TITLE:

How the physical properties of food influence its selection by infant Japanese macaques inhabiting a snow-covered area.

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CITATION:

Taniguchi, Haruka. How the physical properties of food influence its selection by infant Japanese macaques inhabiting a snow-covered area.. American journal of primatology 2014, 77(3): 285-295

ISSUE DATE:

2014-10-05

URL:

<http://hdl.handle.net/2433/200313>

RIGHT:

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- 1 **How the physical properties of food influence its selection by infant Japanese**
2 **macaques inhabiting a snow-covered area**
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18 **ABSTRACT**

19 Dietary differences exist between infant and adult female non-human primates.
20 These differences are considered to be related to the low ability of infants to bite,
21 handle, and obtain food items. This study aimed to provide a comprehensive
22 examination of how the physical properties of food items (fracture toughness, size,
23 processing, and height) influence food selection by infant primates. In this study, 4
24 mother–infant Japanese macaque (*Macaca fuscata*) pairs were investigated in a
25 snow-covered area during winter. The feeding behavior of both mothers and infants
26 was recorded. The size, need for processing, and height of food items were recorded
27 by direct observation, while the fracture toughness of food items (evaluating the
28 required bite force by incisors) was measured using a rheometer. On average, infants
29 spent 14% less time feeding than their mothers, and there were dietary differences
30 between mothers and infants. Compared to their mothers, infants fed relatively more
31 frequently on food items that were small, at a low position, or that could be
32 consumed without processing. In addition, infants spent less time feeding on food
33 items that were tougher than 2000 J/m². Thus, infants fed relatively more frequently
34 on food items that are easy to obtain. This food selection by infants reduced the costs
35 of feeding and allowed them to avoid falling from high trees.

36 **Key words: food characteristics, food access and processing, bite force, relative**
37 **feeding index, age differences**

38

39 INTRODUCTION

40 Many studies of non-human primates indicate that food selection by mothers
41 affects food selection by their infants [for review, see Rapaport & Brown, 2008].
42 When infants start to eat solid foods, they copy the food selected by their mothers
43 [Hikami et al., 1990; Jaeggi et al., 2010]. Yet, some studies have reported the
44 presence of dietary differences between infants and adult females [Nakayama et al.,
45 1999; Tarnaud, 2004], which are attributed to the physical [Altmann, 1980; Gunst et
46 al., 2008; Gunst et al., 2010] and physiological [Nakayama et al., 1999] differences
47 between the 2 age classes. Altmann [1980] observed that “weaning foods” are foods
48 that are easily obtained and are eaten by infants during the transition from
49 dependence on milk to full nutritional independence. Therefore, the physical
50 properties of food items may partly influence food selection by infants during the
51 period of weaning.

52 First, previous studies have shown that the toughness of food items influences
53 food selection by infants. In long-tailed macaques (*Macaca fascicularis*), infants
54 avoid eating fruits with hard rinds [van Schaik & van Noordwijk, 1986]. A
55 craniofacial biomechanical study in rhesus macaques (*Macaca mulatta*) showed that
56 the mean incisor bite force of juveniles is half that of adults [Dechow & Carlson,
57 2005]. Thus, the bite force in infants is considered to be much weaker than that of
58 adults. In recent decades, several studies have used quantitative methods to examine
59 how the toughness of food items influences food selection in primates [Hill & Lucas,
60 1996; Kinzey & Norconk, 1990]. These studies revealed a relationship between the
61 ability to process food items and morphological features via interspecific and
62 intraspecific comparisons [McGraw et al., 2011; Norconk & Veres, 2011; Vogel et al.,

63 2008; Vogel et al., 2014, Wright et al., 2008]. However, previous studies have not
64 quantified the effect of food toughness on food selection by infants.

65 Second, the size of food items may affect food selection by infants. Infant
66 long-tailed macaques eat relatively smaller fruits than adults [van Schaik & van
67 Noordwijk, 1986]. Since bite size can be a body-mass dependent trait of the
68 masticatory apparatus, large-bodied animals generally feed on large food items more
69 efficiently than small-bodied animals. On the other hand, small-bodied animals need
70 to bite large food items many times [Nakagawa, 2008; Shipley et al., 1994;
71 Wrangham et al., 1993].

72 Third, food items that need processing skill may affect food selection by infants.
73 Several studies suggest that infants are less efficient foragers than juveniles and
74 adults [Gunst et al., 2008; Gunst et al., 2010; Rhine & Westlund, 1978; Stone, 2006].
75 For example, compared to juveniles and sub-adults, western lowland gorilla (*Gorilla*
76 *gorilla*) infants tend to feed on food parts that are easier to obtain and that require no
77 processing, because they lack the processing skills and physical strength (e.g., arm
78 strength) necessary to access hard-to-process food items [Nowell & Fletcher, 2008].

79 Fourth, another factor that might influence food selection by infants is the height
80 at which food items are located. Before infants achieve full motor competence,
81 climbing and moving arboreally might increase the probability of fatal falls
82 [Chalmers, 1972; Dunbar & Badam, 1998; Karssemeijer et al., 1990; Sussman, 1977].
83 In addition, compared to other age classes (particularly juveniles), rhesus macaque
84 infants spend more time in low and stable positions [Wells & Turnquist, 2001].

85 Thus, food selection by infants is considered to be affected by the physical
86 properties of food items, including toughness, size, processing, and height. However,

87 previous studies only focused on a limited set of food items [Altmann, 1980; Gunst
88 et al., 2008; Gunst et al., 2010; Nowell & Fletcher, 2008; Rhine & Westlund, 1978]
89 and on certain categories of food parts (e.g., fruits, leaves, and bark) [Nakayama et
90 al., 1999; Tarnaud, 2004]. Few studies have considered all food items when
91 examining the influence of the physical properties of food on dietary differences
92 between infant and adult primates.

