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Author(s)	Hanya, Goro; Fuse, Mieko; Aiba, Shin-Ichiro; Takafumi, Hino; Tsujino, Riyou; Agetsuma, Naoki; Chapman, Colin A
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1 Ecosystem impacts of folivory and frugivory by Japanese macaques in two
2 temperate forests in Yakushima

3

4 GORO HANYA^{1*}, MIEKO FUSE², SHIN-ICHIRO AIBA³, HINO TAKAFUMI⁴,
5 RIYOU TSUJINO⁵, NAOKI AGETSUMA⁶ and COLIN A. CHAPMAN⁷

6

7 ¹ *Primate Research Institute, Kyoto University, Inuyama, Japan*

8 ² *Sasayama Field Station, Kobe University, Sasayama, Japan*

9 ³ *Kagoshima University, Kagoshima, Japan*

10 ⁴ *Rakuno Gakuen University, Ebetsu, Japan*

11 ⁵ *Nara University of Education, Nara, Japan*

12 ⁶ *Field Science Center for Northern Biosphere, Hokkaido University, Kozagawa,
13 Japan*

14 ⁷ *Department of Anthropology and McGill School of Environment, McGill*

15 *University, Montréal, Canada and Wildlife Conservation Society, Bronx, NY, USA*

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19 * Correspondence to: GORO HANYA

20 Primate Research Institute, Kyoto University, Inuyama, Aichi, 484-8506, Japan.

21 E-mail: hanya@pri.kyoto-u.ac.jp

22 Tel: +81-568-63-0542

23 Fax: +81-568-63-0564

24

25 **Abstract**

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

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

48

49 **INTRODUCTION**

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

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

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

92

93 **METHODS**

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

98

99 **Study sites and subjects**

100 We studied in highland (coniferous cool- temperate, 1000-1200 m a.s.l.) and
101 lowland (evergreen broad-leaved warm-temperate, 0-200 m a.s.l.) forests
102 separated by 7 km on the island of Yakushima (30°N, 131°E), Japan. We
103 observed the feeding behavior of the HR group in the highland site and the NA
104 and H groups in the lowland site. The annual home ranges of the HR, NA, and
105 H groups were 2.7, 0.6, and 0.7 km², respectively. The home range of the HR
106 group was a mosaic of primary and logged forest, but primary forest, where
107 forest productivity was studied, comprised 83% of the total area. The home
108 ranges of NA and H groups overlapped extensively and consisted of old
109 secondary forest. Hanya [2004] and Hanya et al. [2007] provide further
110 information about the study sites and subjects.

111 In these forests, biomass of sika deer (*Cervus nippon*) equals that of
112 macaques [Agetsuma et al. 2003] and they influence forest dynamics [Koda et al.
113 2008]. However, we did not compare their impact because deer eat leaves
114 from the ground, where the productivity cannot be estimated by litter trap. In
115 addition, they eat a considerable amount of dead leaves [Agetsuma et al. 2011]
116 they are thus often acting as decomposers. There are no other folivorous or
117 frugivorous large mammals in the island. Marten (*Mustela itatsi*) and field mice
118 (*Apodemus speciosus* and *A. argenteus*) may also eat fruits, but they were also
119 not considered as they are terrestrial. Their biomass seems negligible
120 compared with that of macaques because they are very small (~2 kg for martens
121 and 20-60 g for mice) and very rare, considering the much lower photographic
122 rate (1/10 of macaques) in camera trapping (Hanya et al., unpublished data).

