

1 Fallback foods of red leaf monkeys (*Presbytis rubicunda*) in Danum Valley,

2 Borneo

3

4 Goro Hanya * and Henry Bernard †

5

6 * Primate Research Institute, Kyoto University, Inuyama, Japan

7 † Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah,

8 Kota Kinabalu, Sabah, Malaysia

9

10 Correspondence to: G. Hanya: Primate Research Institute, Kyoto University,

11 Kanrin 41-2, Inuyama, Aichi, 484-8506 Japan. E-mail: hanya@pri.kyoto-u.ac.jp,

12 Tel: +81-568-63-0542, Fax: +81-568-63-0564

13

14 Running title: Diet of red leaf monkey

15

16

17 **Abstract** Animals in Southeast Asia must cope with long periods of fruit
18 scarcity of unpredictable duration between irregular mast fruiting events.
19 Long-term data is necessary to examine the effect of mast fruiting on diet, and
20 particularly on the selection of fallback foods during periods of fruit scarcity. No
21 such data is available for colobine monkeys, which may consume substantial
22 amounts of fruits and seeds when available. We studied the diet of red leaf
23 monkeys (*Presbytis rubicunda*, Colobinae) in Danum Valley, Sabah, northern
24 Borneo, using 25 months of behavioral observation, phenology and vegetation
25 surveys and chemical analysis to compare leaves eaten with non-food leaves.
26 The monkeys spent 46% of their feeding time on young leaves, 38% on seeds,
27 12% on whole fruits, 2.0% on flowers, 1.0% on bark, and 1.2% on pith. They
28 spent more time feeding on seeds and whole fruit when fruit availability was high
29 and fed on young leaves of *Spatholobus macropterus* (liana, Leguminosae) as
30 fallback foods. This species was by far the most important food, constituting
31 27.9% of the total feeding time, and the feeding time on this species negatively
32 correlated with fruit availability. Consumed leaves contained more protein than
33 non-consumed leaves, and variation in time spent feeding on different leaves
34 was explained by their abundance. These results suggest that red leaf monkeys
35 show essentially the same response to the supra-annual increase in fruit
36 availability as sympatric monogastric primates, increasing their seed and
37 whole-fruit consumption. However, they depended more on young leaves, in
38 particular *Spatholobus macropterus*, as fallback foods during fruit-scarce periods
39 than did gibbons or orangutans. Their selection of fallback food appeared to be
40 due to both nutrition and abundance.
41 Key words: diet; fallback foods; functional response; general flowering,

42 *Spatholobus macropterus*

43

44 **Introduction**

45 Seasonal environmental changes can impose serious food shortages or physical
46 stress on animals. For example, animals in Southeast Asia must cope with
47 extreme super-annual seasonality in flowering and fruiting. In lowland
48 dipterocarp forests in the Malay Peninsula, Borneo and Sumatra, many plants
49 come into flower simultaneously for a few weeks to a few months and
50 subsequently set fruit massively (mast fruiting); however, these species of plants
51 rarely flower outside these general flowering events (Sakai 2002; Wich and van
52 Schaik 2000). General flowering events occur at unpredictable intervals every
53 2-6 years (Sakai 2002). Variation also occurs spatially. For example, mast
54 fruiting may occur in only one region, or may occur on the entire Malay
55 Peninsula (Yasuda *et al.* 1999). Between mast fruiting events animals must
56 survive a long flower- or fruit-scarce period of unpredictable duration. The larger
57 inter-annual variability in fruiting in SE Asia than in other regions (van Schaik and
58 Pfannes 2005) is thought to have strong effects on community structure and may
59 be responsible for the low species diversity observed in this region (Reed and
60 Bidner 2004).

