1   Opportunistic feeding strategy in wild immature chimpanzees: Implications for children as active

2   foragers in human evolution

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11

14   **Abstract**

15   Modern human (*Homo sapiens*) children are generally considered to be dependent on older individuals for foods,

16   even after weaning. However, recent studies of hunter-gatherer societies have reported that children can also

17   acquire food by themselves, although the degree of self-provisioning by children differs among groups and is

18   considered a facultative adaptation. To investigate the dependence of children on older individuals for food and

19   the importance of self-provisioning in early hominins, I examined feeding behavior in wild, immature

20   chimpanzees (*Pan troglodytes schweinfurthii*). I studied 19 mother-offspring chimpanzee pairs in the Mahale

21   Mountains National Park, Tanzania for approximately 22 months. Feeding behavior and interactions between

22   mothers and their offspring were recorded. The results supported these three predictions: (1) immature

23   chimpanzees need to feed more frequently than mothers because of increased basal metabolic rate and immature

24   stomach capacity; (2) mothers provide effective opportunities to feed on high-quality food items which are

25   similar to those of the mothers'; and (3) when feeding independently of their mothers, immature chimpanzees

26   consume highly accessibile food including non-adult foods nearby mothers to avoid getting lost and physical

27   burden as with self-provisioning of human children in hunter gatherer societies. During non-simultaneous

28   feeding bouts, immature individuals frequently consumed pith and wood. They may be valuable food items for

29   immature individuals during their growth stage because they can be consumed year round and contain relatively

30   higher crude ash and protein amounts, which may enable immature chimpanzees to manage the confines of their

31   immature bodies, preventing them from matching adult feeding rhythms. This opportunistic feeding strategy is

32   similar to self-provisioning by human children in hunter-gatherer societies. These results suggested that early

33   hominin children performed self-provisioning based on opportunistic feeding strategies, and contributed to their

34   food consumption by snacking in accordance with their metabolic needs and physical confines.

Introduction

Many life history models suggest that one of the unique features of human (*Homo sapiens*) life-history is childhood, during which time they must be provided with specially prepared foods and require intensive care by older individuals, even after weaning (Bogin and Smith, 1996; Bogin, 1997, 2009; Humphrey, 2010). However, recent field studies of self-provisioning (i.e., foraging without adult supervision; Crittenden, 2009) by children (i.e., immature individuals aged 2 to 12 years including the developmental stages of childhood and juvenility; Crittenden, 2016) in hunter-gatherer societies indicated that they were not simply passive recipients but were actively engaged in acquiring foods shortly after weaning (Konner, 2016; but see Kaplan et al., 2000). When adults were away on a foraging trip, the remaining children in hunter-gatherer societies went hunting, gathered food, and consumed it in addition to the foods provided when the adults returned (Hadza: Jones et al., 1997; Meriam: Bird and Bird, 2000, 2005; Nukakau: Swadling and Chowning, 1981). For example, a 3-year-old child in Hadza society met 30% percent of their required caloric intake through self-provisioning (Crittenden et al., 2013).

Children in hunter-gatherer societies reportedly use different feeding strategies from adults, to accommodate their physical development (Hadza: Crittenden et al., 2013; Meriam: Bird and Bird, 2000, 2002; Mikea: Tucker and Young, 2005). As children are weaker and less skilled than adults, they tend to target foods that are easy to acquire and process (e.g., Hadza: Crittenden 2009). Moreover, because children have reduced motor skills and strength, their self-provisioning is conducted near the base camp (Hadza: Jones, 1993; Mikea: Tucker and Young, 2005; Nukakau: Swadling and Chowning, 1981), in places with a low risk of them getting

54 lost (see review by Konner, 2016). They also target food items with high accessibility, some of which are low

55 quality and not usually consumed by adults (Hadza: Jones, 1993; Meriam: Bird and Bird 2000, 2002, 2005;

56 Mikea: Tucker and Young, 2005; Nukakau: Swadling and Chowning, 1981). Therefore, it can be said that self-

57 provisioning by children in hunter-gatherer societies is based on an opportunistic feeding strategy based on the

58 viewpoint that they reduced the costs of moving (i.e., getting lost and physical burden) and target food items

59 less selectively than adults do.

60 Self-provisioning by children in hunter-gatherer societies suggests that they consume foods other than

61 meals provided by adults, and they feed more frequently than adults (Hadza: Crittenden and Zes, 2015, Jones

62 et al., 1997; Meriam: Bird and Bird, 2000; Nukakau: Swadling and Chowning, 1981). Previous studies of human

63 children in industrial societies showed that the timing of feeding, rather than the amount of foods, is most

64 important before and after weaning. Increased basal metabolic rate means that children require more energy per

65 body weight than adults do (Holiday, 1986). However, children's stomach capacity limits the amount of food

66 that can be consumed in a single feeding (Dewey, 2013). Therefore, although adults usually eat substantial meals

67 several times a day (Mattson et al., 2014), it is difficult for children to match the timings of meals with those of

68 adults (Chiva, 1997). Although there is considerable variation between societies and over time, in modern

69 societies children usually have snacks between meals (Jacquier et al., 2017). A study of Japanese macaques

70 (*Macaca fuscata*) also suggested that smaller stomach capacity prompted a larger number of feedings in

71 immature individuals than in adults (Mori, 1995). Self-provisioning by immature individuals may function as

72 snacking (i.e., feeding between meals/feedings shared with adults).

73   Although there is no doubt that food items shared with adults are important for children in hunter-

74   gatherer societies, understanding self-provisioning by children contributes to our understanding of childhood

75   and provides insight into models of human evolution (Crittenden et al., 2013). For example, the risk of getting

76   lost, existence of predators, and scarcer resources close to camp areas contribute to lower self-provisioning by

77   children (Jones et al., 1997; Kramer, 2005; Konner 2016). Konner (2016) reviewed the differences among

78   hunter-gatherer societies in the contribution of self-provisioning by children (!Kung, Hadza, Efe, Aka, Ache,

79   Bofi, Marutu, and Toba) and suggested that it is a facultative adaptation. To examine whether self-provisioning

80   was conducted by children of early hominins, it is useful to investigate self-provisioning by immature

81   individuals (i.e., including the developmental stages of infancy and juvenility) in non-human primate species

82   that are genetically close to humans. This study aimed to evaluate the dependence of children on older

83   individuals for food and the importance of self-provisioning in early hominins against implicit assumptions that

84   children depend heavily on food provisioning from older individuals in human evolution.

85   In theories of childhood, non-human primates are generally regarded as independent foragers after

86   weaning in contrast to human children (Bogin, 2009). Although food transfer from mothers to their offspring

87   has been reported in many non-human primates (Jaeggi and van Schaik, 2011), constant and direct food

88   provisioning for nutrition has rarely been reported in non-human primates (except callitrichids; see Brown et

89   al., 2004). Additionally, transferred foods are usually the leftovers from maternal chewing and/or only a small

90   amount, which may not provide much nutrition (e.g., chimpanzees, *Pan troglodytes*: Nishida and Turner, 1996,

91   Bornean orangutans, *Pongo pygmaeus*; Jaeggi et al., 2008). Therefore, transferred foods may not contribute

92 much to caloric intake for immature non-human individuals. On the other hand, even after weaning, immature

93 individuals of non-human primates do not forage completely independently from mothers or older individuals.

94 Some previous studies have suggested that simultaneous feeding with older individuals, i.e., feeding at the same

95 time as older individuals belonging to the same group, is important for immature individuals who have not yet

96 learned which plants are edible and where to find foods within their home range (Rapaport and Brown, 2008).

97 Traveling with older individuals and simultaneous feeding with older individuals (mainly mothers) may provide

98 appropriate opportunities for nutrition intake and to learn about food items or the feeding rhythms of adults

99 (eastern gorilla, *Gorilla beringei*: Watts, 1985; Bornean orangutans, *Pongo pygmaeus*: Jaeggi et al., 2010;

100 Mayotte brown lemurs: *Eulemur fulvus*; Tarnaud, 2008; and Japanese macaques, *Macaca fuscata*: Ueno, 2005).

101 In short, simultaneous feeding with older individuals is assumed to be dependent on older individuals, and non-

102 simultaneous feeding is assumed to be independent of older individuals and comparable to self-provisioning

103 (i.e., foraging by themselves without adult supervision) by human children in hunter-gatherer societies.

104 However, few previous studies of non-human primates have focused on non-simultaneous feeding with adults

105 because their main topics are nutrition intake and learning in food transfer and simultaneous feeding with adults

106 (but see Taniguchi, 2016 for Japanese macaques). In chimpanzees—one of the two species genetically closest

107 to humans—there is no detailed study on feeding strategies of immature chimpanzees from the viewpoint of

108 simultaneity with older individuals.

109   Chimpanzees generally travel in fission–fusion groups to search for fruits that vary seasonally

110 (Wrangham, 1975; Itoh and Nakamura, 2015b). Immature individuals under 8 years of age, almost always travel

111 with their mothers (Hayaki, 1988) and sometimes with just the two of them; the mother and offspring watch

112 each other's position and behavior and the immature chimpanzees scream when they become separated from

113 their mothers. Therefore, the behavior and range of immature individuals are restricted by the position and range

114 of their mothers (Goodall, 1986; Matsumoto and Hayaki, 2015). Previous studies at several sites reported that

115 there were two peaks of feeding bouts for adult chimpanzees in a day (e.g., Newton-Fisher, 1999). Although

116 adult chimpanzees do not always only feed twice daily, they feed for a long time, which can generally be divided

117 into two phases.