93 In temperate regions, it is important to survive in winter when the climate is harsh
94 (i.e., cold and snow) and food availability is low [Nakagawa, 1997]. The Japanese
95 macaque is the best-studied temperate primate, with its seasonal reproductive and
96 foraging patterns being well-documented [Nakagawa et al., 2010]. Thus, this species
97 presents an ideal model for studying age-related differences on revealing the feature
98 of food selection by infants. Infant Japanese macaques (*Macaca fuscata*) are born in
99 spring and need to eat solid foods before the onset of winter to meet their nutritional
100 requirements, because the daily rate of milk transfer from mothers decreases by 50%
101 at around 6 months of age [Tanaka, 1992]. Indeed, infant macaques start to increase
102 solid food intake at 5–6 months of age [Iwamoto, 1982]. In snow-covered areas with
103 cool-temperate deciduous forests, macaques are limited to bark and dormant buds as
104 their main food items in winter [Suzuki, 1965]. Dietary differences between infant
105 and adult female Japanese macaques have been previously reported. For instance,
106 infants primarily feed on buds in winter, whereas adult females mainly feed on bark
107 [Nakayama et al., 1999].

108 This study aimed to provide a comprehensive examination of the physical
109 properties that influence food selection by infant Japanese macaques. I hypothesize
110 that, compared to their mothers, infants feed more frequently on food items that are

111 easily obtainable, because infant have a lower ability to bite, handle, and acquire
112 food items. Specifically, I hypothesize that, in comparison to their mothers, Japanese
113 macaque infants feed relatively more frequently on food items that (1) are softer; (2)
114 can be eaten in 1 bite; (3) do not need processing; and (4) are located at a lower
115 position in trees. In particular, it may be easy to validate the effect of the height of
116 food items in snow covered areas, because macaques tend to be limited to using food
117 items on trees (as ground vegetation is covered in snow) [Suzuki, 1965]. In addition,
118 a large number of studies have been conducted on the morphological development of
119 Japanese macaques, in terms of teeth and locomotor apparatus [Hamada, 1982;
120 Hamada, 1983; Ishida, 1972; Iwamoto, 1977; Iwamoto et al., 1984; Iwamoto, 1987].
121 Thus, the feeding pattern observed in the current study is discussed in relation to the
122 morphological development of this species, to validate my hypotheses.

123

124 **METHODS**

125 This study complied with the research guidelines of the Primate Research Institute
126 of Kyoto University, Japan, and adhered to Japanese legal requirements. I also
127 adhered to the Principles for the Ethical Treatment of Nonhuman Primates delineated
128 by the American Society of Primatologists.

129

130 **Study area and subjects**

131 The study was conducted in the southwestern part of the Shimokita Peninsula
132 (41°30'N, 141°00'E) from December 27, 2008 to March 29, 2009. The forest located
133 at an altitude higher than 400 m above sea level (a.s.l.) is dominated by *Fagus*
134 *crenata* and *Sasa* species on the forest floor. In comparison, the forest located at an

135 altitude below 400 m a.s.l. is a mosaic dominated by *Thujopsis dolabrata* and
136 *Quercus crispula*. Approximately one-quarter of the forest is covered in plantations
137 or secondary forests of *Cryptomeria japonica*, *Pinus densiflora*, *Larix kaempferi*, and
138 *Abies sachalinensis* [Kanuma et al., 2000].

139 The daily mean temperatures during the study period were 1.1 ± 2.6 °C (mean $\pm$
140 SD, range = -4.5–10.9 °C), and the daily mean minimum temperatures were $-2.2 \pm$
141 2.2 °C (range = -7.3–6.7 °C) (Japanese Meteorological Agency;
142 <http://www.jma.go.jp/jma/index.html>; accessed 2013-10-31). The study area was
143 covered in snow during this period; however, snow was sometimes absent in certain
144 places (e.g., roads).

145 The study group was the A87 troop of Japanese macaques, comprising 51
146 individuals, including 13 adult females (estimated as being either over 7 years of age
147 or parous) and 7 infants (less than 1 year of age). Four mother–infant pairs (Pairs ID1,
148 ID2, ID3, and ID4) were investigated in this study. The ages of the infants ranged
149 between 7 and 10 months during the study period. The focal infants consisted of 2
150 males and 2 females.

151 The focal mother–infant pairs were investigated by the focal animal sampling
152 method [Altmann, 1974]. Either a mother or her infant was observed as the focal
153 animal. Then, each animal was observed for 10 hours every 3 weeks. The total
154 observation time for each animal was 40 hours during the study period. Each animal
155 was continuously observed for 1 hour at a time. I changed focal animals each hour,
156 unless no other subject individuals were within view of the observer.

157 The focal animal's activities (feeding, grooming, resting, traveling, and other),
158 maternal carriage, and nipple contact were recorded by instantaneous sampling

[Altmann, 1974] at 3-min intervals. In this study, I present data for infants relating to the time spent in contact with the mother's nipple and carriage by the mother. The definition of "feeding" included not only taking food items into the mouth, but also processing (e.g., removal of a husk or digging an item out of the ground), and searching for (e.g., raking fallen leaves) food items by hand. When feeding was observed, I recorded the food item species, the food parts, the size of the food items, the need for processing, and the height at which feeding activity occurred. The food item parts were categorized as bark, dormant buds, leaves, seeds (including acorns and pinecones), roots (including rhizomes), twigs, and other. The size of food items was classified into 2 categories: (1) small: a food item entering an infant's mouth in 1 bite (less than approximately 1 cm in width), and (2) large: 2 or more bites required. The processing of food items was divided into 2 categories: (1) no processing required before a food item was taken into the mouth, and (2) processing required before a food item was taken into the mouth. The average height of food items was classified into 5 categories: (1) 0 m (i.e., on the ground), (2) 0–2 m, (3) 2–5 m, (4) 5–10 m, and (5) more than 10 m.

