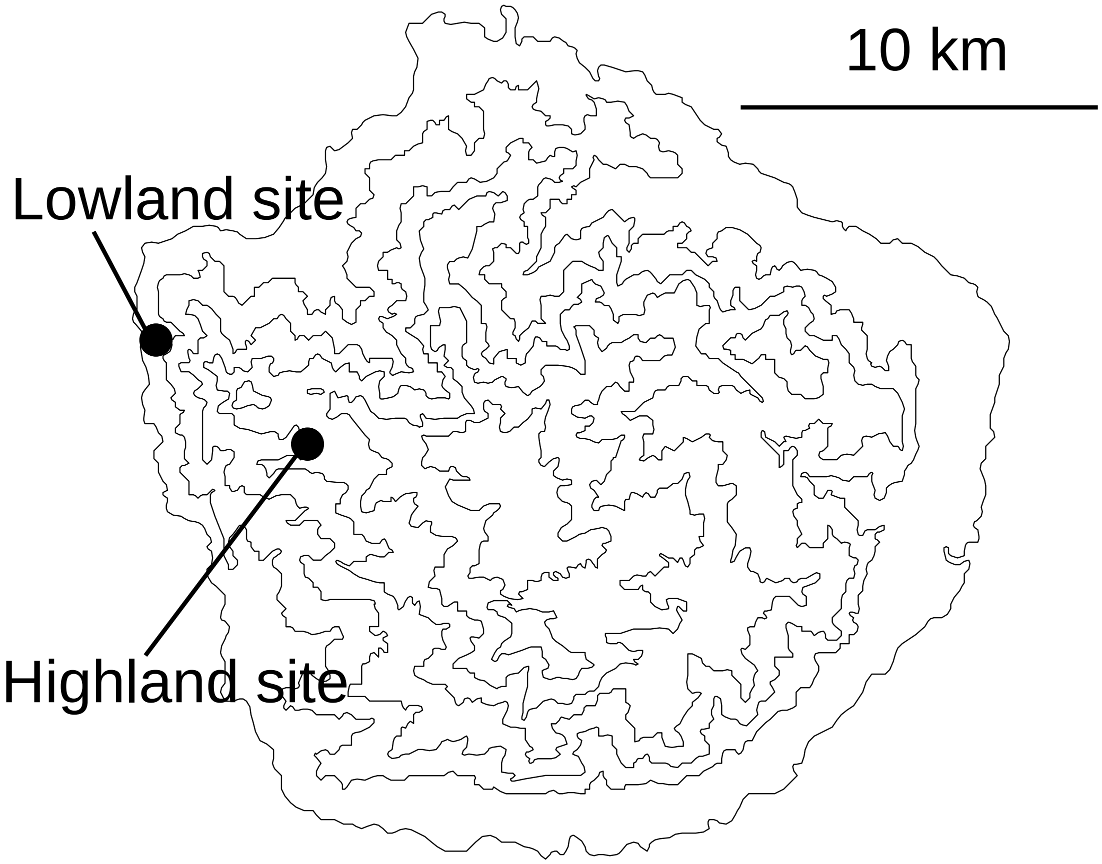

Fig. 1

Table 1. Comparison of leaf consumption by macaques and estimated leaf production

a. Lowland forest of Yakushima

Target	Leaf fall	Corrected leaf fall*	Corrected leaf fall+estimated consumption by insects**	Leaf consumption by macaques
	kg/km^2/year	kg/km^2/year	kg/km^2/year	kg/km^2/year (% to leaf production)
All species	431000	544000	605000	226 (0.037%)
Food species	76100	96100	107000	226 (0.21%)
Symplocos lucida	1480	1870	2120	35 (1.7%)
Daphniphyllum teijsmannii	410	518	614	35 (5.7%)

b. Highland forest of Yakushima

Target	Leaf fall	Corrected leaf fall*	Corrected leaf fall+estimated consumption by insects**	Leaf consumption by macaques
	kg/km^2/year	kg/km^2/year	kg/km^2/year	kg/km^2/year (% to leaf production)
All species	352000	444000	495000	1910 (0.39%)
Food species	150000	189000	212000	1910 (0.90%)
Symplocos myrtacea	12100	15300	17200	160 (0.93%)
Eurya japonica	4230	5340	6080	130 (2.1%)
Trochodendron aralioides	36600	46200	51400	78.2 (1.5%)
Symplocos prunifolia	81.3	103	129	13 (10%)

* Corrected leaf fall was calculated by dividing the gross leaf fall by 0.792, which indicated estimated leaf weight before the translocation of organic and inorganic matter from the abscised leaves.