118 In this study, I describe the feeding behaviors of immature chimpanzees according to their simultaneity

119 with mothers. Specifically, I aim to test three predictions: (1) immature chimpanzees need to feed more

120 frequently than mothers (i.e., feeding non-simultaneously with mothers) because of their increased basal

121 metabolic rate and immature stomach capacity; (2) mothers facilitate access to the same food items that they

122 eat, i.e., mothers provide effective opportunities to feed on high quality food items; and (3) when feeding

123 independently of their mothers, immature chimpanzees feed on foods with high accessibility including non-

124 adult foods, these foods are related to their restricted foraging area and limited motor skills and strength, as with

125 self-provisioning by human children in hunter gatherer societies. Finally, the role of mothers and opportunistic

126 feeding strategies by immature individuals in human evolution are examined by comparing self-provisioning

127 by immature individuals in humans and chimpanzees.

128

Methods

129

130   Permission to study wild chimpanzees in Mahale Mountains National Park was granted by the Tanzanian

131   Commission for Science and Technology, the Tanzanian Wildlife Research Institute, Tanzania National Parks,

132   and the Mahale-Gombe Wildlife Research Centre (permit numbers 2010-215-NA-2009-26, 2011-166-ER-2006-

133   26, 2012-409-ER-2009-26, and 2015-165-ER-2009-26). The subjects were chimpanzees (*Pan troglodytes*

134   *schweinfurthii*) of the M group in the Mahale Mountains National Park in Tanzania (6°15′ S, 29°55′ E;

135   Nakamura and Itoh, 2015). Individuals of the M group have almost all been identified since 1980 (Hiraiwa-

136   Hasegawa et al., 1984). The core area of chimpanzee habitat was the west side of the Mahale mountains at 780

137   to 1300 m asl (Nakamura et al., 2013), which consisted of a mosaic of lowland forest patches comprising

138   *Erythrophleum* forest and *Xylopia−Pycnanthus* forest, colonizing forest dominated by species such as *Senna*

139   *spectabilis* and *Croton sylvaticus*, Miombo (*Brachystegia bussei*) woodland, woodland comprising

140   *Combretum* spp., and swamp (Itoh and Nakamura, 2015b). Plant species in the area, including those not

141   consumed by chimpanzees, are well known (Nishida and Uehara, 1981, 1983; Itoh, 2004, 2015b; Turner,

142   2006; Itoh and Muramatsu, 2015; Itoh and Nakamura, 2015b; Itoh et al., 2015). In general, the dry season

143   begins in early October and the wet season in mid-May (Itoh, 2015a).

144   At six months of age, chimpanzees are at least partially dependent on non-milk foods (Hiraiwa-

145   Hasegawa, 1990b). The weaning age (i.e., the border between infancy and juvenility) of chimpanzees is usually

146   around 4−5 years, which is defined as the time of re-conception by the mother and cessation of nipple contact

147   (Goodall, 1986; Lee et al., 1991; Emery Thompson et al., 2007; Kramer, 2010; Emery Thompson, 2013).

148   However, recent studies suggest that 3-year-old chimpanzees drastically reduce nutritional dependence on

149   breastfeeding based on stable isotope analysis (Bădescu et al., 2017), eruption of the first molar (Smith et al.,

150   2013), greater survivorship of orphans (Nakamura and Hosaka, 2015), and developmental changes in feeding

151   behavior (Matsumoto, 2017). Therefore, in this study it was assumed that the nutritional weaning age of

152   chimpanzees was at 3 years. It is noteworthy that after 3 years of age, chimpanzees can process and feed on

153   almost all food items in the food repertoire of their natal group by themselves, for example, fruits covered by a

154   hard shell and piths of terrestrial herbaceous vegetation (THV) covered by hard outer layer (Matsumoto, 2017;

155   Corp and Byrne, 2002). Therefore, I define individuals younger than 3 years of age as 'lactational individuals'

156   and those older than 3 years of age as 'weaned individuals.'

157   The study period was from January to September 2011, from October 2012 to July 2013, and from

158   June to August 2015. I observed 20 immature individuals aged 0.5−6 years using the focal animal sampling

159   method (Altmann, 1974). I usually followed and observed the immature individual that I found first on each

160   day. If I found multiple immature individuals, I selected the immature individual for which I had fewer data. I

161   did not change the target until I lost sight of them. The total following time was 537 h, 40 min. For the analysis,

162   I excluded the time when I could not tell if immature individuals processed something by mouth or not for more

163   than 30 s. One severely disabled infant was excluded from the analysis (see Matsumoto et al., 2016). Therefore,

164   the total analysis time was 416 h, 11 min. I calculated the age of immature individuals by subtracting the month

165   of observation from the month of their first observation. Detailed information about individuals and analysis

166   times is shown in Table 1.

167 I recorded processing by mouth, including instances where food was put on the lips or into the mouth,

168 biting, licking, and chewing. I also recorded the start and end times and the target of mouth processing. If the

169 target was a plant, I recorded the plant part that was targeted (namely fruit, leaf, petiole, flower, seed, resin, pith,

170 wood, bark, or other). When chimpanzees ate wood and pith, they often put bark, cambium, and outer layers

171 into their mouth, and it was difficult to distinguish between them. Therefore, I defined the stem as the plant part

172 that included at least wood and/or pith. For example, stems included wood of woody vine and pith of THV. I

173 recorded plant species mainly in the local language and identified them according to available lists of plant

174 species (Nishida and Uehara, 1981, 1983; Itoh, 2015b; Noriko Itoh, unpublished data).

175 When the mother engaged in feeding, a research assistant told me the target food item. If the mother

176 fed on plants, I recorded the plant species and parts. I recorded food items of adult chimpanzees using ad libitum

177 sampling. I defined 'maternal foods,' 'adult foods,' and 'non-adult foods' as food items selected by mothers of

178 focal offspring-mother pairs, those selected by adults other than mothers by ad libitum sampling during the

179 research period, and those which mothers and other adults did not select, respectively.

180 To record processing by mouth, I defined chewing as feeding that excluded play feeding (Watts, 1985),

181 which does not provide nutritional value, for example, just putting food into the mouth without swallowing.

182 Additionally, I recorded drinking water and licking decaying wood, rock, and sap as feeding. These behaviors

183 are usually observed among adult chimpanzees (Itoh and Nakamura, 2015a; Itoh et al., 2015).

184 End time of feeding was determined as the end of chewing and/or licking. If immature individuals

185 started to play or travel continuously, the end time was determined as the start of play or travel. I defined 'feeding

186 time' as continuous if immature individuals performed some processing by mouth of the same food item again

187 within 30 s. I also recorded the feeding behavior of other individual(s) within my sight and their food items at

188 the start of focal subjects' feeding.

189 I defined feeding time with mother as the feeding time during which feeding by the mother was

190 recorded and/or the immature individuals fed on foods transferred from the mother (Nishida and Turner, 1996)

191 regardless of the distance between mother and offspring. Though this definition does not include a distance

192 between mother and offspring, immature chimpanzees always travel with mothers and rarely go out of mothers'

193 sight unless they are lost. See Supplementary Online Material (SOM) Figure S1 for the close maternal distance

194 at the beginning of feeding of immature individuals.

195 If the interval between the end of feeding time and the beginning of the next feeding on the same food

196 item was less than 10 min, I defined them both as the same feeding bout. The 10 min threshold was determined

197 from the minimum value of density curves of all intervals between feeding times within the same day. I defined

198 a feeding bout with and without the mother as a feeding bout including feeding time with the mother and not,

199 respectively.

200

201 *Encounter frequency of the plant species*

202 The ubiquity of food items should contribute to accessibility for immature chimpanzees who must travel

203 with mothers rather than to be locally distributed. Therefore, to evaluate the accessibility of food items, I

204 conducted a census of plants and defined the encounter frequency of each plant species. I established a rectangle

205   (5 × 2.5 m, the 5 m side was parallel to the transect) at a distance of 250 m on both sides of a transect, which

206   was established in the core area of the chimpanzee M-group range (about 20 km^2; Nakamura et al., 2013;

207   Nakamura and Itoh, 2015; Itoh and Nakamura, 2015b). I treated the two points on both sides of the transect as

208   one quadrat (5 × 5 m) and established 80 quadrats (2000 m^2 in total). In each quadrat, I recorded all plant species

209   that were more than 50 cm high. I calculated the encounter frequency of a plant species as the number of quadrats

210   in which the plant species was confirmed per total number of quadrats (80). For example, if plant A was

211   confirmed in 40 quadrats, the encounter frequency was 40/80 = 0.5. As I did not count the number of plants,

212   encounter frequency does not exactly reflect the abundance or the density, but the ubiquity of plant species in

213   the core ranging area of M-group chimpanzees. Immature individuals could find plant species of higher

214   encounter frequency with comparative ease wherever they were located with their mothers in the core ranging

215   area of the M-group chimpanzees.

216

217   *Statistical analysis*

218   I used chi-square tests to investigate differences in the rates of feeding on each plant part and for each

219   food items divided by commonality with adult or maternal food, between 'lactational or weaned individuals'

220   and 'feeding with or without mother.' If there was a significant difference, I used residual analysis of the pair to

221   examine which plant part and food category differed significantly. The *p*-values were Bonferroni corrected and

222   were considered statistically significant when $p < 0.05$.