175

176 **Measurement of fracture toughness**

177 Previous studies have found that forces at the molars are 2–2.5 times greater than
178 those at the incisors [Dechow & Carlson, 2005]. Therefore, in this study, I limited the
179 measurement of fracture toughness to food items where macaques were observed to
180 use their incisors to make the initial bites. I measured the fracture toughness of the 32
181 food items that macaques fed on for more than 1.0% of total feeding time. I could not
182 collect or measure 3 food items (bark of *Helwingia japonica*, acorns of *Q. crispula*,

183 *Trametes* spp.) among them. The bite force for bark, dormant buds, leaves, roots, and
184 twigs was measured using a rheometer (COMPAC100II; SUN Scientific Co., Ltd. TM,
185 Setagaya-ku, Tokyo, Japan). The rheometer measures a series of loads when a single
186 blade cuts a food item. The load data were transferred to a computer using an
187 analogue-digital converter (ADA16-32/2(CB)F, CONTEC Co., Ltd.®,
188 Nishiyodogawa-ku, Osaka, Japan). The load was measured every millisecond during
189 the cutting process. The total workload was calculated as the integral of the series of
190 loads. Before taking rheometer measurements, the cross-sectional area was measured
191 using a digital caliper (CD-15PSX; Mitutoyo Corporation ®, Kawasaki-shi,
192 Kanagawa, Japan). The fracture toughness (J/m^2) was determined using the total
193 workload and cross-sectional area. The fracture toughness of each food item was
194 measured more than 7 times, and the average of these measurements was used for
195 analyses. The mechanical tests of food items were performed within 6 hours of
196 collection. The fracture toughness was classified into 6 categories: (1) less than 500
197 J/m^2 , (2) 500–1000 J/m^2 , (3) 1000–1500 J/m^2 , (4) 1500–2000 J/m^2 , (5) 2000–2500
198 J/m^2 , and (6) more than 2500 J/m^2 .

199 Food items for the measurement of fracture toughness were collected from
200 February 5 to 29, 2012. Bark was collected from the same twigs from which the
201 macaques ate bark. The bark was peeled off from the twig with the cambium layer
202 for the analysis. When I was unable to collect the twigs that the macaques fed on, I
203 collected the bark of similar twigs from the same tree. Dormant buds were measured
204 from the boundary between the bud and the twig. Leaves were measured from the
205 middle of the lamina without the midrib, because macaques sometimes did not feed
206 on the midrib. Roots were measured from the boundary between the leaves and roots.

207 Rhizomes were measured at the mid-point between joints. Young twigs were
208 collected from the same tree from which a macaque fed on twigs. Macaques fed on
209 the top part of young twigs. I measured the position of the length 1 cm from the top
210 of young twigs, where macaques often fed. I could not always identify the species
211 name of ferns. The fracture toughness of ferns was based on the average fracture
212 toughness of *Polystichum tripterum*, on which macaques often fed.

213

214 **Relative feeding index**

215 For each mother–infant pair, the difference in time spent feeding on each food
216 item by the mother and its infant was calculated using the following formula
217 [Ichihara, 1990]:

$$218 \quad \text{Relative feeding index of food item X} = \frac{(P_1 - P_2) - 0}{\sqrt{P(1 - P)\left(\frac{1}{n_1} + \frac{1}{n_2}\right)}}$$

219 n_1 = Mother's total number of feeding sample points

220 n_2 = Infant's total number of feeding sample points

221 $n_{1 \text{ food item X}}$ = Mother's number of sample points feeding on food item X

222 $n_{2 \text{ food item X}}$ = Infant's number of sample points feeding on food item X

$$223 \quad P_1 = \frac{n_{1 \text{ food item X}}}{n_1}, P_2 = \frac{n_{2 \text{ food item X}}}{n_2}, P = \frac{n_{1 \text{ food item X}} + n_{2 \text{ food item X}}}{n_1 + n_2}$$

224 A negative number indicates that an infant fed more on a given food item than its
225 mother, whereas a positive number indicates the opposite. To remove the effect of
226 food items on which macaques fed less, the index of the food item where
227 $n_{1 \text{ food item X}} + n_{2 \text{ food item X}}$ was greater than 10 sample points was subject to
228 statistical analysis for each pair.

229

230 **Statistical analysis**

231 To examine the influence of physical properties on the dietary difference between
232 mothers and infants, I used a generalized linear mixed model (GLMM), assuming a
233 normal distribution, with the relative feeding indices as a dependent variable, and 3
234 physical properties (size, processing, and height) as independent variables for each
235 food item. I set the mother–infant pair ID as a random effect. Before using the
236 GLMM, I checked whether the data set for the relative feeding index had a normal
237 distribution using a Kolmogorov–Smirnov test. In addition, I calculated the variance
238 inflation factors (VIF) among 3 factors (size, processing, and height) to check for
239 multicollinearity. Montgomery and Peck [2001] suggest that if the VIF is over 5, the
240 regression coefficients are poorly estimated. The VIF among the 3 factors was low
241 enough for the analyses. Moreover, I added fracture toughness as an independent
242 variable in the GLMM analysis for the measured food items. The normal distribution
243 of the relative feeding indices was checked by the same method presented previously.
244 The VIF among the 4 factors (size, processing, height, and toughness) was low
245 enough for the analyses.