61 Animals in SE Asia cope with this strong seasonality in various ways,
62 including both numerical and functional responses. Numerical response occurs
63 both by migration and reproduction, and thus immediate response is possible for
64 volant and/or fast-reproducing animals, such as giant honey bees (*Apis dorsata*)
65 (Itioka *et al.* 2001) and thrips (Ashton *et al.* 1988). However, a functional
66 response is often the only option for non-volant, slow-reproducing animals. The

67 order primates is a particularly interesting taxon in this context, since primates
68 are among the few large animals that can use the canopy, where most plant
69 reproduction takes place. Most primates do not increase their number in
70 response to the fluctuations of fruit availability, although orangutans may show
71 resource-tracking migration (Buij *et al.* 2002). Instead primates rely on the
72 resources available in their current habitat, meaning that fallback foods play an
73 indispensable role in their survival in seasonal habitats. The two species of
74 orangutan (*Pongo abelii* and *P. pygmaeus*) offer the best examples of primate
75 functional response to mast fruiting. Their diet consists mostly of fruits during
76 mast fruiting, but they fall-back on young leaves and bark during non-fruiting
77 seasons (Kanamori *et al.* 2010; Knott 1998; Wich *et al.* 2006). Furthermore,
78 orangutans accumulate fat during the mast fruiting period and metabolize it
79 when the fruit availability decreases (Knott 1998). However, data for other
80 species are scant, as long-term data are necessary to reveal the effect of mast
81 fruiting.

82 Data on non-frugivores are particularly needed to understand the effect
83 of strong super-annual seasonality in fruit abundance on primate populations.
84 Despite the classical view that primates of the subfamily Colobinae are obligate
85 folivores (Clutton-Brock 1977), colobines are now known to consume substantial
86 amounts of fruits and seeds, with the average fruit- and seed-feeding time of 24
87 colobine species reaching 31% (Kirkpatrick 1999). Although they sometimes
88 feed on fleshy fruits, they typically consume only unripe ones, as acidic fruits
89 may disrupt the forestomach fermenting system (Lambert 1998).

90 We studied the diet of red leaf monkeys (*Presbytis rubicunda*) in the
91 primary lowland dipterocarp forest of Danum Valley, Sabah, Malaysian Borneo,

92 for 25 months. Red leaf monkeys can be classified as folivorous/gramnivorous;
93 their feeding time over 13 months at Sepilok, Sabah, was composed of 36%
94 young leaves, 30% seeds, 19% whole fruits, 11% flowers and other minor foods
95 (Davies 1991). We aimed to (1) describe dietary changes of this species in
96 response to seasonal fluctuations in fruit and young leaf availability, (2) identify
97 the fallback foods they feed on during the fruit scarcity, i.e. foods for which
98 consumption was negatively correlated with the availability of preferred foods
99 (Marshall *et al.* 2009), and (3) elucidate the chemical and distributional
100 properties that explain the differences of consumed vs. non-consumed and
101 frequently vs. rarely consumed young leaves.

102

103 **Methods**

104 Study site

105 The study site is a primary forest around the Danum Valley Field Centre (4°57'N,
106 117°48'E, 300 m above sea level) within the Danum Valley Conservation Area
107 (438 km²) located in eastern Sabah, northern Borneo. During 2007 and 2008,
108 rainfall was 3,115 mm/year and mean daily maximum, minimum and mean
109 temperatures were 31.4°C, 22.5°C and 26.9°C, respectively (Fig. 1; data
110 provided by the Danum Valley Field Centre). The forest is predominantly
111 composed of lowland dipterocarp trees (Newbery *et al.* 1999). Canopy height is
112 approximately 50 m, with emergent trees more than 70 m.

113

114 Behavioral observation

115 We observed one habituated group of red leaf monkeys with 8-12 individuals
116 from around 6:00 until 16:00, 5-10 days per month. We recorded their behavior

117 by scan sampling: every ten minutes we recorded the activity (feeding, moving,
118 resting) of all visible individuals, except for dependent infants. When they were
119 feeding, we recorded the food category and collected samples for later
120 identification. We collected data for 25 months from December 2006 to
121 December 2008. Total observation time was 1141 hours, and the monthly
122 observation time was 16-87 hours (mean: 46 hours). Observation time per day
123 was $7.22 \pm \text{SD } 2.27$ hours. Sometimes we could not find monkeys in the early
124 morning or terminated observation before 16:00 due to heavy rain. Therefore,
125 observation time in the periods of 6:00-7:00 (46 h), 14:00-15:00 (88 h), and
126 15:00-16:00 (79 h) was less than for other hours of the day (104-149 h).
127 However, this bias in observation time is unlikely to have influenced the main
128 results because it was similar across months

129

130 Phenology

131 We used data on monthly tree phenology accumulated by the Danum Valley
132 Field Centre since July 2004, using the same plot set as Norayati (2001) and the
133 same protocol as the census conducted from August 1997 until December 2000
134 (Wong *et al.* 2005). They monitored flushing, flowering and fruiting activities of
135 511-533 identified trees of ≥ 10 cm DBH every month. Plots were situated in
136 primary forest, including the home range of the study group. The monitored area
137 consisted of five transects, each 20×100 m, placed every 400 m along the 2 km
138 trail.