223   I used generalized additive mixed models (GAMMs) to examine the influence of developmental

224   changes (age in months) on the number of feeding bouts in a day, as GAMMs fit smooth functions to non-linear

225   data and use random effects for repeated measures of the same subject. I used the gamm4 package (Wood et al.,

226   2015) in R 3.4.1 (R Core Team, 2017) and constructed GAMMs with a binomial error distribution and a logit

227   link function. I used generalized linear mixed models (GLMMs) to examine the influence of developmental

228   stage (lactational or weaned individuals for categorical data) on encounter frequency of the species of food item

229   consumed by immature individuals. I used the glmer function in the lme4 package (Bates et al., 2014) in R 3.4.1

230   and constructed GLMMs with a binomial error distribution and a log link function. I checked multi-collinearity

231   between explanatory variables using the DAAG package (Maindonald and Braun, 2015). The variance inflation

232   factors (VIF) were low among variables of each model (VIF <3).

233

234   *Model A: number of feeding bouts without mothers*

235   I divided analysis time by individuals and by days. I analyzed the data from the same individual collected

236   on the same day as one data point. I analyzed the data from different individuals collected on the same day as

237   independent data points. The total number of data points was 121 (a total of 'No. of observation days' in Table

238   1 minus number of observation days when feeding by the focal chimpanzee was not observed). I modeled the

239   role of snacking in immature individuals using the number of feeding bouts without mothers/total feeding bouts

240   as the response variable, and age in months (fit smooth function) as the explanatory variable, with individual

241   ID as a random effect. I used Akaike's information criterion (AIC) for model selection (Burnham and Anderson,

242   2002), and selected the model with the smallest AIC value and examined the model(s) that had a ΔAIC (AIC

243 value difference from the best model) of <2 (Burnham and Anderson, 2004).

244

245 *Model B: encounter frequency*

246   I modeled the opportunistic feeding strategy of immature chimpanzees using the encounter frequency

247 of food items as the response variable, and (1) developmental stages (lactational or weaned individuals), (2)

248 simultaneity with mother (feeding bout with or without mothers), interaction between (1) and (2), and (3)

249 commonality with maternal foods (maternal foods or not) as explanatory variables, and individual ID as a

250 random effect. Likelihood ratio tests were used to evaluate the linear model and independent variables affecting

251 categorization.

252

253 **Results**

254   The total number of feeding bouts was 1146. I analyzed 996 bouts that were observed from the beginning to

255 the end of feeding (e.g., I excluded any feeding bouts that started before I began observing the focal individual).

256 Number of feeding bouts and number of feeding bouts without mothers per individuals are shown in Table 1.

257 Figure 1 shows the rate of feeding bouts without mothers. The results of the model selection showed that age

258 did not significantly affect the number of feeding bouts without the mother (Table 2); the rate of feeding bouts

259 without mothers did not vary significantly in individuals of 0.5−6 years old. The estimated rate of the selected

260 model was 38.8% feeding bouts without mothers (61.2% feeding bouts with mothers). Additionally, immature

261 individuals (lactational and weaned) often started feeding alone when feeding without mothers. For lactational

262   individuals, 87% of feeding bouts without mothers began alone, 9% began with other group member(s)

263   excluding adult(s), and 4% began with other group member(s) including adult(s). For weaned individuals, 79%

264   of feeding bouts without mothers began alone, 12% began with other group member(s) excluding adult(s), and

265   8% began with other group member(s) including adult(s). Although immature individuals sometimes started

266   feeding slightly before mothers after arriving at a food patch, mothers or other individuals rarely came and

267   started feeding with immature individuals after they started feeding alone.

268   Figure 2 shows the encounter frequency of the species of food items in each feeding bout. In the

269   analysis of encounter frequency, I used feeding bouts (873) on identified plant species (i.e., I excluded 23, 47,

270   and 53 feeding bouts on unidentified plant foods, insects, and other non-plant foods, respectively). Feeding

271   bouts were classified by developmental stage (lactational or weaned individuals) and by simultaneity with the

272   mother's feeding. In model B, all the explanatory variables in the full model were significant (see Table 3 for

273   detailed parameters), as the effects of developmental changes (lactational individuals to weaned individuals;

274   deviance = 68.5, p < 0.001), simultaneity with maternal feeding (deviance = 317.8, p < 0.001), and maternal

275   foods (deviance = 355.4, p < 0.001) had significant negative effects on encounter frequency. These results

276   suggest that both lactational and weaned individuals tended to feed on items of lower encounter frequency when

277   feeding with mothers, and items with higher encounter frequency when feeding without mothers, and that non-

278   maternal foods tended to be of higher encounter frequency. The interaction also had a significant effect

279   (deviance = 32.0, p < 0.001), suggesting that the difference in encounter frequency in feeding with and without

280   mothers tented to be smaller in weaned individuals than in lactational individuals. Namely, weaned individuals

281   tend to feed on food items of lower encounter frequency (i.e., more selectively) in feeding bouts without mothers

282   than lactational individuals.

283   Figure 3 shows the rate of feeding bouts by food type. Developmental stage (lactational or weaned

284   individuals) did not significantly affect the rate of feeding bouts by food type in either simultaneous or non-

285   simultaneous feeding with the mother (χ^2 = 6.93, df = 4, p > 0.1; and χ^2 = 11.79, df = 4, p > 0.1, respectively).

286   Simultaneity with maternal feeding significantly affected the rate of feeding on different food types in both

287   lactational and weaned individuals (χ^2 = 49.36, df = 4, p <0.001; and χ^2 = 17.95, df = 4, p < 0.01, respectively).

288   As a result of the residual analyses, stems were consumed at significantly higher rates in feeding bouts without

289   mothers than those with mothers in both lactational and weaned individuals (adjusted residual = $\pm$6.52, p

290   <0.001; and adjusted residual = $\pm$4.00, p <0.001, respectively). Additionally, fruits were consumed at a

291   significantly higher rate in feeding bouts with mothers than those without mothers in both lactational and

292   weaned individuals (adjusted residual = $\pm$4.28, p <0.001; and adjusted residual = $\pm$2.68, p <0.05, respectively).

293   Leaves, insects, and other food items did not differ significantly in lactational individuals (adjusted residual =

294    $\pm$1.96, p >0.1; adjusted residual = $\pm$2.03, p >0.1; and adjusted residual = $\pm$0.40, p >0.5, respectively) and in

295   weaned individuals (adjusted residual = $\pm$1.13, p >0.5; adjusted residual = $\pm$0.67, p >0.5; and adjusted residual

296   = $\pm$0.43, p >0.5, respectively).

297   Figure 4 shows the rate of feeding bouts by food commonality with maternal and adult foods. Expected

298   frequency of category 'unidentified' was quite low in the chi-square tests. Therefore, I combined the

299   'unidentified' and 'immature only' data to conduct chi-square tests and residual analysis because mothers and

300   other adults were not observed to feed on the unidentified plant food items. Simultaneity with maternal feeding

301   significantly affected the rate of feeding bouts of food commonality in both lactational and weaned individuals

302   ($\chi 2$ = 89.56, df = 3, p <0.001; and $\chi 2$ = 38.14, df = 3, p < 0.01, respectively). Lactational individuals fed more

303   frequently on maternal foods and adult foods during feeding with mothers than without mothers (adjusted

304   residual = ± 9.34, p <0.001; and adjusted residual = ± 3.08, p <0.001, respectively). Additionally, they fed

305   more frequently on non-adult foods during feeding without mothers than with mothers (adjusted residual = $\pm$

306   6.01, p <0.001). Weaned individuals fed more frequently on maternal foods during feeding with mothers than

307   without mothers (adjusted residual = ± 5.62, p <0.001). Additionally, they fed more frequently on non-adult

308   foods during feeding without mothers than with mothers (adjusted residual = ± 6.78, p <0.001). Feeding on

309   adult foods did not change significantly (adjusted residual = ± 1.70, p >0.1). It is noteworthy that if mothers

310   started feeding on a food item, immature individuals usually showed interest in it and fed on the same items as

311   their mothers were eating in both lactational and weaned individuals.

312   As a complementary analysis, developmental changes (lactational or weaned individuals) significantly

313   affected the rate of feeding bouts by food commonality in both simultaneous and non-simultaneous with mothers

314   ($\chi 2$ = 12.54, df =2, p <0.001; and $\chi 2$ = 24.40, df = 2, p < 0.001, respectively). Weaned individuals fed more

315   times on maternal foods and less on non-adult foods in both simultaneous feeding with mothers (adjusted

316   residual = ±3.35, p <0.01; and adjusted residual = ±3.42, p <0.01, respectively) and non-simultaneous feeding

317   with mothers (adjusted residual = ±4.93, p < 0.001; and adjusted residual = ±4.18, p < 0.001, respectively) than

318   lactational individuals did. Adult food did not change significantly in simultaneous and non-simultaneous

319   feeding with mothers (adjusted residual = ±0.68, $p > 0.5$; and adjusted residual = ±1.48, $p > 0.1$, respectively).