246 All possible combinations of independent factors were examined, and model
247 fitness was assessed by the Akaike Information Criterion (AIC) [Burnham &
248 Anderson, 2002]. I examined only the models that had a ΔAIC (difference from the
249 smallest AIC) of less than 2. To assess the relative likelihood of these models, I
250 calculated the Akaike weight as $\exp(-0.5 \times \Delta\text{AIC score for that model}) / \text{sum of}$
251 $\exp(-0.5 \times \Delta\text{AIC score})$ for all of the models [Burnham & Anderson, 2002]. I
252 presented the coefficient from the maximum-likelihood estimation in the best-fit

model with the smallest AIC. In the physical properties selected for the best-fit model, the statistical difference was determined by the Mann-Whitney test or the Kruskal-Wallis test. For each pair, the dietary differences between the infant and its mother were analyzed using the χ^2 test. Differences with a P value of less than or equal to 0.05 with a two-tailed test were considered significant. I used the software program R 3.0.3 (The R Foundation for Statistical Computing; <http://www.r-project.org/>) for all statistical analyses.

260

261 RESULTS

262 General description of feeding behavior

During the study period, mothers and infants spent $44.8 \pm 6.3\%$ ($N = 4$, range = 40–54%) and $37.9 \pm 4.8\%$ ($N = 4$, range = 32–44%) of time feeding on solid food items in total observation time, respectively. The infant/mother ratio for time spent feeding was 0.86 ± 0.17 ($N = 4$; range = 0.72–1.09). The time spent in contact with the mother's nipple was $21.3 \pm 5.6\%$ ($N = 4$, range = 17–29%) and the time spent carriage by the mother was $0.41 \pm 0.24\%$ ($N = 4$, range = 0.25–0.75%).

For all 4 mother–infant pairs, a dietary difference was present between the mother and its infant in terms of dietary composition of food items that were used in the calculation of relative feeding index (Table I; χ^2 test: pair ID1, $\chi^2 = 193.76$, $P < 0.01$, d.f. = 10; pair ID2, $\chi^2 = 93.76$, $P < 0.01$, d.f. = 12; pair ID3, $\chi^2 = 112.88$, $P < 0.01$, d.f. = 11; pair ID4, $\chi^2 = 133.68$, $P < 0.01$, d.f. = 15). Table I shows the average time spent feeding on each food item by mothers and infants. Among the top 5 food items in terms of the time spent feeding, both mothers and infants contained leaves of Poaceae spp. and acorns of *Q. crispula*. The remaining 3 top food items differed

277 between mothers and infants; infants contained buds of *Sasa kurilensis*, buds of
278 *Zanthoxylum piperitum*, and leaves of *Carex* spp., whereas mothers contained seeds
279 of *P. densiflora*, bark of *Actinidia arguta*, and roots of *Trifolium repens*.

280

281 **Relationship between the relative feeding index and 3 physical properties of** 282 **food items**

283 I examined the relationship between the relative feeding index and 3 physical
284 properties of each food item (size, processing, and height). Fifty-two relative feeding
285 indices ($N_{\text{pair ID1}} = 11$; $N_{\text{pair ID2}} = 13$; $N_{\text{pair ID3}} = 12$; $N_{\text{pair ID4}} = 16$), including 23 different
286 food items, were analyzed (Table I). For mothers, the percentage of time spent
287 feeding on the food items used in this analysis to total feeding time was $79.0 \pm$
288 2.8% ($N = 4$; range = 75–81%), whereas that for infants was $72.3 \pm 6.0\%$ ($N = 4$;
289 range = 69–81%). The data set for the relative feeding index did not differ
290 significantly from a normal distribution (Kolmogorov–Smirnov test, $D = 0.13$, $N =$
291 52 , $P > 0.1$). All 3 properties influenced the difference in time spent feeding by
292 mothers and infants in the best-fit model. Compared to the mothers, infants fed more
293 on food items that could be consumed in 1 bite, that required no processing, and that
294 were located at a lower position (Tables IIa, IIIa and Fig. 1). Food item size and
295 height were selected by the second fit model with a ΔAIC of less than 2, and
296 processing was not selected (Table IIa).

297 The size of the food item significantly affected the difference between mothers and
298 infants (Tables IIIa). Food items that infants could eat with 1 bite mainly included
299 buds (Fig. 1a).

300 Although the need to process food items led to differences in food selection

between infants and mothers, there was no significant difference between food items that did and did not require processing in the relative feeding indices (Tables IIa and IIIa). Food items that required processing contained roots and seeds, and the average relative feeding indices of 2 food items (*Q. crispula* acorns and *P. lobata* seeds) had negative numbers (Fig. 1b). For instance, the average relative feeding index of *Q. crispula* acorns (Table I; Food item No. 2) was -1.04 ± 2.31 ($N = 4$; range = -4.2 – 1.0). Infants did not tend to spend less time feeding on *Q. crispula* acorns, which required the cracking of the shells. In addition, the infants spent more time feeding on *P. lobata* seeds (No. 11), which required the shelling of pods (χ^2 test: pair ID1, $\chi^2 = 21.58$, $P < 0.01$, d.f. = 1).