139

140 Vegetation

141 We took data on the botanical composition of the forest from Lingenfelder (2005).

142 The vegetation plot was different from that used to study phenology but covered
143 a larger area. We used data for a 4-ha plot in the study site, for which all trees
144 ≥ 10 cm DBH were identified to species and their DBH measured. Because these
145 data did not include lianas, we added data on *Spatholobus macropterus*
146 (Leguminosae), an important food source for red leaf monkeys at this site. We
147 set a transect along a circular trail which covers most of the home range (ca 16
148 ha), of 4 m \times 1.2 km and recorded the presence/absence of this liana for all trees
149 along the transect.

150

151 Chemical analysis

152 We compared the chemical properties of young leaves consumed and not
153 consumed by the red leaf monkeys. We sampled young leaves of all species that
154 constituted at least 1% of the feeding time and the top 20 species in abundance
155 (basal area) in the study area of the vegetation survey (Lingenfelder 2005;
156 Newbery *et al.* 1996). We included young leaves of 7 consumed species and 16
157 non-consumed species in analyses.

158 For each tree species consumed, we took young leaf samples from at
159 least four individual trees from which the monkeys had been feeding. We
160 sampled at least 20 leaves for each species. We kept the leaves in plastic bags
161 and took them to the Field Centre where we dried them immediately at 60°C for
162 60 hours using an oven. Afterwards, we stored the leaves in plastic bags and
163 took them to the laboratory at the Primate Research Institute, Kyoto University,
164 where we dried them again at 60°C for 48 hours using a vacuum incubator. After
165 weighing, we milled leaves, put them into a plastic tube and kept them in a
166 desiccator.

167 We determined crude protein using the Kjeldahl procedure for total
168 nitrogen and multiplying by 6.25. Since fiber-bound nitrogen is not taken into
169 account, metabolizable protein may have been lower (Rothman *et al.* 2008). We
170 measured crude lipid as diethyl-ether extract by the Soxhlet method (Soxhlet
171 1879). We determined crude ash by ashing at 550°C. We estimated neutral
172 detergent fibre (NDF) following methods in van Soest (1991). We extracted
173 condensed tannin with 50% methanol and determined its presence / absence
174 using the butanol-HCl method (Porter 1989). We used presence / absence since
175 it is difficult to estimate the concentration of condensed tannin with this method
176 (Rautio *et al.* 2007). We used the ratio of weight of the constituents to the total
177 dry weight for analysis of crude protein, crude lipid, NDF and crude ash.

178

179 Data analysis

180 Due to the high canopy and dense vegetation, the number of individuals we
181 observed in each scan was low (mean: 1.95, SD: 1.12). To avoid over-
182 representation of highly visible behaviors or foods, we divided the number of
183 individuals engaged in each activity (in case of feeding, number of individuals
184 feeding on a particular food item) for each scan by the total number of individuals
185 observed in the scan (Agetsuma 1995; Harrison 1985; Maruhashi 1981). We
186 summed this value for each month for each food item and calculated the
187 proportion this represented of the total feeding record. Patterns in the seasonal
188 variations in the diet evaluated with and without this correction were similar, and
189 the results for the effect of phenology on diet did not change.

190 We examined the effect of the proportion of fruiting and flushing trees in
191 the phenology survey on the proportion of feeding time of the particular food

192 category (or species) using a generalized linear model (GLM). We used data for
193 each month as the unit of analysis (N=25). Since the data were significantly non-
194 normality (Kolmogorov-Smirnov test, $p < 0.05$), we applied the quasi family and
195 calculated quasi AIC (Akaike's Information Criterion) using the 'QAIC' function of
196 the package 'MuMIn' in R 2.13.2 (Burnham and Anderson 2002). We combined
197 fruit and seed feeding because we expected these two categories of foods to
198 respond in a similar way to fruit availability. We used only the food species in the
199 phenology census for the analyses, although we also present data on all food
200 species. The variance inflation factor (VIF) was 1.05, which was less than the
201 cut-off value (5), so collinearity among independent factors did not affect the
202 results. We choose the model with the smallest AIC among all possible
203 combinations of independent factors, including the null model.