320

321   **Discussion**

322   The results support predictions (1), (2), and (3). Immature individuals fed more frequently on maternal foods

323   during feeding bouts with mothers than without mothers. This result suggests that feeding with mothers

324   contributes to opportunities for both lactational and weaned individuals to feed on maternal foods. The results

325   of model A suggest that wild immature chimpanzees under 6 years of age spent 38.8% of observed feeding

326   bouts, feeding without mothers. Additionally, the results of model B suggest that immature individuals fed on

327   more accessible food items (i.e., of high encounter frequency) during feeding bouts without mothers, than during

328   bouts with mothers. The food items eaten during feeding bouts without mothers were often those that mothers

329   or other adults would not select. These results suggest that wild immature chimpanzees fed on 'snacks' less

330   selectively in addition to feeding bouts with mothers. Therefore, immature individuals showed an opportunistic

331   feeding feeding strategy during feeding bouts without mothers, which differed from adult feeding strategies

332   because of lower selectivity and moving costs (i.e., getting lost and physical burden). The immature individuals'

333   opportunistic strategy may be because their positions and movements are restricted by having to travel close to

334   their mothers, as well as their more limited motor skills and strength.

335   Adult chimpanzees of the M group in Mahale selectively feed on some food items from those available

336   in the environment while traveling in fission–fusion patterns (Nishida, 1991; Turner, 2006). Although the food

337   repertoire of adults includes 407 items from 224 plant species (Itoh et al., 2015), fewer food items are utilized

338   throughout the year (see review in Itoh and Nakamura, 2015a). Adults may have selective feeding strategies in

339   which they select appropriate food items of relatively low accessibility and high nutrient content (mainly fruits)

340   according to seasonal variation and environmental changes. Approximately 60% of feeding bouts of immature

341   individuals occurred simultaneously with maternal feeding and they spent more than 80% of feeding bouts

342   feeding on maternal foods. Additionally, if mothers started feeding on a food item, immature individuals usually

343   showed interest in it and started eating it. Therefore, simultaneous feeding with mothers can provide

344   opportunities for immature individuals to consume nutritional foods and learn appropriate food items (Rapaport

345   and Brown, 2008), as suggested by previous studies on other primate species (e.g., Japanese macaques; Ueno,

346   2005). Moreover, a similar tendency was reported in Hadza society, in which children following an adult

347   foraging trip were able to obtain foods of high quality and distant from the base camp (e.g., berries) (Hawks et

348   al., 1995).

349   Conversely, immature chimpanzees under 6 years of age fed without mothers (non-simultaneously

350   with) at a rate of 38.8% of total feeding bouts. These results concur with previous studies of humans that suggest

351   that children with increased basal metabolic rate and smaller stomach capacity need to feed frequently in

352   addition to meals (i.e., snacking; Chiva, 1997). For immature chimpanzees in fission–fusion societies [see

353   Hanamura (2015) for a review] traveling with a group member does not always mean 'traveling with mother'

354   (Matsumoto and Hayaki, 2015), which differs from other primate species in other cohesive grouping patterns

355   (e.g., *Gorilla gorilla*; Yamagiwa,1999). Immature individuals that are parted from their mothers are at risk of

356   predation (Nakazawa et al., 2013). The fission–fusion social structure for immature chimpanzees means that

357   they cannot be far from their mothers. Therefore, feeding on food items of high encounter frequency (high

358   accessibility) is effective during feeding bouts without mothers, who may feed in several phases daily and who

359   may not always rest near a feeding patch.

360   It is also effective for immature chimpanzees to feed on food items that mothers do not feed on. Food

361   items that adults rarely feed on have been reported at several chimpanzee study sites (Mahale: Hiraiwa-

362   Hasegawa, 1990b; Gombe: Bray et al., 2018). This study quantitatively revealed for the first time that immature

363   individuals fed more frequently on non-adult foods during feeding bouts without their mothers than when they

364   were feeding with mothers. As mentioned previously, simultaneous feeding with their mothers is effective as

365   immature individuals can access maternal foods that are likely to be of high quality. Conversely, when mothers

366   do not feed, mothers and offspring are not always near a feeding patch. The results of model B suggest that food

367   items that mothers do not eat tend to be food items of high encounter frequency. This result supports the

368   hypothesis that immature individuals may feed on food items of high encounter frequency, including non-adult

369   foods, as available alternatives. This opportunistic feeding strategy of immature chimpanzees is similar to that

370   of human children in hunter-gatherer societies (see Table 4).

371   The rate of consumption of plant parts during simultaneous feeding bouts was in the order of fruits >

372   leaves > stems. This order was not different from the maternal feeding rate in Mahale (Hiraiwa-Hasegawa,

373   1990b). Conversely, the rate of plant parts consumed during non-simultaneous feeding bouts was higher for

374   stems and lower for leaves and fruits than during simultaneous feeding. Plant parts, such as leaves and stems,

375   are usually available for many months (Itoh and Nakamura, 2015a). Additionally, it is difficult for immature

376 individuals to digest foods containing a large amount of fiber and secondary compounds, especially leaves, due

377 to the immaturity of their digestive organs and small body mass (Hiraiwa-Hasegawa, 1990a; Agetsuma, 2001;

378 Nowell and Fletcher, 2008). However, they can chew them and spit out the fibrous leftovers (Nishida, 1976).

379 Additionally, stems tend to include higher amounts of crude ash per weight unit, although the number of

380 analyzed plant species was only 5 (Nishida, 2012). It is possible that immature individuals obtain minerals from

381 stems for growth. Moreover, pith of THV is regarded as a fallback food for adult chimpanzees (Wrangham et

382 al., 1991) because it can be consumed even when fruits are scarce. Immature individuals need to feed without

383 mothers because of their increased basal metabolic rate and immature stomach capacity, which do not change

384 seasonally. Pith should be suitable for feeding bouts without mothers because it can be consumed throughout

385 the year in Mahale (Itoh et al., 2015) and is found relatively easily throughout the core area of chimpanzee

386 habitat. The same tendency was reported in humans, as children in Hadza society frequently targeted foods that

387 were available throughout the year (e.g., baobab; Crittenden, 2009). Moreover, stems (as defined in this study)

388 included the pith of THV, which is a rich source of protein (Nishida, 2012; Rogers et al., 1990; but see

389 Wrangham et al., 1991). Therefore, the pith (stem) of THV may be a valuable food item for immature individuals

390 during their growth stage.

391   Interactions in model B suggest that weaned individuals fed more frequently on food items of low

392 encounter frequency than lactational individuals. Additionally, weaned individuals spent more time feeding on

393 maternal and adult food items than lactational individuals. The distance between mothers and offspring increases

394 as immature individuals develop and grow (Matsumoto and Hayaki, 2015), which may enable immature

395   individuals to select food items commonly eaten by mothers during feeding bouts without them. For example,

396   I observed that immature individuals discovered a maternal food fruit and moved a considerable distance to feed

397   on it when traveling with their mothers, thereafter returning to their mothers. Weaned individuals fed on food

398   items more selectively, similarly to adults, as they always traveled with their mothers in fission–fusion patterns.

399   However, it should be pointed out that developmental changes investigated by chi-square tests and residual

400   analysis did not control for individuals. Additional data are needed to reach conclusion about developmental

401   changes taking individual variance into account.

402   Previous studies on primates, including humans, assumed that feeding without adults and feeding on

403   non-adult foods were not important for development, and that they were a result of a lack of experience and

404   learning (e.g., Tarnaud, 2008). However, this study suggests that feeding without adults and feeding on non-

405   adult foods may be beneficial for physically immature individuals (with small digestive organs and immature

406   motor skills and strength) that are not able to match the feeding rhythms of adults or travel too far from their

407   mothers. These results support the suggestion that human children are not simply inferior to adults in experience

408   and knowledge, but are active foragers (Bird and Bird, 2002).

409   Immature Bornean orangutans (*Pongo pygmaeus*) always travel together with their mothers in fission–

410   fusion society, like chimpanzees. Lactational individuals of Bornean orangutans rarely feed at different patches

411   and/or non-simultaneously with mothers (fewer than 10% of all feeding bouts). However, feeding bouts at

412   different patches from mothers and/or non-simultaneously with mothers increased to more than 60% after

413   weaning (Jaeggi et al., 2008, 2010). Notably, even before nutritional independence, lactational individuals of

414   chimpanzees often fed non-simultaneously with mothers, contrary to Bornean orangutans (Jaeggi et al., 2010).

415   One possible reason for this difference is that Bornean orangutans are more arboreal than chimpanzees.

416   Immature orangutans under 5 years old cannot move between trees freely (Mendonça et al., 2016). Moreover,

417   this study showed that stems, including pith of THV, are important during feeding bouts without mothers in

418   chimpanzees. It is possible that Bornean orangutans rarely feed at different patches and/or non-simultaneously

419   with mothers because they do not have opportunities to feed on terrestrial plants but weaned Bornean orangutans

420   are physically able to feed on food items selectively without mothers. However, there are differences in the

421   definitions and methods between these studies. There may be a different degree of dependence on milk between

422   these species; no comparable data have been reported, however. Additionally, I cannot exclude differing

423   definitions of feeding as a possible explanation: I distinguished feeding from play-feeding according to mouth

424   processing in this study but no detailed definition on feeding was presented by Jaeggi et al. (2010).