Finally, the height of the food item significantly affected the difference between mothers and infants (Tables IIIa). All average relative feeding indices of food items that were located at a height of more than 5 m were positive numbers (Fig. 1c), except for *A. arguta* buds (No. 9). Infants spent more time feeding on *A. arguta* buds (χ^2 test: pair ID4, $\chi^2 = 11.75$, $P < 0.01$, d.f. = 1). For the 23 food items (Table I), mothers and infants spent $24.9 \pm 4.1\%$ ($N = 4$; range = 21–31%) and $7.9 \pm 3.3\%$ ($N = 4$; range = 4.8–12%) time, respectively, feeding on food items that were located at a height of more than 5 m in the tree in total feeding time. For all 4 mother–infant pairs, infants spent significantly less time feeding on food items that were located at a height of more than 5 m than their mothers (χ^2 test: pair ID1, $\chi^2 = 34.59$, $P < 0.01$, d.f. = 1; pair ID2, $\chi^2 = 26.83$, $P < 0.01$, d.f. = 1; pair ID3, $\chi^2 = 19.46$, $P < 0.01$, d.f. = 1; pair ID4, $\chi^2 = 21.98$, $P < 0.01$, d.f. = 1).

323

324 **Relationship between the relative feeding index and 4 physical properties of**

325 food items

326 To clarify the influence of fracture toughness on dietary differences between
327 mothers and infants, I examined the relationship between the relative feeding index
328 and 4 physical properties (fracture toughness, size, processing, and height) of the
329 food items. Thirty-nine relative feeding indices were analyzed ($N_{\text{pair ID1}} = 7$; $N_{\text{pair ID2}}$
330 $= 10$; $N_{\text{pair ID3}} = 9$; $N_{\text{pair ID4}} = 13$), including 19 different food items for which
331 macaques were observed to use their incisors in taking the initial bites (Table I). For
332 mothers, the percentage of time spent feeding on the food items used in this analysis
333 to total feeding time was $57.5 \pm 8.1\%$ ($N = 4$; range = 46–65%), whereas that for
334 infants was $50.1 \pm 13.1\%$ ($N = 4$; range = 31–60%). This dataset contained only 1 of
335 4 food items that required processing. The dataset relating to the relative feeding
336 index did not differ significantly from a normal distribution (Kolmogorov–Smirnov
337 test, $D = 0.15$, $N = 39$, $P > 0.1$). In the best-fit model (Tables IIb and IIIb), size,
338 height, and processing affected the difference in the time spent feeding by mothers
339 and infants, and each effect had the same tendency as the above analysis (Tables IIa
340 and IIIa). Fracture toughness was not selected in the best-fit model (Table IIb).
341 However, the second fit model with a ΔAIC of less than 2 contained fracture
342 toughness.

343 Although fracture toughness did not cause a major difference in the selection of
344 food between mothers and infants, all average relative feeding indices of the food
345 items that were tougher than 2000 J/m^2 were positive numbers (Fig. 1d). Among the
346 32 food items for which fracture toughness was measured, all infants spent
347 significantly less time feeding on food items that had a toughness of more than $2,000$
348 J/m^2 (Fig. 2; χ^2 test: pair ID1, $\chi^2 = 5.37$, $P < 0.05$, d.f. = 1; pair ID2, $\chi^2 = 30.87$, $P <$

0.01, d.f. = 1; pair ID3, $\chi^2 = 35.01$, $P < 0.01$, d.f. = 1; pair ID4, $\chi^2 = 34.34$, $P < 0.01$,
d.f. = 1). Food items that were tougher than 2000 J/m² included some bark, *Z.*
piperitum twigs, *S. kurilensis* leaves, and *Miscanthus sinensis* roots.

352

DISCUSSION

The results of this investigation were almost concordant with my hypothesis. In
summary, compared with their mothers, Japanese macaque infants fed relatively
more on food items that are small, that require no processing, or that are located at a
lower position. In addition, infants spent less time feeding on food items with a
toughness greater than 2,000 J/m².

359

Feeding and suckling by infants

Throughout the study period, Japanese macaque infants still spent as much as
21.3% of their time suckling, and the average time spent feeding was 0.86 times that
observed in mothers. This result is almost consistent with the findings of a previous
study. In winter, Japanese macaque infants inhabiting a snow-covered areas, spent
approximately 30% less time feeding than adult females [Nakayama et al., 1999].
Nakayama and others [1999] suggest that the estimated fuel reserves do not meet the
cumulative energy deficit of infants and adult females during winter, and the energy
deficit of infants might be met by consuming milk from their mothers. Thus, infants
need to feed on solid food, in addition to spending more time suckling during winter.

370

Relationship between food fracture toughness and food selection by infants

(Hypothesis 1)

373 Although infants did not feed relatively more frequently on food items that were
374 softer, they spent less time feeding on food items that were tougher than 2000 J/m²
375 compared to their mothers. These quantitative results are consistent with those of
376 previous studies of long-tailed macaques that were conducted using qualitative
377 methods [van Schaik & van Noordwijk, 1986]. The ability to process food is known
378 to be linked with the morphology of different species or age–sex class [McGraw et
379 al., 2011; Norconk & Veres, 2011; Vogel et al., 2008; Vogel et al., 2014; Wright et al.,
380 2008]. Deciduous dentition is complete at around 7.5 months of age in Japanese
381 macaques, and the age of eruption of the permanent teeth is around 18 months
382 [Iwamoto et al., 1984; Iwamoto, 1987]. Therefore, the infants observed during the
383 present study period had completed deciduous dentition, but did not have permanent
384 teeth. According to a craniofacial biomechanical study [Dechow & Carlson, 2005],
385 when juveniles reach complete deciduous dentition, but occlusion of the first
386 permanent incisors has yet to occur, the mean forces of juvenile incisors are only half
387 those of adults. Thus, differences in the fracture toughness ranges of food items
388 selected by mothers and infants might be the result of differences in their
389 morphological features.