123

124 **Behavioral observations**

125 We collected data between April 2000 and March 2001 for HR group in the
126 highland site (510 hr) and between October 2003 and August 2004 for NA group
127 in the lowland site (1080 hr). To supplement the September data lacking for the
128 NA group, we also used the data of H group in September 1998. We collected
129 behavioral data using focal animal sampling (duration of 1 hr) of seven adult
130 females and six males for the highland group (mean \pm SD of observation time:
131 39 \pm 12 hr/individual), and five adult females for the NA group (216 \pm 75
132 hr/individual) and for five adult males in the H group (18 \pm 0.86 hr/individual).
133 Data on the diet are available elsewhere [Hanya 2003; Hanya 2004; Hanya et al.
134 2007] (Appendix 1). We defined a feeding bout as starting when the animal put
135 food into the mouth and stopping when 20 seconds had elapsed without the
136 subject moving in the tree or manipulating food or when the animal left the tree
137 or started eating other items. We recorded the number of food units that the
138 animal ingested for as long as possible. One food unit was operationally
139 defined depending on the particular item and plant species (e.g. one leaf, one
140 fruit, one cluster of fruits).

141

142 **Estimating food consumption**

143 We estimated the dry weight intake of all stages of leaves (both mature and
144 young leaves) and fruits (including seeds). We considered consumption as the
145 removed biomass and included the weight of indigestible parts that were
146 discarded before ingestion. For feeding bouts where the number of food units
147 ingested could not be recorded, we estimated ingestion by multiplying the
148 duration of the feeding bouts and the average feeding rate (#units/second) of all

149 feeding bouts for that item of the species. To calculate this average, we
150 discarded data when the duration of a feeding bout was less than 2 min unless
151 this was the only datum available for the food species/item. This was because
152 data of short duration were less reliable. Then, we multiplied the number of
153 food units ingested (estimated or actually counted) during each feeding bout by
154 its unit dry weight and summed the results for all feeding bouts of each focal
155 observation. We multiplied the estimated dry weight intake per observation
156 hour with the average day length of the month and the number of days in the
157 month, to obtain the total estimated dry weight intake in the month. This could
158 be justified as the distribution of observations was not biased to a particular time
159 of the day or month: we made from dawn to dusk [Hanya 2004; Hanya et al.
160 2007] and equally distributed observation days in each month. We calculated
161 total annual intake by summing the values of the 12 months. We summarized
162 data of the unit weight and feeding rate in Appendix 2.

163 We estimated intake for age-sex classes that we did not observe
164 assuming that macaque consumption was proportional to the 0.75 power of
165 average body mass for the age/sex [Kleiber 1987] using body weight data from
166 Watanabe [1975] (Appendix 3). For the highland site, data on adult males and
167 females were available, so we estimated the average intake using the pooled
168 data. For the lowland site, only the female data were available, so we
169 estimated the male intake following the power rule. We used age-sex
170 composition of the HR and NA groups to estimate the proportion of individuals of
171 each age-sex class in the population. We used the data of these two particular
172 groups, rather than the data on age-sex composition collected over a larger
173 scale. This was because we needed to use data that were comparable with the

174 behavioral and litter trap data, which were taken within the home range of these
175 two particular groups. We calculated food consumption of each age-sex class
176 at the population level by multiplying (1) the estimated food consumption of the
177 class, (2) proportion of the class in the population and (3) the population density.
178 We derived density from Yoshihiro et al. [1999] and Hanya et al. [2003b]
179 (Appendix 3). We calculated food consumption at the population-level as the
180 sum of all the age-sex classes. In the highland site, we also recorded the
181 amount of leaves that macaques dropped during feeding. We estimated total
182 amount of dropped leaves in that month by an adult individual by multiplying the
183 amount of leaves (g) per observation time, average day length of the month and
184 the number of days in the month. We estimated amount dropped at the
185 population level over the year in the same way as we did for leaf intake.

186

187 **Litter trap**

188 We established two vegetation plots within the home ranges of the groups and
189 identified and measured all tree stems with a diameter at breast height (DBH) >
190 5 cm. Plot size was 50m * 50m in the highland site (0.09% of the home range
191 of the HR group) and 100m * 50m in the lowland site (0.8% of the home range of
192 the NA group). Aiba et al. [2007] and Hanya and Aiba [2010a] described details
193 of the plots. These plots included both ridge and valley and phenological
194 change recorded in these plots predicted the seasonal variation in the macaque
195 diet [Hanya 2004; Hanya et al. 2007]. Therefore these plots seemed to be
196 representative of the home range. We placed 25 and 20 litter traps (nylon
197 mesh of <0.5 mm, 0.58 m² in size and 1-1.5 m above the ground) evenly
198 distributed in highland and lowland site plots respectively. The minimum