425   Feeding bouts without mothers usually began when immature individuals were alone. This differs

426   from self-provisioning by human children, in which a small party without adults was formed (e.g., Hadza:

427   Crittenden et al., 2013). Although the two are not directly comparable, the tendency for human children to travel

428   to self-provision with other children or juveniles/adolescents may be fundamentally associated with the

429   psychological development of cooperation and reciprocity in humans (Olson and Spelke, 2008; Kato-Shimizu

430   et al., 2013). However, immature chimpanzees did feed with other individual(s) in a few feeding bouts without

431   mothers. Zamma et al. (2011) reported that a 9-year-old adolescent shared non-adult foods with a 2-year-old

432   infant. More research on feeding by other group members is needed for a better understanding of feeding

433   strategies of immature individuals.

434   In the Mahale Mountains National Park, environmental resources should be relatively richer than in

435   other chimpanzee habitats, such as dry forests. Therefore, more studies of self-provisioning by immature

436   individuals in other habitats are needed to compare different chimpanzee groups and establish whether feeding

437   without mothers is common and important among chimpanzees in general, or varies according to environmental

438   resources, similarly to facultative adaptation in human societies (Konner, 2016). Nevertheless, this study

439   provides the first confirmation that immature chimpanzees consume highly accessible food items, including

440   non-adult foods, via opportunistic feeding. This snacking behavior may resolve issues caused by the immaturity

441   of their digestive organs (which prevent them from matching adult feeding rhythms), the social structure of

442   chimpanzees (having to travel with mothers), and immature motor skills and strength that restrict the area of

443   activity of immature chimpanzees. Immature chimpanzees are dependent on simultaneous feeding with mothers

444   even after weaning (see also Nakamura et al., 2014), but are also active foragers according to their physical and

445   social restrictions. These traits are similar to those of human children in some hunter-gatherer societies (Table

446   4), which strongly supports the suggestion by Crittenden et al. (2013) that immature individuals, including

447   children and juveniles, are not solely dependent on foods provided by adults but are themselves active

448   foragers—a hypothesis that has largely been ignored in models of human evolution. Namely, this study suggests

449   that self-provisioning was conducted by children of early hominins based on opportunistic feeding strategies

450   and contributes to their food consumption, in the role of snacking corresponding with their metabolic need and

451   their physical limitations.

References

Agetsuma, N., 2001. Relation between age–sex classes and dietary selection of wild Japanese monkeys.

Ecological Research 16, 759-763.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227-267.

Bădescu, I., Katzenberg, M.A., Watts, D.P., Sellen, D.W., 2017. A novel fecal stable isotope approach to

determine the timing of age-related feeding transitions in wild infant chimpanzees. American Journal of

472   Physical Anthropology 162, 285-299.

473 Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G.,

474   Green, P., Bolker, M.B., 2014. Linear Mixed-Effects Models using 'Eigen' and S4. R package version 1.1-

475   17. http://CRAN.R-project.org/package=lme4.

476 Bird, D.W., Bird, R.B., 2000. The ethnoarchaeology of juvenile foragers: shellfishing strategies among Meriam

477   children. Journal of Anthropological Archaeology 19, 461-476.

478 Bird, D.W., Bird, R.B., 2002. Children on the reef. Human Nature 13, 269-297.

479 Bird, D.W., Bird, R.B., 2005. Martu children's hunting strategies in the Western Desert, Australia. In: Hewlett,

480   B., Lamb, M. (Eds.), Hunter-Gatherer Childhoods. Aldine, New York, pp. 129-146.

481 Bogin, B., 1997. Evolutionary hypotheses for human childhood. American Journal of Physical Anthropology

482   40, 63-89.

483 Bogin, B., 2009. Childhood, adolescence, and longevity: a multilevel model of the evolution of reserve capacity

484   in human life history. American Journal of Human Biology 21, 567-577.

485 Bogin, B., Smith, B.H., 1996. Evolution of the human life cycle. American Journal of Human Biology 8, 703-

486   716.

487 Bray, J., Emery Thompson, M., Muller, M.N., Wrangham, R.W., Machanda, Z.P., 2018. The development of

488   feeding behavior in wild chimpanzees (*Pan troglodytes schweinfurthii*). American Journal of Physical

489   Anthropology 165, 34-46.

490 Brown, G.R., Almond, R.E.A., van Bergen, Y., 2004. Begging, stealing, and offering: food transfer in nonhuman

491   primates. Advances in the Study of Behavior 34, 265-295.

492   Burnham, K.P., Anderson, D.R., 2002. Information and likelihood theory: a basis for model selection and

493   inference. In: Burnham, K.P., Anderson, D.R. (Eds.), Model Selection and Multimodel Inference. Springer,

494   New York, pp. 49-97.

495   Burnham, K.P., Anderson, D.R., 2004. Multimodel inference: understanding AIC and BIC in model selection.

496   Sociological Methods & Research 33, 261-304.

497   Chiva, M., 1997. Cultural aspects of meals and meal frequency. British Journal of Nutrition 77, S21-S28.

498   Corp, N., Byrne, R.W., 2002. Leaf processing by wild chimpanzees: Physically defended leaves reveal complex

499   manual skills. Ethology 108, 673-696.

500   Crittenden, A.N., 2009. Allomaternal care and juvenile foraging among the Hadza: Implications for the

501   evolution of cooperative breeding in humans. Ph.D. Dissertation, University of California San Diego.

502   Crittenden, A.N., 2016. Children's foraging and play among the Hadza: the evolutionary significance of "work

503   play". In: Meehan, C.L., Crittenden, A.N. (Eds.), Childhood: Origins, Evolution, and Implications.

504   University of New Mexico Press, Albuquerque, pp. 155-171.

505   Crittenden, A.N., Conklin-Brittain, N.L., Zes, D.A., Schoeninger, M.J., Marlowe, F.W., 2013. Juvenile foraging

506   among the Hadza: implications for human life history. Evolution and Human Behavior 34, 299-304.

507   Crittenden, A.N., Zes, D.A., 2015. Food sharing among Hadza hunter-gatherer children. PLoS One 10,

508   e0131996.

509   Dewey, K.G., 2013. The challenge of meeting nutrient needs of infants and young children during the period of

complementary feeding: an evolutionary perspective. The Journal of Nutrition 143, 2050-2054.

Emery Thompson, M., 2013. Reproductive ecology of female chimpanzees. American Journal of Primatology 75, 222-237.

Emery Thompson, M., Jones, J.H., Pusey, A.E., Brewer-Marsden, S., Goodall, J., Marsden, D., Matsuzawa, T., Nishida, T., Reynolds, V., Sugiyama, Y., Wrangham, R.W., 2007. Aging and fertility patterns in wild chimpanzees provide insights into the evolution of menopause. Current Biology 17, 2150-2156.

Goodall, J., 1986. The chimpanzees of Gombe: Patterns of Behavior. Belknap Press of Harvard University Press, Boston.

Hanamura, S., 2015. Fission–fusion grouping. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 106-118.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., 1995. Hadza children's foraging: juvenile dependency, social arrangements, and mobility among hunter-gatherers. Current Anthropology 36, 688-700.

Hayaki, H., 1988. Association partners of young chimpanzees in the Mahale Mountains National Park, Tanzania. Primates 29, 147-161.

Hiraiwa-Hasegawa, M., 1990a. Maternal investment before weaning. In: Nishida, T. (Ed.), The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies. Tokyo University Press, Tokyo, pp. 257-266.

Hiraiwa-Hasegawa, M., 1990b. A note on the ontogeny of feeding. In: Nishida, T. (Ed.), The Chimpanzees of the Mahale Mountains: Sexual and Life History Strategies. Tokyo University Press, Tokyo, pp. 277-283.

Hiraiwa-Hasegawa, M., Hasegawa, T., Nishida, T., 1984. Demographic study of a large-sized unit-group of

529   chimpanzees in the Mahale Mountains, Tanzania: A preliminary report. Primates 25, 401-413.

530   Holliday, M.A., 1986. Body composition and energy needs during growth, In: Falkner, F., Tanner, J.M. (Eds.),

531   Postnatal Growth Neurobiology. Springer US, Boston, pp. 101-117.

532   Humphrey, L.T., 2010. Weaning behaviour in human evolution. Seminars in Cell & Developmental Biology 21,

533   453-461.

534   Itoh, N., 2004. Plant phenology and chimpanzee fission–fusion grouping system in Mahale Mountains National

535   Park. Ph.D. Dissertation, Kyoto University, Kyoto.

536   Itoh, N., 2015a. Climate and climatological trends in the Kasoje forest. In: Nakamura, M., Hosaka, K., Itoh, N.,

537   Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge,

538   pp. 143-149.

539   Itoh, N., 2015b. Floral list. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees:

540   50 Years of Research. Cambridge University Press, Cambridge, pp. 717–739.

541   Itoh, N., Muramatsu, D., 2015. Patterns and trends in fruiting phenology: some important implications for

542   chimpanzee diet. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years

543   of Research. Cambridge University Press, Cambridge, pp. 174-194.

544   Itoh, N., Nakamura, M., 2015a. Diet and feeding behavior. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K.

545   (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 227-245.

546   Itoh, N., Nakamura, M., 2015b. Mahale flora: its historical background and long-term changes. In: Nakamura,

547   M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge

548	University Press, Cambridge, pp. 150-173.

549	Itoh, N., Zamma, K., Matsumoto, T., Nishie, H., Nakamura, M., 2015. Dietary list. In: Nakamura, M., Hosaka,

550	K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press,

551	Cambridge, pp. 717–739.

552	Jacquier, E.F., Gatrell, A., Bingley, A., 2017. "We don't snack": Attitudes and perceptions about eating in-

553	between meals amongst caregivers of young children. Appetite 108, 483-490.