204 We examined young leaf food selection at two different levels using
205 GLMs. We examined the following six independent factors: crude protein, NDF,
206 crude ash, crude lipid, presence/absence of condensed tannin, and abundance
207 (number of stems/4 ha, using the vegetation data). First, we examined the effect
208 of these properties on whether the monkeys fed on a species (1) or not (0)
209 (binomial distribution). Then we examined the effects on the proportion of
210 feeding time for food leaves. We started from the full model and then decreased
211 the number of independent factors until the AIC did not decrease any further
212 (backward stepwise). The maximum variance inflation factor (VIF) was 2.35,
213 which was less than the cut-off value (5), so collinearity among independent
214 factors did not affect the results.

215 We used R 2.13.2. (© The R Foundation for Statistical Computing) for
216 all the statistical analyses. We set the alpha level at $P < 0.05$.

217

218 **Results**

219 Phenology

220 There was one clear peak of fruiting during the 25 month study, from May to
221 October 2007 (Fig. 2a). This was the largest peak in the period August 1997 to
222 December 2000 (Wong *et al.* 2005). During this high fruiting period, 2.8-6.7% of
223 trees bore fruits while only 0-1.9% of trees did so out of this period. The number
224 of flushing trees also fluctuated considerably (Fig. 2b).

225

226 Overall diet

227 Red leaf monkeys fed on young leaves (46% of feeding time), seeds (38%),
228 whole fruits (12%), flowers (2.0%), bark (1.0%), pith (1.2%) and other foods
229 (unspecified foods and mature leaf, 0.2%). The monkeys ate all whole fruits
230 unripe and masticated the seeds. They consumed plant parts from at least 122
231 different species (identified at least to genus level) belonging to 50 different
232 families, 103 of which we identified to species (Table 1). The main food families
233 were Leguminosae (10 species), Lauraceae (10), Euphorbiaceae (8), Meliaceae
234 (8) and Sapindaceae (7). Young leaves of *Spatholobus macropterus*
235 (Leguminosae, liana) were by far the most important foods, which constituted
236 27.9% of the total feeding time, followed by the seeds of *Chionanthus pluriflorus*
237 (Oleaceae, 4.2%) and *Nothaphoebe umbelliflora* (Lauraceae, 4.1%; Table 2).

238

239 Seasonal variation

240 Red leaf monkeys increased seed and fruit consumption and decreased
241 young leaf consumption when fruit availability was high (Fig. 4). The best-fit

242 model predicting fruit+seed consumption included only a positive effect of the
243 percentage of trees fruiting (Table 2a). The best-fit model predicting young leaf
244 consumption also included only the percentage of trees fruiting but with a
245 negative effect (Table 2b). The percentage of trees flushing was not included in
246 these best-fit models (Fig. 5). The model that included only the percentage of
247 flushing trees was the second-best fit to explain the fruit+seed consumption and
248 young leaf consumption, which had Δ QAIC values (difference from the QAIC of
249 the best-fit model) of 0.40 and 0.33, respectively. The model that included both
250 the percentage of flushing and fruiting trees was the third-best fit, and it had a
251 Δ QAIC value of 1.98, for fruit+seed consumption as well as for young leaf
252 consumption.

253 When fruit availability decreased red leaf monkeys consumed young leaves
254 of *S. macropterus*. Feeding time on young leaves on *S. macropterus* (27.9%)
255 was much longer than for the second most important leaf species (*Ziziphus*
256 *angustifolia*, 1.5%, Table 3) and *S. macropterus* was consumed in each of the 25
257 study months. Feeding time on the young leaves of *S. macropterus* was
258 significantly negatively correlated with the percentage of fruiting trees (N=25,
259 $r=-0.49$, $P=0.012$, Pearson's correlation), but the sum of the feeding time of the
260 other species was not ($r=-0.27$; $P=0.17$). Feeding time on young leaves of the
261 second- and third-most consumed species, which constituted more than 1% of
262 the total feeding time, also did not correlate with the percentage of fruiting trees
263 (*Xanthophyllum affine*: $r=-0.15$, $P=0.48$; *Ziziphus angustifolia*: $r=0.06$, $P=0.77$).