390

391 **Relationship between food size and food selection by infants (Hypothesis 2)**

392 Infants fed relatively more frequently on food items that could be eaten in 1 bite
393 compared to their mothers. Bite size (amount of food eaten with a single bite)
394 constrains the feeding rate [Nakagawa, 2008, Shipley et al., 1994]. The bite size of
395 large food items increases with body size. Consequently, mothers feed more on larger
396 food items than their infants. In addition, small animals are considered to need more

time to process large food items than large animals [Nakagawa, 2008; Wrangham et al., 1993]. For instance, the feeding rate on buds was greater than that on bark in 0 year olds and 1 year olds whereas there was no difference in the feeding rate of these 2 food parts by older Japanese macaque classes [Nakayama et al., 1999]. Infants may increase their feeding efficiency by selecting smaller food items.

402

Relationship between food processing and food selection by infants (Hypothesis 3)

Infants tended to feed relatively more frequently on food items requiring no processing than their mothers. However, processing was not selected by the second fit model, with no significant difference between food items that did and did not require processing in the relative feeding index.

Food items that require processing included roots, which that need to be dug out, and pinecones, the scales of which need to be peeled off. It might be difficult for infants to feed on food items that require high arm strength and/or bite force for processing. Juvenile chacma baboons (*Papio hamadryas ursinus*) are significantly less efficient foragers than adult baboons primarily for difficult-to-extract resources [Johnson & Bock, 2004]. In addition, adult Japanese macaques carry and wash grass roots, while juveniles have rarely been observed to dig roots [Nakamichi et al., 1998]. Nakamichi and others [1998] discussed the possibility that it may be difficult for juveniles to dig out roots. In brown capuchins (*Cebus apella*), infants do not have adult levels of proficiency at ripping bamboo stalks to extract larvae, with infants devoting more time than adults and juveniles to foraging on other food items (shoots, pith, and non-embedded insects) that are easy to obtain [Gunst et al., 2008]. It has

421 been suggested that foraging efficiency and time allocation are linked to parallel
422 changes in body size and dentition [Gunst et al., 2008]. The results of this study are
423 generally consistent with these preceding studies.

424 Yet, the average relative feeding indices of 2 food items (*Q. crispula* acorns and *P.*
425 *lobata* seeds) had negative numbers. For both mothers and infants, *Q. crispula* acorns
426 (No. 2) were among the top 5 food items, and infants tended not to spend less time
427 on this food item than their mothers. In addition, infants fed more frequently on *P.*
428 *lobata* (No. 11) seeds, which required the pods to be shelled. Out of the food items
429 available in winter, acorns and seeds have higher energy or protein content compared
430 to other food items (e.g., bark, leaves, and buds) [Nakagawa, 1989; Nakagawa, 1997].
431 In particular, primate infants have a higher requirement for protein compared to
432 adults [Oftedal et al., 1991]. If infants are able to access energy- or protein-rich food
433 items that need processing, infants may feed at the same time as their mothers or may
434 feed on these items more frequently than their mothers. However, to confirm these
435 hypotheses, I must conduct a more detailed examination of on the processing of food
436 items, and the relationship between the physical properties and nutritional content of
437 food items.

438

439 **Relationship between food height and food selection by infants (Hypothesis 4)**

440 Infants fed relatively more frequently on food items that were located at low
441 positions than their mothers. Since infants were only carried for 0.41% of the time,
442 infants had to climb trees by themselves to feed on solid foods in winter. In addition,
443 Japanese macaque infants over 4 months of age tend to decrease their proximity to
444 their mothers when feeding [Ueno, 2005]. Infant rhesus macaques also use the

445 ground and low or horizontal arboreal settings more than adults and juveniles [Wells
446 & Turnquist, 2001]. Wells and Turnquist [2001] noted that ontogenetic changes in
447 morphology are closely paralleled by changes in locomotor behavior.

448 In studies on the growth of the locomotor apparatus of Japanese macaques, the
449 most notable ontogenetic changes in the musculoskeletal system occur during the
450 first year of life. There is a shift from the newborn pattern of the propulsive mass of
451 the hind limb in yearlings [Hamada, 1982; Hamada, 1983] and the locomotor
452 apparatus acquires approximately the pattern of adults when monkeys are around 2
453 years of age [Ishida, 1972]. As infants grow up, their upper limb muscles develop for
454 forward propulsion, including pulling up the body when climbing, in addition to
455 improving the control of the movement of segments at the shoulder, elbow, and wrist
456 joints. In contrast, the necessity for finger extension and flexion with power
457 decreases [Hamada, 1982; Hamada, 1983; Ishida, 1972]. Thus, it may be more
458 difficult for infants to move in trees because their locomotor apparatus is shifted
459 toward quadrupedalism.

460 Compared to their mothers, infants fed more frequently on food items located less
461 than 5 m above the ground. Infants may avoid the risk of falling from a high position
462 by selecting the lower positions as feeding sites. However, compared to their mothers,
463 infants fed more on *A. arguta* buds (No. 9), which are positioned more than 5 m high.
464 *A. arguta* is a woody liana that twines around itself and forms a stable foothold. Thus,
465 *A. arguta* may be more accessible to infants than other food items that are located at
466 a height of over 5 m.

467 Incidentally, it has been reported that the time allocated to arboreal travelling was
468 longer for juveniles than adults [Hanya, 2003; Watanuki & Nakayama, 1993].