554	Jaeggi, A.V., Dunkel, L.P., van Noordwijk, M.A., Wich, S.A., Sura, A.A.L., van Schaik, C.P., 2010. Social

555	learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. American

556	Journal of Primatology 72, 62-71.

557	Jaeggi, A.V., van Noordwijk, M.A., van Schaik, C.P., 2008. Begging for information: mother-offspring food

558	sharing among wild Bornean orangutans. American Journal of Primatology 70, 533-541.

559	Jaeggi, A.V., van Schaik, C.P., 2011. The evolution of food sharing in primates. Behavioral Ecology and

560	Sociobiology 65, 2125.

561	Jones, N.B., 1993. The lives of hunter-gatherer children: effects of parental behavior and parental reproductive

562	strategy. In: Michael E.P., Lynn A.F. (Eds.), Juvenile primates: life history, development and behavior.

563	University of Chicago Press, Chicago, IL, pp. 309-326.

564	Jones, N.G.B., Hawkes, K., O'Connell, J.F., 1997. Why do Hadza children forage? In: Segal, N.L., Weisfeld,

565	G.E.R., Weisfeld, C.C. (Eds.), Uniting Psychology and Biology: Integrative Perspectives on Human

566	Development. American Psychological Association, Washington, DC, pp. 279-313.

567   Kaplan, H., Hill, K., Lancaster, J., Hurtado, A.M., 2000. A theory of human life history evolution: diet,

568   intelligence, and longevity. Evolutionary Anthropology 9, 156-185.

569   Kato-Shimizu, M., Onishi, K., Kanazawa, T., Hinobayashi, T., 2013. Preschool children's behavioral tendency

570   toward social indirect reciprocity. PLoS One 8, e70915.

571   Konner, M., 2016. Hunter-gatherer infancy and childhood in the context of human evolution. In: Meehan, C.L.,

572   Crittenden, A.N. (Eds.), Childhood: Origins, Evolution, and Implications. University of New Mexico Press,

573   Albuquerque, pp. 123-154.

574   Kramer, K.L., 2005. Children's help and the pace of reproduction: cooperative breeding in humans. Evolutionary

575   Anthropology 14, 224-237.

576   Kramer, K.L., 2010. Cooperative breeding and its significance to the demographic success of humans. Annual

577   Review of Anthropology 39, 417-436.

578   Lee, P.C., Majluf, P., Gordon, I.J., 1991. Growth, weaning and maternal investment from a comparative

579   perspective. Journal of Zoology 225, 99-114.

580   Maindonald, J.H., Braun, W.J., 2015. Data Analysis and Graphics Data and Functions. R package version 1.22.

581   http://CRAN.R-project.org/package=DAAG.

582   Matsumoto, T., 2017. Developmental changes in feeding behaviors of infant chimpanzees at Mahale, Tanzania:

583   Implications for nutritional independence long before cessation of nipple contact. American Journal of

584   Physical Anthropology 163, 356-366.

585   Matsumoto, T., Hayaki, H., 2015. Development and growth: with special reference to mother–infant

586   relationships. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of

587   Research. Cambridge University Press, Cambridge, pp. 313–325.

588   Matsumoto, T., Itoh, N., Inoue, S., Nakamura, M., 2016. An observation of a severely disabled infant

589   chimpanzee in the wild and her interactions with her mother. Primates 57, 3-7.

590   Mattson, M.P., Allison, D.B., Fontana, L., Harvie, M., Longo, V.D., Malaisse, W.J., Mosley, M., Notterpek, L.,

591   Ravussin, E., Scheer, F.A., Seyfried, T.N., Varady, K.A., Panda, S., 2014. Meal frequency and timing in

592   health and disease. Proceedings of the National Academy of Sciences USA 111, 16647-16653.

593   Mendonça, R.S., Takeshita, R.S., Kanamori, T., Kuze, N., Hayashi, M., Kinoshita, K., Bernard, H., Matsuzawa,

594   T., 2016. Behavioral and physiological changes in a juvenile Bornean orangutan after a wildlife rescue.

595   Global Ecology and Conservation 8, 116-122.

596   Mori, A., 1995. Rank and age related feeding strategy observed through field experiments in the Koshima group

597   of Japanese macaques. Primates 36, 11-26.

598   Nakamura, M., Corp, N., Fujimoto, M., Fujita, S., Hanamura, S., Hayaki, H., Hosaka, K., Huffman, M.A., Inaba,

599   A., Inoue, E., Itoh, N., Kutsukake, N., Kiyono-Fuse, M., Kooriyama, T., Marchant, L.F., Matsumoto-Oda,

600   A., Matsusaka, T., McGrew, W.C., Mitani, J.C., Nishie, H., Norikoshi, K., Sakamaki, T., Shimada, M., Turner,

601   L.A., Wakibara, J.V., Zamma, K., 2013. Ranging behavior of Mahale chimpanzees: a 16 year study. Primates

602   54, 171-182.

603   Nakamura, M., Hayaki, H., Hosaka, K., Itoh, N., Zamma, K., 2014. Orphaned male chimpanzees die young

604   even after weaning. American Journal of Physical Anthropology 153, 139-143.

605   Nakamura, M., Hosaka, K., 2015. Orphans and allomothering. In: Nakamura, M., Hosaka, K., Itoh, N., Zamma,

606   K. (Eds.), Mahale Chimpanzees: 50 Years of Research. Cambridge University Press, Cambridge, pp. 421-

607   432.

608   Nakamura, M., Itoh, N., 2015. Overview of the field site: Mahale Mountains and their surroundings. In:

609   Nakamura, M., Hosaka, K., Itoh, N., Zamma, K. (Eds.), Mahale Chimpanzees: 50 Years of Research.

610   Cambridge University Press, Cambridge, pp. 7-20.

611   Nakazawa, N., Hanamura, S., Inoue, E., Nakatsukasa, M., Nakamura, M., 2013. A leopard ate a chimpanzee:

612   first evidence from East Africa. Journal of Human Evolution 65, 334-337.

613   Newton-Fisher, N.E., 1999. The diet of chimpanzees in the Budongo Forest Reserve, Uganda. African Journal

614   of Ecology 37, 344-354.

615   Nishida, T., 1976. The bark-eating habits in primates, with special reference to their status in the diet of wild

616   chimpanzees. Folia Primatologica 25, 277-287.

617   Nishida, T., 1991. Primate gastronomy: Cultural food preferences in nonhuman primates and origins of cuisine.

618   In: Friedman, M.I., Tordoff, M.G., Kare, M.R. (Eds.), Chemical Senses. Marcel Dekker, New York, pp. 195-

619   209.

620   Nishida, T., 2012. Chimpanzees of the Lakeshore: Natural History and Culture at Mahale. Cambridge University

621   Press, Cambridge.

622   Nishida, T., Turner, L.A., 1996. Food transfer between mother and infant chimpanzees of the Mahale Mountains

623   National Park, Tanzania. International Journal of Primatology 17, 947-968.

624 Nishida, T., Uehara, S., 1981. Kitongwe name of plants: a preliminary listing. African Study Monographs 1,

625   109-131.

626 Nishida, T., Uehara, S., 1983. Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*): Long-term record

627   from the Mahale Mountains, Tanzania. African Study Monographs 3, 109-130.

628 Nowell, A.A., Fletcher, A.W., 2008. The development of feeding behaviour in wild western lowland gorillas

629   (*Gorilla gorilla gorilla*). Behaviour 145, 171-193.

630 Olson, K.R., Spelke, E.S., 2008. Foundations of cooperation in young children. Cognition 108, 222-231.

631 Rapaport, L.G., Brown, G.R., 2008. Social influences on foraging behavior in young nonhuman primates:

632   learning what, where, and how to eat. Evolutionary Anthropology 17, 189-201.

633 Rogers, E.M., Maisels, F., Williamson, E.A., Fernandez, M., Tutin, C.E.G., 1990. Gorilla diet in the Lopé

634   Reserve, Gabon. Oecologia 84, 326-339.

635 Smith, T.M., Machanda, Z., Bernard, A.B., Donovan, R.M., Papakyrikos, A.M., Muller, M.N., Wrangham, R.,

636   2013. First molar eruption, weaning, and life history in living wild chimpanzees. Proceedings of the National

637   Academy of Sciences USA 110, 2787-2791.

638 Swadling, P., Chowning, A., 1981. Shellfish gathering at Nukalau Island, West New Britain Province, Papua

639   New Guinea. Journal de la Société des Océanistes 37, 159-167.

640 Taniguchi, H., 2016. Effects of the habitat differences on feeding behavior and co-feeding relationships in infant

641   Japanese macaques (*Macaca fuscata*) during weaning period. Ph.D. Dissertation, Kyoto University.

642 Tarnaud, L., 2008. Mother-young feeding synchrony and early food selection differences in *Eulemur fulvus*.

643   International Journal of Primatology 29, 1687-1695.

644   Tucker, B., Young, A.G., 2005. Growing up Mikea: Children's time allocation and tuber foraging in

645   southwestern Madagascar. In: Hewlett, B.S., Lamb, M.E. (Eds.), Hunter-Gatherer Childhoods: Evolutionary,

646   Developmental, and Cultural Perspectives. Transaction Publishers, New Jersey, pp. 147-171.

647   Turner, L.A., 2006. Vegetation and chimpanzee ranging in the Mahale Mountains National Park, Tanzania.

648   Memoirs of the Faculty of Science, Kyoto University 18, 45-82.

649   Ueno, A., 2005. Development of co-feeding behavior in young wild Japanese macaques (*Macaca fuscata*).

650   Infant Behavior and Development 28, 481-491.

651   Watts, D.P., 1985. Observations on the ontogeny of feeding behavior in mountain gorillas (*Gorilla gorilla*

652   *beringei*). American Journal of Primatology 8, 1-10.