264

265 Young leaf selection

266 Red leaf monkeys chose young leaves which contained more crude protein than

267 leaves of common species as food, and consumed the most abundant species *S.*
268 *macropterus* most frequently. The best-fit model for the difference between
269 consumed and non-consumed leaves included only a positive effect of crude
270 protein content (Table 4a). The second- and third-best fit models included crude
271 ash or lipid in addition to crude protein, and these had $\Delta\text{AIC}=1.97$ or 2.00 ,
272 respectively. A high protein content increased the likelihood that a leaf species
273 was selected as food. The protein content of young *S. macropterus* leaves was
274 the third highest (20.5%) and 1.5 times higher than the mean value of the 23
275 species examined (13.8%). The difference between consumed and
276 non-consumed species was not significant for NDF ($t=1.72$, $P=0.10$), crude ash
277 ($t=1.18$, $P=0.25$), crude lipid ($t=1.04$, $P=0.31$), and abundance ($t=0.59$, $P=0.56$),
278 but significant for crude protein ($t=4.78$, $P=0.0001$; Fig. 6).

279 GLM model selection did not identify the most significant factors
280 explaining the variation in feeding time among food species because the best-fit
281 model included 5 independent factors (Table 4b). The second-best-fit model had
282 an extremely larger value of ΔAIC (28.9). However, we found a significant
283 correlation with feeding time for abundance ($N=7$, $r=0.99$, $P<0.0001$) but not for
284 the other factors (NDF: $r=0.52$, $P=0.23$; crude protein: $r=0.16$, $P=0.72$; crude
285 ash: $r=0.63$, $P=0.12$; crude lipid: $r=0.01$, $P=0.98$). In addition, there was no
286 difference in feeding time between tannin-free and tannin-bound species ($t=1.33$,
287 $P=0.24$). This suggests that the effect of abundance was more important than
288 other factors.

289

290 **Discussion**

291 Response to fruiting seasonality

292 Red leaf monkeys increased whole fruit and seed consumption in response to
293 increased fruit availability, and increased young leaf consumption when fruit
294 availability was low. Qualitatively, these findings are essentially the same
295 response as that shown by monogastric Bornean orangutans and Müller's
296 gibbons (*Hylobates muelleri*) (Kanamori *et al.* 2010; Vogel *et al.* 2009), which live
297 sympatrically with red leaf monkeys in various parts of Borneo, and indicate that
298 fruits and seeds are preferred foods for all of these primates. However, the
299 responses of red leaf monkeys and sympatric apes differ quantitatively, although
300 caution is required here because the studies were not conducted at the same
301 time and in the same place. Orangutans in Danum Valley decrease their
302 fruit-feeding time to less than 50% only infrequently (7 of 27 months (Kanamori
303 *et al.* 2010) and fruit feeding time for gibbons at Tuanan was more than 50%
304 even at the lowest fruit availability (Vogel *et al.* 2009). Red leaf monkeys were
305 apparently less dependent on fruits and seeds. Fruit and seed feeding time was
306 less than 50% for the majority of the study period (16 out of 25 months). During
307 the period of fruit scarcity, red leaf monkeys shifted their diet from fruits and
308 seeds to leaves, while gibbons continue to search for fruits, such as figs.
309 Orangutans are intermediate to these two species.

310

311 Fallback foods

312 Red leaf monkeys in Danum Valley used the young leaves of *Spatholobus*
313 *macropterus* as a fallback food, as consumption of these leaves was negatively
314 correlated with the availability of preferred foods (Marshall *et al.* 2009). Young
315 leaves of other species were not fallback foods, as their feeding time was not
316 related to fruit availability.

317 Fallback foods can be classified into 'low-quality' and 'high-quality'
318 foods (Lambert 2007), and the fallback strategies of red-leaf monkeys and
319 gibbons seem to rely on 'low-' and 'high-quality' foods, respectively. Dependence
320 on 'low-quality' foods is often associated with digestive and dental adaptations
321 that allow the extraction of sufficient energy from the low-quality foods (Marshall
322 *et al.* 2009), including the foregut fermentation of red leaf monkeys (Lambert
323 1998). Unlike brachiating gibbons, who can move quickly in the canopy (Vogel *et*
324 *al.* 2009), it is difficult for red leaf monkeys to effectively search for rare
325 resources, such as fruiting fig trees, making abundance a particularly important
326 factor in finding fallback foods in their habitat.