** Insect folivory was assumed to be 10% of the leaf production.

Table 2. Number of species decreasing/not decreasing over 13 years

a. Lowland forest of Yakushima (between 1990 and 2003)

	Decrease	Not decrease
Food species	2	3
Non-food species	10	32

a. Highland forest of Yakushima (between 1999 and 2012)

	Decrease	Not decrease
Food species	0	3
Non-food species	0	7

Table 3. Comparison of fruit/seed consumption by Japanese macaques and birds to amount of fruit litter

a. Lowland forest of Yakushima

Target	Fruit fall	Fruit consumption by Japanese macaques
	kg/km^2/year	kg/km^2/year
All species	59900	5230
Food species	52200	5230
Litsea acuminata	887	603

b. Highland forest of Yakushima

Target	Fruit fall	Fruit consumption kg/km^2/year (% to fruit production)	
	kg/km^2/year	by Japanese macaques	by birds
All species	10700	381	-
Food species	3810	381	-
Distylium racemosum	1980	176	-
Eurya japonica	24.2	33.4	27.6
	(28.4%)	(39.2%)	(32.3%)
Cleyera japonica	27.1	4.01	92.6
	(21.9%)	(3.24%)	(74.9%)
Symplocos myrtacea	8.95	2.11	25.0
	(24.8%)	(5.85%)	(69.3%)

Appendix 1. Diet composition of the three study groups

	HR		NA		H (September only)	
	% feeding time	intake g dry weight/h	% feeding time	intake g dry weight/h	% feeding time	intake g dry weight/h
Fruit	13%	3.74	34%	11.35	39%	7.03
Seed	4%	1.89	32%	8.40	52%	3.95
Mature leaf	38%	12.76	5%	0.67	2%	0.09
Young leaf	3%	0.24	2%	0.19	0%	0.01
Flower	15%	Not estimated	2%	Not estimated	0%	Not estimated
Pith, stem, bark and roc	4%	Not estimated	2%	Not estimated	2%	Not estimated
Fungi	14%	Not estimated	1%	Not estimated	0%	Not estimated
Animal	1%	Not estimated	18%	Not estimated	5%	Not estimated
Other	7%	Not estimated	3%	Not estimated	1%	Not estimated

Appendix 2. Estimated unit weights, feeding rates, and percentage of feeding time for plants consumed by Japanese macaques living in lowland and highland forest areas

a. Lowland of Yakushima

Category	Species	Unit weight (g)	Feeding rate (#unit/sec)	% to total feeding time
fruit	*Ficus superba*	0.150	0.22	9.0%
fruit	*Ficus erecta*	0.152	0.29	7.0%
fruit	*Eurya emarginata*	0.019	0.60	4.5%
fruit	*Actinidia rufa*	0.920	0.05	2.4%
fruit	*Ficus microcarpa*	0.148	0.15	2.2%
fruit	*Myrica rubra*	0.067	0.10	2.1%
fruit	*Litsea acuminata*	0.395	0.35	1.9%
fruit	*Ficus pumila*	0.352	0.03	1.6%
fruit	*Neolitsea sericea*	0.147	0.25	1.1%
fruit	*Morinda umbellata*	0.088	0.47	0.9%
fruit	*Vitis ficifolia*	0.013	0.27	0.6%
fruit	*Melia azedarach*	0.405	NA	0.6%
fruit	*Cinnamomum camphora*	0.048	0.28	0.4%
fruit	*Eurya japonica*	0.012	0.63	0.4%
fruit	*Diospyros japonica*	0.352	0.10	0.4%
fruit	*Elaeocarpus sylvestris*	0.356	0.09	0.2%
fruit	*Psychotria serpens*	0.008	0.10	0.2%
fruit	*Taxillus yadoriki*	0.041	0.10	0.1%
fruit	*Glochidion obovatum*	0.195	NA	0.1%
fruit	*Ardisia sieboldii*	0.055	0.21	0.1%
mature leaf	*Daphniphyllum teijsmannii*	0.110	0.07	1.9%
mature leaf	*Symplocos lucida*	0.110	0.17	0.6%
mature leaf	*Oreocnide pedunculata*	0.022	0.34	0.4%
mature leaf	*Ficus superba*	0.270	0.11	0.4%
mature leaf	*Trema orientalis*	0.230	0.07	0.4%
mature leaf	*Ficus erecta*	0.170	0.06	0.2%
mature leaf	*Callicarpa shikokiana*	0.022	0.43	0.2%
mature leaf	*Maesa tenera*	0.120	0.11	0.1%
mature leaf	*Hydrangea grosseserrata*	0.037	NA	0.1%
seed	*Rhus succedanea*	0.093	0.42	8.8%
seed	*Zanthoxylum ailanthoides*	0.007	0.81	5.4%
seed	*Rhaphiolepis umbellata*	0.195	0.22	4.3%
seed	*Lithocarpus edulis*	0.386	0.06	3.8%
seed	*Cinnamomum camphora*	0.048	0.45	3.1%
seed	*Mallotus japonicus*	0.009	0.48	2.4%
seed	*Ardisia sieboldii*	0.055	0.28	0.8%
seed	*Litsea acuminata*	0.001	0.25	0.7%
seed	*Quercus phillyraeoides*	0.490	0.12	0.7%
seed	*Oreocnide pedunculata*	0.007	0.49	0.6%
seed	*Euscaphis japonica*	0.030	0.23	0.6%
seed	*Neolitsea sericea*	0.147	0.36	0.2%
seed	*Castanopsis sieboldii*	0.498	NA	0.2%
seed	*Glochidion obovatum*	0.195	NA	0.1%
young leaf	*Rhus succedanea*	0.039	0.14	1.2%
young leaf	*Elaeagnus glabra*	0.044	0.40	0.2%
young leaf	*Oreocnide pedunculata*	0.006	0.64	0.1%