653   Wood, S., Scheipl, F., Wood, M.S., 2015. Generalized additive mixed models using mgcv and lme4. R package

654   version 0.2-3. http://CRAN.R-project.org/package=gamm4.

655   Wrangham, R.W., 1975. Behavioural ecology of chimpanzees in Gombe National Park, Tanzania. Ph.D.

656   Dissertation, University of Cambridge.

657   Wrangham, R.W., Conklin, N.I., Chapman, C.A., Hunt, K.D., Milton, K., Rogers, E., Whiten, A., Barton, R.A.,

658   1991. The significance of fibrous foods for Kibale Forest Chimpanzees [and Discussion]. Philosophical

659   Transactions of the Royal Society of London B 334, 171-178.

660   Yamagiwa, J., 1999. Socioecological factors influencing population structure of gorillas and chimpanzees.

661   Primates 40, 87-104.

662   Zamma, K., Nakashima, M., Romadhani, A., 2011. Mahale chimpanzees start to eat oil palm. Pan Africa News

663   18, 6-8.

664 **Figure legends**

665 **Figure 1.** Feeding bouts of infant chimpanzees without mothers. Data points represent observations from one

666 individual per day. The horizontal line represents the best fit of model A (38.8 %).

667

668 **Figure 2.** Encounter frequency of food items during feeding bouts of lactational and weaned individuals, with

669 or without mothers. Each data point represents one feeding bout. The numbers above each box plot represent

670 the number of feeding bouts.

671

672 **Figure 3.** Food types consumed by immature chimpanzees. Numbers above the bars represent the total number

673 of feeding bouts.

674

675 **Figure 4.** Feeding bouts of immature chimpanzees separated by food commonality (maternal foods, adult foods,

676 and non-adult foods). Numbers above the bars represent the number of feeding bouts.

677

678 **Figure S1.** Distance (meters) from mother at the beginning of feeding bouts of immature individuals. Numbers

679 above the bars represent the number of feeding bouts. I excluded feeding bouts when the mother was followed

680 by a research assistant but out of my sight. I excluded 2, 6, 1, and 14 bout(s) from left. The medians of lactational

681 and weaned individuals were 1 meter and 3 meters both in simultaneous and non-simultaneous feeding bouts

682 with mothers, respectively.

683 **Table 1**

684 Details of individual chimpanzee infants at Mahale National Park in this study.

Name	Abbreviation	Sex	Mother	Developmental stage	Analysis time (min)	No. of observation days	Age in months	No. of feeding bouts [No. of feeding bouts without mother]
Asahi	AH	♀	Multiparous	Lactational	748	6	14-19	29 [17]
				Weaned	377	1	47	14 [6]
Ayu	AY	♀	Multiparous	Lactational	2306	10	9-35	95 [63]
				Weaned	177	1	37	6 [3]
Cissy	CI	♀	Multiparous	Weaned	2293	11	36-61	123 [53]
Cyon	CN	♂	Multiparous	Lactational	175	2	13	7 [5]
Figaro	FG	♂	Multiparous	Lactational	1832	8	12-35	75 [30]
				Weaned	742	6	36-42	33 [13]

Name	Code	Sex	Parity					
Iris	IR	♀	Multiparous	Lactational	593	4	18-24	17 [6]
				Weaned	591	3	38-42	28 [11]
Jura	JR	♀	Multiparous	Lactational	257	1	23	17 [2]
Lilim	LM	♀	Primiparous	Weaned	464	2	67-70	16 [7]
Omali	OL	♂	Primiparous	Lactational	1053	8	6-28	22 [6]
Peace	PC	♂	Primiparous	Lactational	307	2	14	6 [1]
Quinoko	QN	♀	Multiparous	Lactational	713	3	29-31	20 [8]
Quilt	QL	♀	Multiparous	Weaned	576	3	50-70	22 [12]
Shinji	SJ	♂	Multiparous	Lactational	1191	6	13-34	47 [27]
				Weaned	431	2	36-43	8 [3]
Teto	TO	♀	Multiparous	Lactational	110	1	34	9 [6]
				Weaned	2493	12	37-59	104 [58]
–	TZ09[a]	♀	Multiparous	Lactational	2286	10	16-23	77 [41]

Upepo	UP	♀	Primiparous	Lactational	2525	13	9-35	82 [33]
				Weaned	699	3	37	27 [3]
Xyla	XL	♀	Primiparous	Lactational	1153	4	6-32	53 [13]
Zorufa	ZF	♀	Multiparous	Weaned	647	4	44-70	22 [5]
Zamma	ZA	♂	Multiparous	Lactational	231	1	26	8 [2]

685 [a] Researchers at Mahale do not name infants under 3 years of age because of high infant mortality; therefore, I used the mothers' abbreviation, plus the latter

686 two digits of the birth years to label unnamed infants. TZ09 died before 3 years of age.

687   **Table 2**

688   Parameter estimates, Akaike's information criterion (AIC), and ΔAIC values for model A.

Order	AIC (ΔAIC)	Parameter estimate/SE	
		Intercept	Age in months[a]
1	392.6 (0.0)	-0.84/0.08	—
2	395.6 (3.0)	-0.84/0.08	selected

689   [a] 'Age in months' is smoothed for modeling, as the coefficient could not be evaluated.

690

691

692　**Table 3**

693　Parameter estimates, deviance, and *p*-values for model B. An asterisk (*) indicates their interaction.

	Intercept	Weaned	Without mother	Weaned*Without mother	Mother food
Parameter estimate/SE	-1.44/0.10	-0.17/0.04	0.58/0.02	-0.31/0.04	-0.49/0.02
Deviance	—	88.3	398.8	51.6	458.4
p	—	< 0.001	< 0.001	< 0.001	< 0.001

694

695

696 **Table 4**

697 Comparison of 'self-provisioning' in immature chimpanzees and humans.

Subjects	Definition	Food	Social aspect	Confines	Contribution
Immature (0.5–6 years of age) chimpanzees of the M group in Mahale	Feeding non-simultaneously with mothers (i.e., feeding without mothers)	Higher accessibility than food consumed when feeding with mothers Frequently target food available throughout year (e.g., stems) Includes food not usually consumed by adults	87% and 79% of feeding bouts start alone for <3-year-old and ≥3-year-old individuals, respectively	Near mothers for travel in fission-fusion society Immature motor abilities	38.8% of total feeding bouts of immature chimpanzees in Mahale, but no data for other areas
Children (2–12 years of age) of modern humans in hunter-gatherer societies	Foraging without adult supervision	Higher accessibility than food usually consumed by adults[a] At least in Hadza society, frequently target food available throughout year (e.g., baobab)[b] Includes food species or plant parts not usually consumed by adults[c]	In mixed-age groups without adults[d]	Near the base camp[e] Immature motor skills and strength (i.e., slower walking speed)[f]	Facultative adaptation: lower risk of getting lost and richer environment leads to higher rate of self-provisioning[g]

698 [a] Hadza: Jones (1993); Mardu: Bird and Bird (2005); Meriam: Bird and Bird (2000, 2002); Mikea: Tucker and Young (2005); Nukakau: Swadling and

699 Chowning (1981).

700 [b] Hadza: Crittenden (2009).

701 [c] Meriam: Bird and Bird (2000, 2002); Mikea: Tucker and Young (2005); Nukakau: Swadling and Chowning (1981).

702 [d] Hadza: Crittenden et al. (2013), Jones (1993), Jones et al. (1997); Mardu: Bird and Bird (2005); Meriam: Bird and Bird (2000, 2002); Mikea: Tucker and