327 Red leaf monkeys appear to depend on young leaves of *S.*
328 *macropterus* as fallback food for two reasons: high protein content and high
329 abundance. There is a universal trend among colobus monkeys to prefer leaves
330 with more protein (Chapman and Chapman 2002; Kar-Gupta and Kumar 1994;
331 Yeager *et al.* 1997), and this includes red leaf monkeys in Sepilok (Davies *et al.*
332 1988). Condensed tannins or other phenolic compounds do not usually affect
333 food selection of colobus monkeys (Chapman and Chapman 2002; Kool 1992;
334 Maisels *et al.* 1994; Mowry *et al.* 1996), in contrast to monogastric primates such
335 as macaques (Hanya *et al.* 2007). *S. macropterus* differed from other
336 protein-rich leaves by its extreme abundance. The stem density of *S.*
337 *macropterus* (302/ha) was much higher than those of other leaf food species
338 (0.25-34/ha). Animals can reduce searching cost by eating abundant species
339 (Hanya *et al.* 2007). This is particularly important for red leaf monkeys, which do
340 not have special adaptations for quick movement through the canopy like
341 gibbons (Vogel *et al.* 2009). Interestingly, the young leaf of *S. macropterus* is

342 also one of the important fallback foods for sympatric orangutans, constituting
343 more than 20% of their feeding time during periods of fruit scarcity (Kanamori *et*
344 *al.* 2010). In response to decreased fruit availability, orangutans decrease their
345 feeding time on fruits to less than 20% and shift to eating young leaves and bark
346 (Kanamori *et al.* 2010). They also cannot move as quickly in the canopy as
347 gibbons (Vogel *et al.* 2009) and may select young leaves of *S. macropterus* as
348 fallback foods for a similar reason to that of red leaf monkeys. However, red leaf
349 monkeys in Sepilok consume young leaves of another species of *Spatholobus*
350 (*latistipulus*), but no single species constituted most of the feeding time (Davies
351 *et al.* 1988), unlike *S. macropterus* in the Danum Valley. The selection of fallback
352 food may be strongly affected by the local flora, and it is not consistent within
353 species.

354 Marshall and Wrangham (2007) defined fallback foods as food that is
355 low-quality but abundant. Our finding that the leaves of this species contain more
356 protein than common species seems to contradict their definition superficially.
357 However, Marshall and Wrangham (2007) used the term 'low-quality' only when
358 compared with preferred food items. If we suppose that the quality of young
359 leaves, including *S. macropterus*, is lower than that of fruits and seeds, and red
360 leaf monkeys chose *S. macropterus* among those 'low-quality' foods, our finding
361 and their definition do not contradict. However, leaves and seeds, which are the
362 two most important foods for Colobinae (Kirkpatrick 1999), have different
363 nutritional and distribution properties (Janson and Chapman 1999), and so it is
364 difficult to judge which is lower in quality than the other. In fact, another species
365 of colobine (*Trachypithecus francoisi*) shows a positive correlation between the
366 availability and feeding time of young leaves, but this is not the case for fruits

367 and seeds (Zhou *et al.* 2009). A comprehensive comparison is necessary
368 between these two types of foods in order to evaluate the value as food for
369 colobines.

370

371 In conclusion, we found that the red leaf monkey increased seed and whole-fruit
372 consumption in response to the supra-annual increase in fruit availability, which
373 is the essentially the same response as that found in sympatric monogastric
374 primates. However, they depended more on young leaves, in particular
375 *Spatholobus macropterus*, as fallback foods than did gibbons or orangutans.
376 This species appeared to be eaten so often due to its high protein content and
377 extreme abundance.