199 inter-trap distance was 10 m. We collected litter once a month, oven-dried it at
200 60 °C for 96 hr and weighed and sorted items into broad-leaf, conifer needle,
201 fruits, and others. Fruits included the whole or partial ripe fruits, unripe fruits
202 and seeds separated from pulp. We sorted them by species and weighed them.
203 We separated bird feces from 'others' in the highland plot.

204

205 **Estimation of fruit and leaf production**

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

213

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

222 In principle, annual leaf production is equal to annual leaf litter fall when
223 the leaf biomass of the forest reaches equilibrium [Clark et al. 2001]. However,

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

234

235 *Fruit production:* We calculated the production of fruit for the highland site as the
236 sum of fruit fall and consumption by macaques and birds. However, in the
237 lowland site, data on bird consumption were lacking so macaque frugivory was
238 compared only with the fruit fall. The current estimation in the highland was
239 based on the data used also in Hanya [2005], who calculated only the total
240 number of seeds removed by birds. However, in the current analysis, we
241 present data for each species of plant. We confined the estimation of bird
242 consumption to the three species (*E. japonica*, *C. japonica*, and *S. myrtaceae*)
243 that constituted 92.5% of the fleshy fruit production in the highland site. These
244 species have small seeds (<5 mm long) which were swallowed by macaques
245 [Otani & Shibata 2000]. Thus, in the estimation, we could regard the pulpless
246 seeds of these species dropped into the trap as having dispersed by birds
247 [Kominami et al. 2003], along with the seeds found in bird feces. We did not
248 find any macaque feces in the traps in the highland site. We confirmed that

249 macaque feces were recognizable for at least one month after defecation by
250 experimentally putting feces in a trap. We estimated the weight of fruits
251 removed by birds using the data of (1) the number of seeds trapped, (2) the
252 average number of seeds in one fruit for each species and (3) average weight of
253 one fruit, of which data we collected by measuring >100 fruits for each species.

254

255 **Long-term changes of forest composition**

256 To assess the impact of macaque folivory on forest tree species dynamics, we
257 established a 2.4 ha vegetation plot (4% of the home range of the NA group) in
258 1990 in the lowland site. The plot consisted of 10 line transects (5 m wide,
259 30-150 m long) set every 100 m within the entire home range of the NA and the
260 H groups. We recorded the species and the DBH of all trees >5 cm DBH in
261 1990 and 2003. In the highland site, for the analysis of forest composition
262 dynamics, we used the plot of 0.25 ha that we set to collect litter. We
263 established this plot in 1999 and resampled in 2012. We examined changes in
264 density between the two periods using a G-test for species with more than 9
265 stems in one of the years. We tested a null hypothesis which assumed no
266 difference in the proportion of decreasing species between food and non-food
267 species. We examined 47 lowland (5 food and 42 non-food species) and 10
268 highland species (3 food and 7 non-food species).

269

270 **RESULTS**

271 **Folivory**

272 In both the lowland and highland sites, the impact of macaque folivory at the
273 community level was negligible relative to leaf production or assumed folivory by

274 insects. The leaf biomass consumed by macaques was only 0.037% and
275 0.39% of the estimated total leaf production in the lowland and highland sites,
276 respectively (Table 1). These values increased if we considered only food
277 species, but it still remained low (0.21% in the lowland site and 0.90% in the
278 highland site). At the species level, however, macaque leaf consumption
279 reached 5.7% of the estimated leaf production in the lowland site
280 (*Daphniphyllum teijsmannii*) and 10.1% in the highland site (*Symplocos*
281 *prunifolia*). For other species, macaques consumed between 0.93% and
282 2.14% of the leaves produced. In the highland site, we estimated the biomass
283 of dropped leaves as 3.93 kg/km²/year, which was 0.21% of the consumed
284 leaves.