703 Young (2005); Nukakau: Swadling and Chowning (1981).

704 [e] Hadza: Jones (1993); Mikea: Tucker and Young (2005); Nukakau: Swadling and Chowning (1981).
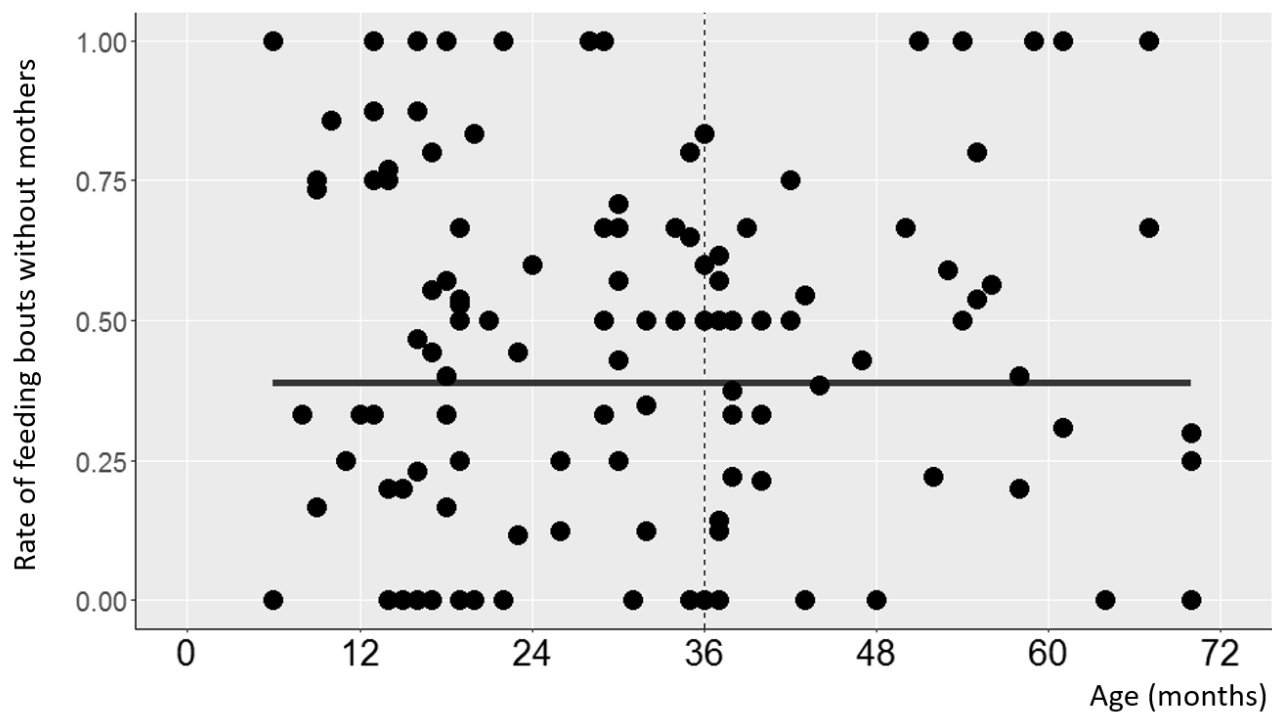
705 [f] Mardu: Bird and Bird (2005); Meriam: Bird and Bird (2000, 2002).

706 [g] Jones et al. (1997); Kramer (2005); Konner (2016).
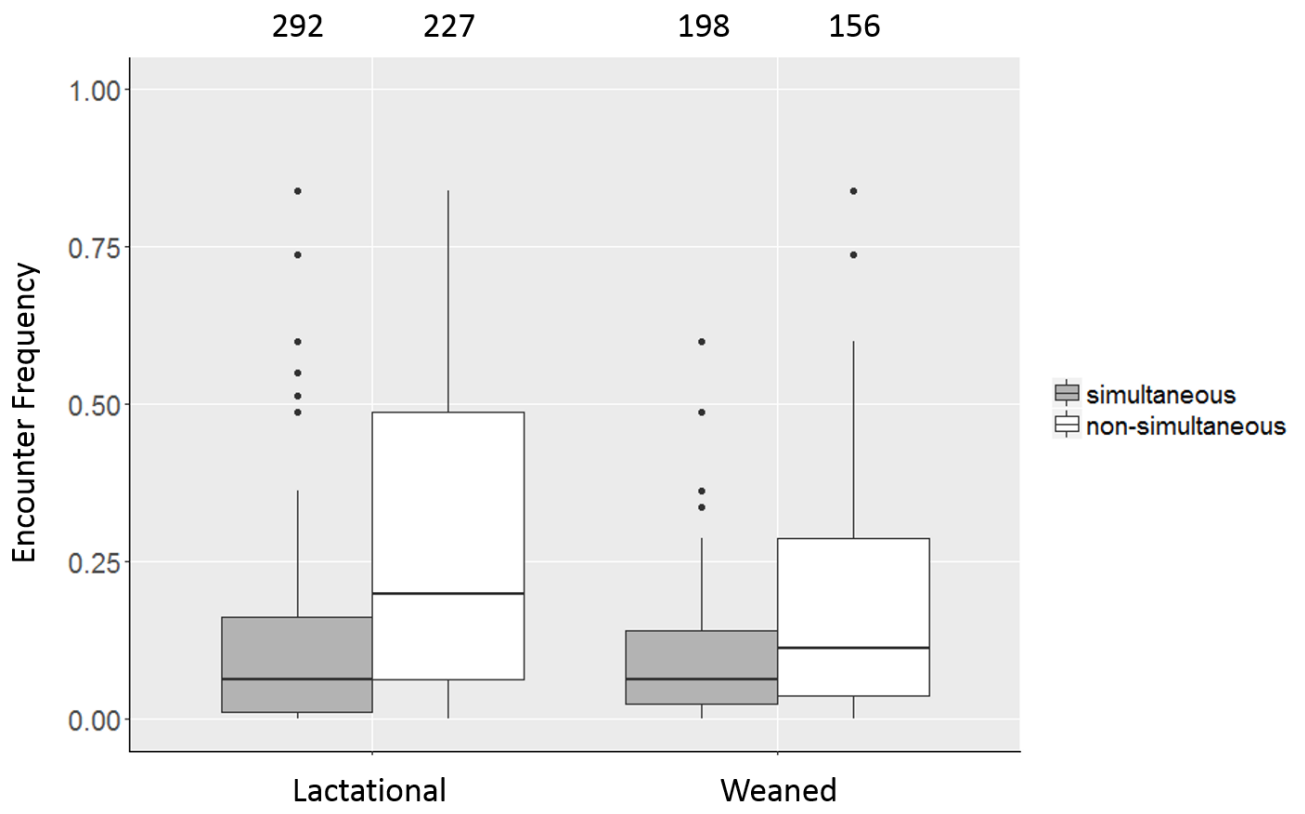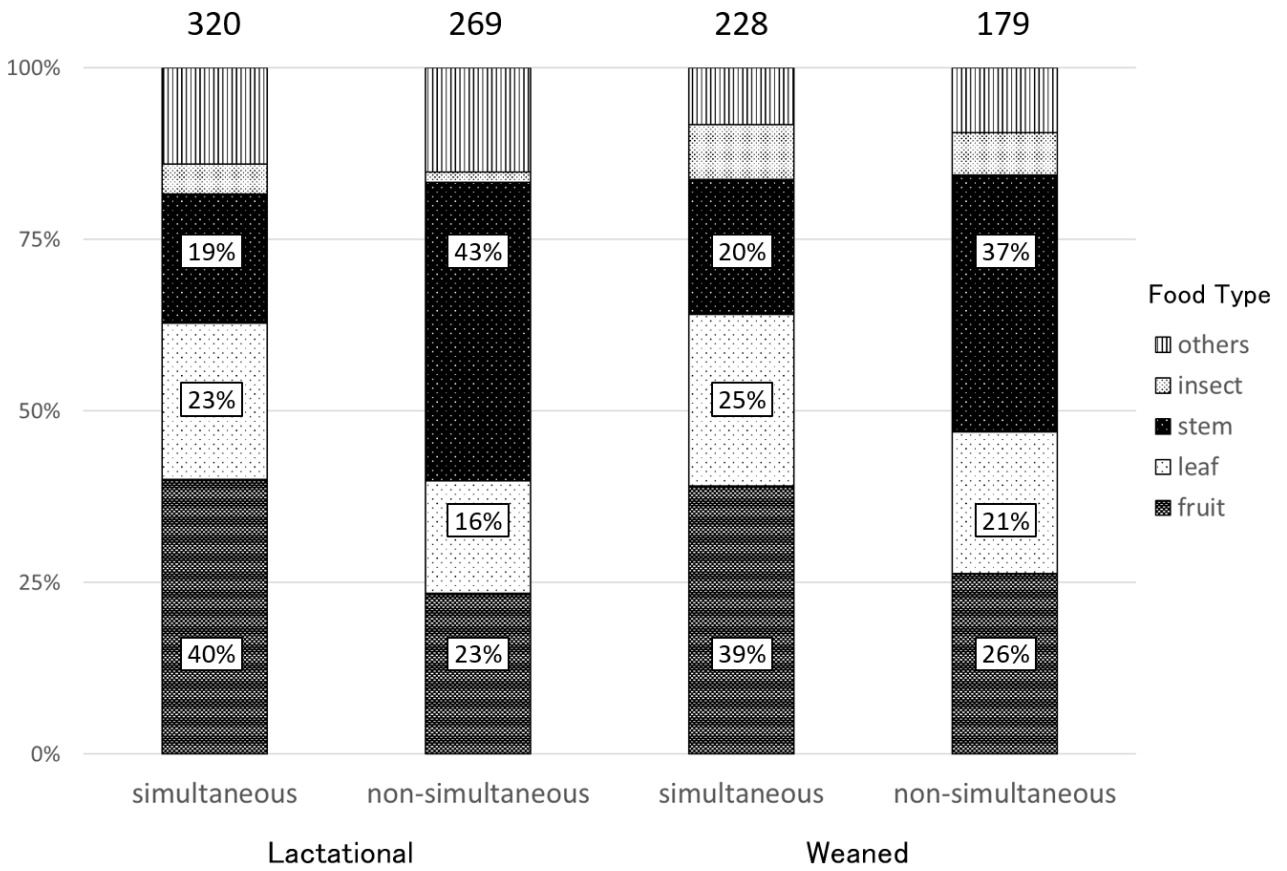
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708   **Figure 1**

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710   **Figure 2**

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712   **Figure 3**

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714 **Figure 4**

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716   **Figure S1**

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