378

379 **Acknowledgements**

380 This study would not have been possible without the hard work of our field
381 assistants, Syamsudin Jail, Sharry bin Mustah, Saharudin Idos, Unding Jami,
382 Sallehudin Jail and Rayner Jupili. We are greatly indebted to the staff of the
383 Danum Valley Field Centre and our colleagues there for their hospitality and help,
384 in particular Jimmy Omar, Mike Bernadus, Glen Reynolds, Tomoko Kanamori,
385 Noko Kuze and Siew Te Wong. Constructive comments by Drs. Joanna Setchell,
386 Oliver Shülke and an anonymous reviewer were really helpful in improving the
387 manuscript. The Economy Planning Unit of Malaysia and the State of Sabah and
388 the Danum Valley Management Committee of Yayasan Sabah permitted our
389 study. This study was financed by the JSPS Core-to-Core Program (HOPE), the
390 MEXT Grant-in-Aid for JSPS Overseas Fellows, Grant-in-Aid for Young
391 Scientists (No. 20770195 and No. 22687002) to GH, Primate Society of Japan,
392 the 21st Century COE Program (A14) and Global COE Program “Formation of a
393 Strategic Base for Biodiversity and Evolutionary Research: from Genome to
394 Ecosystem.”

395

396 **References**

- 397 Agetsuma, N. (1995). Foraging strategies of Yakushima macaques (*Macaca*
398 *fuscata yaku*). *International Journal of Primatology*, 16, 595-609.
- 399 Ashton, P. S., Givnish T. J. & Appanah S. (1988). Staggered flowering in the
400 Dipterocarpaceae: new insights into floral induction and the evolution of mast
401 fruiting in the aseasonal tropics. *American Naturalist*, 132, 44-66.
- 402 Buij, R., Wich S. A., Lubis A. H. & Sterck E. H. M. (2002). Seasonal movements
403 in the Sumatran orangutan (*Pongo pygmaeus abelii*) and consequences for
404 conservation. *Biological Conservation*, 107, 83-87.
- 405 Burnham, K. P. & Anderson D. R. (2002). *Model Selection and Multi-model*
406 *Inference. 2nd Edition*. Springer, New York.
- 407 Chapman, C. A. & Chapman L. J. (2002). Foraging challenges of red colobus
408 monkeys: influence of nutrients and secondary compounds. *Comparative*
409 *Biochemistry And Physiology A-Molecular And Integrative Physiology*, 133,
410 861-875.
- 411 Clutton-Brock, T. H. (1977). *Primate Ecology: Studies of Feeding and Ranging*
412 *Behaviour in Lemurs, Monkeys and Apes*. Academic Press, Brighton.
- 413 Davies, A. G., Bennett E. L. & Waterman P. G. (1988). Food selection by 2
414 southeast Asian colobine monkeys (*Presbytis rubicunda* and *Presbytis*
415 *melalophos*) in relation to plant chemistry. *Biological Journal of the Linnean*
416 *Society*, 34, 33-56.
- 417 Davies, G. (1991). Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in
418 dipterocarp forest of northern Borneo. *International Journal of Primatology*, 12,
419 119-144.
- 420 Hanya, G., Kiyono M., Takafumi H., Tsujino R. & Agetsuma N. (2007). Mature

- 421 leaf selection of Japanese macaques: effects of availability and chemical content.
422 *Journal of Zoology*, 273, 140-147.
- 423 Harrison, M. J. S. (1985). Time budget of the green monkey, *Cercopithecus*
424 *sabaeus*: some optimal strategies. *International Journal of Primatology*, 6,
425 351-376.
- 426 Itioka, T., Inoue T., Kaling H., Kato M., Nagamitsu T., Momose K., Sakai S.,
427 Yumoto T., Mohamad S. U., Hamid A. A. & Yamane S. (2001). Six-year
428 population fluctuation of the giant honey bee *Apis dorsata* (Hymenoptera :
429 Apidae) in a tropical lowland dipterocarp forest in Sarawak. *Annals of the*
430 *Entomological Society of America*, 94, 545-549.
- 431 Janson, C. & Chapman C. (1999). Resources and primate community structure.
432 In J. Fleagle, C. Janson & K. Reed (eds), *Primate Communities* (pp. 237-267).
433 Cambridge: Cambridge Univ Press.
- 434 Kanamori, T., Kuze N., Bernard H., Malim T. P. & Kohshima S. (2010). Feeding
435 ecology of Bornean orangutans (*Pongo pygmaeus morio*) in Danum Valley,
436 Sabah, Malaysia: A 3-year record including two mast fruitings. *American Journal*
437 *of Primatology*, 72, 820-840.
- 438 Kar-Gupta, K. & Kumar A. (1994). Leaf chemistry and food selection by common
439 langurs (*Presbytis entellus*) in Rajaji National Park, Uttar Pradesh, India.
440 *International Journal of Primatology*, 15, 75-93.
- 441 Kirkpatrick, R. C. (1999). Colobine diet and social organization. In P. Dolhinow &
442 A. Fuentes (eds), *The Nonhuman Primates* (pp. 93-105). Mountain View:
443 Mayfield Publishing Company.
- 444 Knott, C. D. (1998). Changes in orangutan caloric intake, energy balance, and
445 ketones in response to fluctuating fruit availability. *International Journal of*