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

290

291 **Frugivory**

292 In contrast to leaves, macaques consumed a considerable portion of the total
293 fruit production. For the three fleshy-fruited species in the highland site, for
294 which we quantified both bird and macaque consumption, macaque
295 consumption was 3.2-39% of the total fruit production depending on plant
296 species, whereas birds consumed between 32 and 75% of the fruit production
297 (Table 3b). Macaques and birds together consumed more than two-thirds of
298 the fruit production for all the species. In the lowland site, fruit consumption by

299 macaques constituted 8.8%, 10.1%, and 68.8% of fruit fall for all species, food
300 species, and the most frequently eaten species, respectively (Table 3a).

301 Although there were 12 fruiting species that constituted more than 1% of the
302 annual feeding time (sum of the duration of the feeding bouts) for the lowland
303 site macaques, fruits of only one of them appeared in the litter trap.

304

305 **DISCUSSION**

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

307 Our data suggested that at the community level the amount of leaves consumed
308 by Japanese macaques in Yakushima was negligible compared with the leaf
309 production. Total leaf consumption by macaques constituted less than 0.4% of
310 the total leaf production. However, for some species, the impact of macaque
311 folivory reached 10% in the highland site, which was comparable to the
312 community-level impact of insect folivory known for various types of forests
313 (3-17%) [Landsberg & Ohmart 1989]. Because some tree species can survive
314 even if they lose all their leaves by browsing [Rooke & Bergstrom 2007], we
315 need further study to confirm the effect of folivory on plant longevity, growth,
316 and/or reproduction.

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

324 In contrast to our results, Chapman et al. [2013] reported that in Kibale
325 National Park, Uganda, there was a tendency for tree species that were eaten by
326 two species of colobus monkeys to decrease in abundance but no such
327 tendency was found for the species that colobus did not eat. The difference
328 between Yakushima and Kibale is likely due to difference in primate biomass.
329 Primate biomass in Kibale (2759 kg/km^2) [Chapman et al. 1999] is 6.77 and 24.2
330 times larger than that in the lowland and highland sites of Yakushima
331 respectively and folivorous colobines make up the greatest portion (75%) of that
332 biomass [Chapman et al. 1999]. Total litter fall (including leaves, branch, and
333 reproductive parts) in Yakushima was $565,000 \text{ kg/km}^2/\text{year}$ in the lowland site
334 and $473,000 \text{ kg/km}^2/\text{year}$ in the highland site. This represented 71% and 59%
335 of the average documented for 12 tropical forests (average = $966,200 \text{ kg/}$
336 km^2/year , maximum: $1,235,000 \text{ kg/km}^2/\text{year}$) [Hanya & Aiba 2010b]. Therefore,
337 if we suppose that leaf production in Kibale is average for a tropical forest, leaf
338 production in Kibale is calculated only as 1.41 times larger than that in the
339 lowland site and 1.69 times of that in the highland site of Yakushima.
340 Supposing further that the amount of leaf consumption is proportional to primate
341 biomass; leaf consumption/production ratio in Kibale is 4.80 ($6.77/1.41$) times
342 larger than in lowland site and 17.1 ($24.2/1.41$) times larger than in the highland
343 site of Yakushima. Given that 75% of the primate biomass in Kibale is
344 folivorous colobines, this is likely to be a conservative estimate. That is, if
345 Japanese macaques in Yakushima consume ca. 10% of produced leaves for
346 some species, more folivorous Kibale primates would impose more serious
347 damage to many species. In addition, latitudinal variations in leaf turn-over
348 cycle [Reich et al. 1996] may affect the different impact of folivory in Yakushima

349 (temperate) and Kibale (tropical). More detailed data on leaf production and
350 consumption by Kibale primates are needed to confirm our estimates. In any
351 case, however, comparisons of Yakushima and Kibale suggest that the threshold
352 value of primate biomass above which primate folivory has a critical impact on
353 the forest lies somewhere between Yakushima and Kibale.