469 Arboreal feeding is advantageous for juveniles when eating buds and fruits on
470 terminal twigs, because increased body mass may restrict immediate access to
471 terminal twig areas [Hanya, 2003; Watanuki & Nakayama, 1993]. However, the
472 results of this study indicate that smaller body mass may not be an advantage for
473 infants when moving to terminal twigs at heights of over 5 m. In rhesus macaques,
474 juveniles (12–18 months of age) spent more time in the arboreal environment than
475 adults and infants [Wells & Turnquist, 2001]. This difference in the behavior pattern
476 of juveniles and adults may be explained by the inverse relationship between body
477 size and joint mobility, because there is a rapid decline in passive joint mobility until
478 an age of approximately 15 months [DeRousseau et al., 1983]. In addition, juveniles
479 are able to move more freely than infants, which do not have fully developed
480 locomotor apparatus [Dunbar & Badam, 1998]. In comparison with mothers and
481 juveniles, infants probably spend more time feeding on food items at lower positions
482 in the tree after decreasing maternal carriage.

483

484 The results of the current study were almost concordant with my hypothesis that
485 infants feed more frequently on food items that are easily obtainable than their
486 mothers, because of the lower ability of infants to bite, handle, and access food items.
487 These preferences, which are associated with the physical abilities of infants, save
488 the costs of time and energy required for feeding [Janson et al., 1993; Johnson &
489 Bock, 2004], and help infants to avoid falling from high trees. During the weaning
490 period, infants may acquire information about available foods or foraging skills from
491 their mothers [Tarnaud & Yamagiwa, 2008], while they spend more time feeding on
492 easily obtainable foods, termed “weaning foods.”

493 **ACKNOWLEDGMENTS**

494 I thank the Shimokita Forest Office for the permission to conduct research on
495 the Shimokita Peninsula. I am grateful to Prof. Juich Yamagiwa, Dr. Naofumi
496 Nakagawa, and Dr. Eiji Inoue for their support and guidance during this research. I
497 am indebted to Mr. Haruki Kinoshita and Ms. Kiku Kinoshita for use of a house
498 during my field research and to Mr. Shiro Matsuoka, Ms. Atsuko Matsuoka, Ms.
499 Naka Nakashima, and Ms. Kouko Hanayama for their help with my research life and
500 safety checks. I also thank Ms. Yuri Nakayama and members of the Japanese
501 Macaques' Field Station in Shimokita Peninsula for their help and support in the
502 field. I am grateful to Prof. Hiroshi Ihobe, Dr. Daisuke Shimizu, and Dr. Daisuke
503 Koyabu for their support and guidance with the rheometer. I thank Mr. Shunkichi
504 Hanamura, Dr. Yuji Iwata, Dr. Wataru Yano, Dr. Yoshihiro Nakashima, Dr. Elizabeth
505 Nakajima, two reviewers and the editor of this journal, and members of the
506 Laboratory of Human Evolution Studies, Kyoto University, for their advice and
507 support. Finally, I gratefully acknowledge the A87 troop, my study troop, which
508 endured my persistent observations. This study was financed in part by the
509 Cooperative Research Program of the Primate Research Institute of Kyoto University,
510 the grants to Excellent Graduate schools program of MEXT, Japan, grants for Global
511 COE Program (A06) to Kyoto University from MEXT, Japan, a Grant-in-Aid for
512 Scientific Research (B, No. 23370099) from JSPS to N. Nakagawa and a
513 Grant-in-Aid for JSPS Fellows (No. 241479) to H. Taniguchi.

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656 toughness of ingested leaves and feeding behavior among four Colobinae in
657 Vietnam. *International Journal of Primatology* 29:1455-1466.

TABLE I. Percentage of time spent feeding by infants and mothers, the relative feeding index, and the physical properties of food items. Percentage of time spent feeding on food items was averaged for 4 focal infants and 4 focal mothers. The food items were arranged according to the time that infants spent feeding on them. The relative feeding index of the food item was averaged among mother–infant pairs that were used in the calculation of the relative feeding index.

Food item No.	Food item species name	Food part	Percentage of time spent feeding				Relative feeding index		Physical properties of the food item			
			Infant	※	Mother	※	※※ (Pair ID name)		Size	Processing	Height	※※※ Toughness
1	Poaceae spp.	Leaf	<u>23.1</u>	1	<u>24.7</u>	1	0.43	4 (All)	2	1	1	2
2	<i>Quercus crispula</i>	Seed (Acorn)	<u>12.0</u>	2	<u>9.1</u>	3	-1.04	4 (All)	2	2	1	-
3	<i>Sasa kurilensis</i>	Bud	<u>8.2</u>	3	1.9		-3.69	4 (All)	1	1	1	-
4	<i>Zanthoxylum piperitum</i>	Bud	<u>8.2</u>	3	2.3		-3.47	4 (All)	1	1	2	2
5	<i>Carex</i> spp.	Leaf	<u>5.1</u>	5	3.6		-1.05	3 (ID1, 3, 4)	2	1	1	3
6	<i>Fraxinus lanuginosa</i>	Bud	2.8		1.9		-0.97	4 (All)	1	1	3	3
7	<i>Viburnum dilatatum</i>	Bud	2.3		1.2		-1.40	2 (ID2, 3)	1	1	2	3
8	<i>Celastrus orbiculatus</i>	Bud	2.0		2.1		1.52	2 (ID2, 4)	1	1	4	2
9	<i>Actinidia arguta</i>	Bud	2.0		0.1		-3.51	1 (ID4)	1	1	4	2
10	Fern	Leaf	1.7		0.7		-1.38	1 (ID2)	2	1	1	2
11	<i>Pueraria lobata</i>	Seed	1.6		0		-4.76	1 (ID1)	1	2	3	-
12	<i>Actinidia arguta</i>	Bark	1.6		<u>7.5</u>	4	4.37	3 (ID2, 3, 4)	2	1	4	5
13	<i>Actinidia polygama</i>	Bud	1.5		0.4		-2.42	1 (ID4)	1	1	3	1
14	<i>Trifolium repens</i>	Root (Rhizome)	1.3		<u>5.5</u>	5	3.22	3 (ID1, 3, 4)	2	2	1	4
15	<i>Euonymus oxyphyllus</i>	Bark	1.1		1.2		-0.21	2 (ID2, 4)	2	1	3	4
16	<i>Evodiopanax innovans</i>	Bud	1.0		1.2		-1.67	1 (ID1)	1	1	3	2
17	<i>Pinus densiflora</i>	Seed (Pinecone)	0.7		<u>10.4</u>	2	5.10	4 (All)	1	2	5	-