b. Highland of Yakushima

Category	Species	Unit weight (g)	Feeding rate (#unit/sec)	% to total feeding time
fruit	*Eurya japonica*	0.012	1.01	5.2%
fruit	*Prunus sargentii*	0.082	0.30	2.4%
fruit	*Boehmeria longispica*	0.067	0.38	1.7%
fruit	*Eurya japonica* var. *yakushimensis*	0.008	0.71	0.9%
fruit	*Cornus kousa*	0.700	0.14	0.8%
fruit	*Cleyera japonica*	0.038	0.52	0.4%
fruit	*Dendropanax trifidus*	0.030	0.34	0.3%
fruit	*Symplocos myrtacea*	0.030	0.51	0.3%
fruit	*Neolitsea aciculata*	0.036	0.50	0.2%
fruit	*Vitis ficifolia*	0.042	0.17	0.2%
fruit	*Ilex pedunculosa*	0.074	0.16	0.2%
fruit	*Euonymus yakushimensis*	0.018	0.27	0.2%
fruit	*Ilex crenata*	0.065	0.55	0.2%
mature leaf	*Symplocos myrtacea*	0.039	0.56	12.5%
mature leaf	*Eurya japonica*	0.118	0.34	5.3%
mature leaf	*Histiopteris incisa*	0.123	0.25	4.0%
mature leaf	*Actinidia arguta*	0.103	0.24	3.3%
mature leaf	*Symplocos prunifolia*	0.055	0.20	2.2%
mature leaf	*Sorbus commixta*	0.045	0.60	1.7%
mature leaf	*Rubus croceacanthus*	0.008	0.61	1.5%
mature leaf	*Lepisorus onoei*	0.066	0.59	1.5%
mature leaf	*Trochodendron aralioides*	0.325	0.12	1.1%
mature leaf	*Rubus minusculus*	0.035	0.58	1.0%
mature leaf	*Ficus oxyphylla*	0.075	0.17	0.8%
mature leaf	*Mitchella undulata*	0.008	0.76	0.8%
mature leaf	*Pyrrosia lingua*	0.133	0.05	0.4%
mature leaf	*Zoysia japonica*	0.007	0.77	0.4%
mature leaf	*Miscanthus sinensis*	0.034	0.87	0.3%
mature leaf	*Chloranthus serratus*	0.074	0.27	0.3%
mature leaf	*Gleichenia japonica*	0.123	0.23	0.2%
mature leaf	*Ilex pedunculosa*	0.100	0.23	0.1%
mature leaf	*Clethra barbinervis*	0.103	0.38	0.1%
seed	*Distylium racemosum*	0.001	0.10	2.5%
seed	*Cornus kousa*	0.096	0.54	1.0%
seed	*Camellia japonica*	0.019	0.54	0.2%
seed	*Quercus salicina*	0.124	0.50	0.2%
young leaf	*Symplocos myrtacea*	0.779	0.00	2.9%
young leaf	*Actinidia arguta*	1.022	0.02	0.4%

Appendix 3. Parameters used in the estimation of the population-level food consumption by Japanese macaques

a. Average day length of each month

Month	Day length (hour)
January	13.0
February	13.2
March	14.2
April	14.0
May	13.3
June	12.5
July	11.5
August	10.7
September	10.2
October	10.3
November	11.1
December	12.0

b. Parameters specific to different age-sex categories

Category	Body mass (kg)	Energy requirement relative to an adult female	Proportion in the population (NA group)	Proportion in the population (HR group)
Adult male	15.39	1.10	16%	25%
Adule female	13.55	1	28%	35%
Juvenile	6.54	0.58	56%	32%
Infant	NA	0	0%	8%

c. Abundance of Japanese macaques

Site	Population density (macaque/km^2
Lowland	81.1
Highland	11.8