354

355 **Impact of frugivory**

356 Of the three fleshy-fruited species evaluated at the highland site, Japanese
357 macaques were the most important fruit consumer for one (*E. japonica*),
358 consuming approximately 40% of production. As for the two other species, bird
359 consumption was 11-23 times larger than that of macaques. These two groups
360 of frugivores consumed up to two thirds of the fruit production. Although one
361 third of the fruits were not eaten, we think that fruits may nevertheless be a
362 limited resource. According to our data on the seasonality of fruit fall, a majority
363 (91%) of the uneaten fruits of these species dropped before the macaques and
364 birds stop feeding on them (by November) and it appeared that finding fruits was
365 difficult. When frugivores stopped feeding on these fruits, there were only very
366 few fruits remaining. In addition, considering the degree of inter-annual
367 variability in diet, frugivores could have depleted the uneaten fruit biomass.
368 Hanya [2005] showed that the fruit consumption by macaques and birds in 1999
369 reached 1.66 times higher than in 2000. Tsuji et al. [2006] reported even higher
370 inter-annual variation in the amount of fruits consumed by wild Japanese
371 macaques in Kinkazan, northern Japan.

372 The impact of macaque frugivory at the community level remains to be
373 further investigated, but we can expect that it would be larger than the case of

374 folivory, but smaller than the case of intensively-fed *E. japonica* fruits. This is
375 because macaques consumed only 10% of the fruit fall for all the food species.
376 In addition, most (65%) of the fruit fall for the species eaten by macaques
377 comprised two gravity-dispersed species (*Distylium racemosum* and *Camellia*
378 *japonica*) [Hanya & Aiba 2010a], which were unlikely to be eaten by birds (Hanya,
379 per. obs). Macaques might be seed predators for these species.

380 We cannot fully assess the impact of the frugivory by Japanese
381 macaques in the lowland site because there are no data on bird consumption
382 there. For several reasons, however, it is likely that the tendency would be the
383 same in the lowland site as in the highland sites. First, most (58%) of the fruit
384 fall of food species for macaques in the lowland site was acorns [Hanya & Aiba
385 2010a], which most birds in Yakushima do not consume. Second, at the
386 species level, macaques are likely important fruit consumers for some species.
387 For example, fruits of *Litsea acuminata* consumed by macaques reached 68% of
388 the fruit fall, which is a similar level to that of *E. japonica* in the highland site.
389 Fruits of *L. acuminata* are among the largest in Yakushima and only a few bird
390 species can swallow the seeds [Noma & Yumoto 1997]. In addition, it has
391 already been clarified that fruit consumption by macaques in the lowland site
392 Yakushima is much larger (>32 times) than that by birds for two fleshy-fruited
393 species (*Ficus superba* and *Myrica rubra*) [Otani 2001; Terakawa et al. 2008].
394 Third, 11 out of 12 major food fruit species for Japanese macaques were 'rare'
395 species whose fruit abundance cannot be accurately estimated by litter traps.
396 Since they are rare, the fruit production of these species is likely to be lower than
397 the common species, such as *L. acuminata*. Therefore, the ratio of macaque
398 frugivory to fruit production would be higher for these species than *L. acuminata*.

399 It is already known that the Japanese macaques in Yakushima provide effective
400 seed dispersal services with respect to the quality, such as dispersal distance
401 and topography [Noma & Yumoto 1997; Otani & Shibata 2000; Terakawa et al.
402 2009; Tsujino & Yumoto 2009; Yumoto et al. 1998]. Seed dispersal
403 effectiveness could be evaluated as the product of quantity and quality of seed
404 dispersal [Schupp et al. 2010]. Our results suggest the quantitative importance
405 of seed dispersal by macaques and thus suggest they play an important role in
406 forest regeneration through seed dispersal.