18	<i>Hydrangea petiolaris</i>	Bud	0.7	1.9	1.08	2 (ID1, 3)	1	1	4	2
19	<i>Fraxinus lanuginosa</i>	Bark	0.7	2.6	2.31	2 (ID2, 4)	2	1	3	6
20	<i>Zanthoxylum ailanthoides</i>	Bark	0.7	1.5	3.21	1 (ID3)	2	1	4	3
21	<i>Euonymus oxyphyllus</i>	Bud	0.7	1.5	3.28	1 (ID4)	1	1	3	2
22	<i>Actinidia polygama</i>	Bark	0.7	1.5	3.83	1 (ID2)	2	1	3	5
23	<i>Celastrus orbiculatus</i>	Bark	0.2	1.4	2.84	1 (ID4)	2	1	4	6

- ※ Ranking in the time spent feeding for the top five underlined food items.
- ※※ Number of mother–infant pairs used in the calculation of the relative feeding index
- ※※※ “-” indicates that I did not measure the fracture toughness of the food item

TABLE II. Summary of the generalized linear mixed models for the effect of physical properties on the relative feeding index.

Adopted factor	AIC	ΔAIC	Akaike weight (%)
(a) 52 relative feeding indices involving 23 different food items			
Size +, Height +, Processing +	249.5	0	72
Size +, Height +	251.4	1.88	28
(b) 39 relative feeding indices involving 19 different food items, including toughness as the independent variable			
Size +, Height +, Processing +	185.3	0	59
Size +, Height +, Processing +, Toughness +	187.3	1.97	22

ΔAIC is the difference with the smallest Akaike information criterion (AIC). Akaike weight: $\exp(-0.5 \times \Delta AIC) / \sum \exp(-0.5 \times \Delta AIC)$

[Burnham & Anderson, 2002].

“−” denotes a negative correlation between the relative feeding index and the physical property, while “+” denotes a positive correlation between them. A positive number for the relative feeding index indicates that infants fed less than their mothers did on a food item.

TABLE III. Best-fit generalized linear mixed model for the effect of physical properties on the relative feeding index.

Adopted factors	Partial regression coefficient	SE	Statistical test	Test statistic	<i>P</i>
(a) 52 relative feeding indices involving 23 different food items					
Size	3.25	0.71	Mann-Whitney test ($N_1 = 27$; $N_2 = 25$)	$z = 2.04$	< 0.05
Processing	1.58	0.79	Mann-Whitney test ($N_1 = 40$; $N_2 = 12$)	$z = 1.67$	0.09
Height	1.57	0.26	Kruskal-Wallis test ($N_1 = 19$; $N_2 = 6$; $N_3 = 13$; $N_4 = 10$; $N_5 = 4$)	$\chi^2 = 16.7$ d.f. = 4	< 0.01
(b) 39 relative feeding indices involving 19 different food items, including toughness as the independent variable					
Size	3.21	0.77	Mann-Whitney test ($N_1 = 18$; $N_2 = 21$)	$z = 2.62$	< 0.01
Processing	3.78	1.47	Mann-Whitney test ($N_1 = 36$; $N_2 = 3$)	$z = 1.42$	0.15
Height	1.38	0.35	Kruskal-Wallis test ($N_1 = 11$; $N_2 = 6$; $N_3 = 12$; $N_4 = 10$)	$\chi^2 = 9.2$ d.f. = 3	< 0.05

The coefficient is from maximum-likelihood estimation. SE is the standard error of the coefficient.

Figure Legends

Fig. 1. Relationship between the relative feeding index and physical properties.

A negative number indicates that infants fed more than their mothers did on a food item, while a positive number indicates that infants fed less than their mothers did on a food item. The means of each food item in Table I are plotted. The number on the right side of the plot represents the food item number in Table I.

(a) Size: Food item size was classified into 2 categories: (1) small: eaten by infants in 1 bite, and (2) large: eaten by infants in two or more bites.

(b) Processing: The need for processing food items was divided into 2 categories: (1) no processing required before a food item was taken into the mouth, and (2) processing required before a food item was taken into the mouth.

(c) Height: The average height of food items where feeding was observed was classified into 5 categories: (1) 0 m (i.e., on the ground), (2) 0–2 m, (3) 2–5 m, (4) 5–10 m, and (5) more than 10 m.

(d) Fracture Toughness: The average fracture toughness of the food items was classified into 6 categories: (1) less than 500 J/m², (2) 500–1000 J/m², (3) 1000–1500 J/m², (4) 1500–2000 J/m², (5) 2000–2500 J/m², and (6) more than 2500 J/m²

Fig. 2. Relationship between fracture toughness and the percentage of time spent feeding.

The fracture toughness of 32 food items that the macaques were observed to use their incisors to make the initial bites was measured.

Fig. 1. Relationship between the relative feeding index and physical properties.

Fig.2. Relationship between fracture toughness and the percentage of time spent feeding.