407

408 **Robustness of the results**

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

413 First, although our dietary data were based on detailed observation of
414 feeding behavior, food intake at the population level was estimated based on
415 many assumptions. Error may have occurred when we (1) estimated food
416 intake of one age-sex class from the data of different classes, (2) estimated
417 age-sex composition of the population, and (3) calculated population-level intake
418 from the population density. As for the first assumption, Hanya [2003] has
419 confirmed that variation in the mass of food ingested by wild Japanese
420 macaques of different age classes are roughly consistent with our assumption.
421 We believe the second assumption did not cause serious error, as we used the
422 age-sex composition of the subject groups, which was the most likely
423 composition of the macaques using the area within the home ranges of the

424 subject groups. As for the third assumption, the density data seemed correct
425 because they agreed with the the long-term record of the distribution of identified
426 groups [Yoshihiro et al. 1999; Hanya et al. 2003]. Error could have occurred if
427 there was heterogeneity in density within the study site and the home range of
428 the study group was situated where density was particularly high or low,
429 although it seemed unlikely that this was the case given the distribution of
430 groups in the study area.

431 Second, data on productivity were derived from plots of only 0.25 ha or
432 0.5 ha. This area was much smaller than the home ranges of the study groups,
433 and may not reflect productivity across the entire home range area. We note,
434 however, that productivity measured in plots within the same altitudinal zones of
435 Yakushima differed at most by a factor of two [Aiba et al. 2007]. This difference
436 is much smaller than the difference in leaf productivity and macaque
437 consumption. Therefore, the qualitative conclusion of our analysis - that
438 macaque folivory is negligible - is not likely to be affected by plot size.
439 However, the conclusion at the population level needs further examination, as
440 certain plant species may show a non-random in the monkeys' home range.
441 Focal tree observation might be a better approach to assess consumption and
442 productivity for rare species.

443 Third, the small plot size in the highland site constrained the analysis of
444 tree species dynamics. Therefore, our evaluation of forest dynamics in the
445 highland site is preliminary. However, given that none of the species decreased
446 in abundance, it is unlikely that larger plot sizes would produce contrary findings.
447 We cannot discard the possibility that macaques can have significant negative
448 impact on rare species which did not appear in the vegetation plot. Various

449 plots are established in different altitudinal zones of Yakushima [Aiba et al. 2007],
450 so meta-analysis of tree species dynamics with respect to macaque folivory will
451 be feasible in the future. The plot size in the lowland site was rather large (2.4
452 ha) and cover the entire home range, so the results from here seemed reliable.

453 Finally, there were no data from the NA group for one month, so we
454 filled in missing values with data from another year and another group.

455 Considering the large seasonal variation in the diet in Yakushima [Hanya 2004;
456 Hill], we believe this is a better solution than calculating the intake in this month
457 as an average of the other 11 months. Because the home ranges of the two
458 groups overlapped extensively, we assumed that dietary differences were
459 minimal. Main foods in this month were fruits of figs and *Rhus succedanea*,
460 both of which exhibit small supra-annual variations in fruiting intensity.

461 Therefore, large supra-annual variations in the diet in this month also seem
462 unlikely. In addition, the actual over- or underestimation related to using the
463 data of other year/group should be small because it constitutes only one of the
464 twelve months.

465

466 In conclusion, macaque folivory was negligible compared to leaf production at
467 the community level because macaque consumption constituted only ~0.04% of
468 the leaf production and macaque food species did not decrease over 13 years.

469 However, the impact of macaque frugivory has more important consequences for
470 the plants consumed.

471

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487

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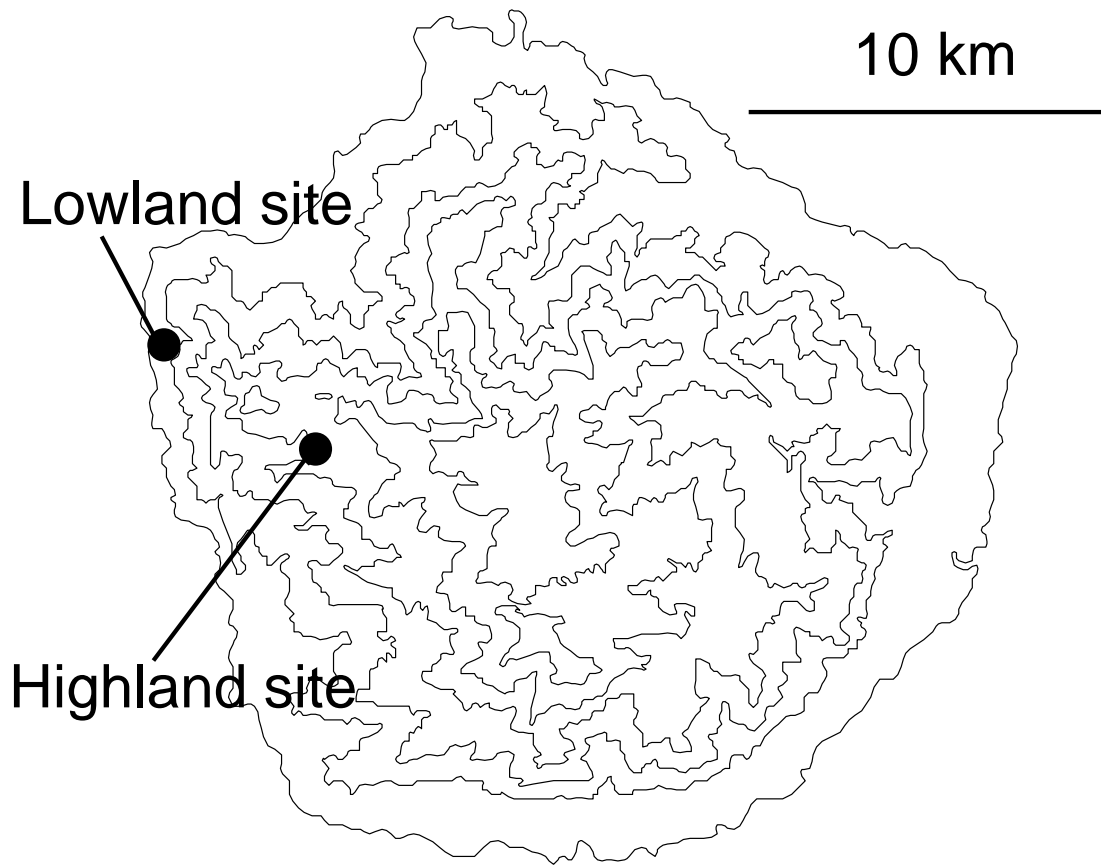
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644 Legend to the figure

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

647



648

649 Fig. 1

650

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%)
<i>Symplocos lucida</i>	1480	1870	2120	35 (1.7%)
<i>Daphniphyllum teijsmannii</i>	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%)
<i>Symplocos myrtacea</i>	12100	15300	17200	160 (0.93%)
<i>Eurya japonica</i>	4230	5340	6080	130 (2.1%)
<i>Trochodendron aralioides</i>	36600	46200	51400	78.2 (1.5%)
<i>Symplocos prunifolia</i>	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.

651

652

653

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

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

	<u>Decrease</u>	<u>Not decrease</u>
Food species	2	3
Non-food species	10	32

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

	<u>Decrease</u>	<u>Not decrease</u>
Food species	0	3
654 Non-food species	0	7

655

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 kg/km ² /year	Fruit consumption
		by Japanese macaques kg/km ² /year
All species	59900	5230
Food species	52200	5230
<i>Litsea acuminata</i>	887	603

b. Highland forest of Yakushima

Target	Fruit fall kg/km ² /year	Fruit consumption kg/km ² /year (% to fruit production)	
		by Japanese macaques	by birds
All species	10700	381	-
Food species	3810	381	-
<i>Distylium racemosum</i>	1980	176	-
<i>Eurya japonica</i>	24.2 (28.4%)	33.4 (39.2%)	27.6 (32.3%)
<i>Cleyera japonica</i>	27.1 (21.9%)	4.01 (3.24%)	92.6 (74.9%)
<i>Symplocos myrtacea</i>	8.95 (24.8%)	2.11 (5.85%)	25.0 (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	<i>Ficus superba</i>	0.150	0.22	9.0%
fruit	<i>Ficus erecta</i>	0.152	0.29	7.0%
fruit	<i>Eurya emarginata</i>	0.019	0.60	4.5%
fruit	<i>Actinidia rufa</i>	0.920	0.05	2.4%
fruit	<i>Ficus microcarpa</i>	0.148	0.15	2.2%
fruit	<i>Myrica rubra</i>	0.067	0.10	2.1%
fruit	<i>Litsea acuminata</i>	0.395	0.35	1.9%
fruit	<i>Ficus pumila</i>	0.352	0.03	1.6%
fruit	<i>Neolitsea sericea</i>	0.147	0.25	1.1%
fruit	<i>Morinda umbellata</i>	0.088	0.47	0.9%
fruit	<i>Vitis ficifolia</i>	0.013	0.27	0.6%
fruit	<i>Melia azedarach</i>	0.405	NA	0.6%
fruit	<i>Cinnamomum camphora</i>	0.048	0.28	0.4%
fruit	<i>Eurya japonica</i>	0.012	0.63	0.4%
fruit	<i>Diospyros japonica</i>	0.352	0.10	0.4%
fruit	<i>Elaeocarpus sylvestris</i>	0.356	0.09	0.2%
fruit	<i>Psychotria serpens</i>	0.008	0.10	0.2%
fruit	<i>Taxillus yadoriki</i>	0.041	0.10	0.1%
fruit	<i>Glochidion obovatum</i>	0.195	NA	0.1%
fruit	<i>Ardisia sieboldii</i>	0.055	0.21	0.1%
mature leaf	<i>Daphniphyllum teijsmannii</i>	0.110	0.07	1.9%
mature leaf	<i>Symplocos lucida</i>	0.110	0.17	0.6%
mature leaf	<i>Oreocnide pedunculata</i>	0.022	0.34	0.4%
mature leaf	<i>Ficus superba</i>	0.270	0.11	0.4%
mature leaf	<i>Trema orientalis</i>	0.230	0.07	0.4%
mature leaf	<i>Ficus erecta</i>	0.170	0.06	0.2%
mature leaf	<i>Callicarpa shikokiana</i>	0.022	0.43	0.2%
mature leaf	<i>Maesa tenera</i>	0.120	0.11	0.1%
mature leaf	<i>Hydrangea grosseserrata</i>	0.037	NA	0.1%
seed	<i>Rhus succedanea</i>	0.093	0.42	8.8%
seed	<i>Zanthoxylum ailanthoides</i>	0.007	0.81	5.4%
seed	<i>Rhaphiolepis umbellata</i>	0.195	0.22	4.3%
seed	<i>Lithocarpus edulis</i>	0.386	0.06	3.8%
seed	<i>Cinnamomum camphora</i>	0.048	0.45	3.1%
seed	<i>Mallotus japonicus</i>	0.009	0.48	2.4%
seed	<i>Ardisia sieboldii</i>	0.055	0.28	0.8%
seed	<i>Litsea acuminata</i>	0.001	0.25	0.7%
seed	<i>Quercus phillyraeoides</i>	0.490	0.12	0.7%
seed	<i>Oreocnide pedunculata</i>	0.007	0.49	0.6%
seed	<i>Euscaphis japonica</i>	0.030	0.23	0.6%
seed	<i>Neolitsea sericea</i>	0.147	0.36	0.2%
seed	<i>Castanopsis sieboldii</i>	0.498	NA	0.2%
seed	<i>Glochidion obovatum</i>	0.195	NA	0.1%
young leaf	<i>Rhus succedanea</i>	0.039	0.14	1.2%
young leaf	<i>Elaeagnus glabra</i>	0.044	0.40	0.2%
young leaf	<i>Oreocnide pedunculata</i>	0.006	0.64	0.1%

b. Highland of Yakushima

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