- 446 *Primates*, 19, 1061-1079.
- 447 Kool, K. M. (1992). Food selection by the silver leaf monkey, *Trachypithecus*
448 *auratus sondaicus*, in relation to plant chemistry. *Oecologia*, 90, 527-533.
- 449 Lambert, J. E. (1998). Primate digestion: Interactions among anatomy,
450 physiology, and feeding ecology. *Evolutionary Anthropology*, 7, 8-20.
- 451 Lambert, J. E. (2007). Seasonality, fallback strategies, and natural selection: a
452 chimpanzee and Cercopithecoid model for interpreting the evolution of the
453 hominin diet. In P. S. Ungar (ed. *Evolution of the human diet: the known, the*
454 *unknown, and the unknowable* (pp. 324-343). Oxford: Oxford University Press.
- 455 Lingensfeldt, M. (2005) Rain forest dynamics and response to drought in a
456 Bornean primary lowland dipterocarp forest (PhD thesis) pp. 179. University of
457 Bern, Bern.
- 458 Maisels, F., Gauthier-Hion A. & Gautier J. P. (1994). Diets of 2 sympatric
459 colobines in Zaire: more evidence on seed-eating in forests on poor soils.
460 *International Journal of Primatology*, 15, 681-701.
- 461 Marshall, A. J. & Wrangham R. W. (2007). Evolutionary consequences of
462 fallback foods. *International Journal of Primatology*, 28, 1218-1235.
- 463 Marshall, A. J., Boyko C. M., Feilen K. L., Boyko R. H. & Leighton M. (2009).
464 Defining fallback foods and assessing their importance in primate ecology and
465 evolution. *American Journal of Physical Anthropology*, 140, 603-614.
- 466 Maruhashi, T. (1981). Activity patterns of a troop of Japanese monkeys (*Macaca*
467 *fuscata yakui*) on Yakushima Island, Japan. *Primates*, 22, 1-14.
- 468 Mowry, C. B., Decker B. S. & Shure D. J. (1996). The role of phytochemistry in
469 dietary choices of Tana River red colobus monkeys (*Procolobus badius*
470 *rufomitratu*). *International Journal of Primatology*, 17, 63-84.

- 471 Newbery, D. M., Campbell E. J. F., Proctor J. & Still M. J. (1996). Primary lowland
472 dipterocarp forest at Danum Valley, Sabah, Malaysia. Species composition and
473 patterns in the understorey. *Vegetatio*, 122, 193-220.
- 474 Newbery, D. M., Kennedy D. N., Petol G. H., Madani L. & Ridsdale C. E. (1999).
475 Primary forest dynamics in lowland dipterocarp forest at Danum Valley, Sabah,
476 Malaysia, and the role of the understorey. *Philosophical Transactions of the*
477 *Royal Society B-Biological Sciences*, 354, 1763-1782.
- 478 Norhayati, A. (2001) Frugivores and fruit production in primary and logged
479 tropical rainforests (PhD thesis). In: *Faculty of Science and Technology* pp. 269.
480 Universiti Kebangsaan Malaysia, Bangi, Malaysia.
- 481 Porter, L. J. (1989). Tannins. In P. M. Dey & J. B. Harborne (eds), *Methods in*
482 *Plant Biochemistry, vol.1. Plant Phenolics* (pp. 389-419). London: Academic
483 Press.
- 484 Rautio, P., Bergvall U. A., Karonen M. & Salminen J. P. (2007). Bitter problems in
485 ecological feeding experiments: Commercial tannin preparations and common
486 methods for tannin quantifications. *Biochemical Systematics And Ecology*, 35,
487 257-262.
- 488 Reed, K. E. & Bidner L. R. (2004). Primate communities: past, present, and
489 possible future. *Yearbook of Physical Anthropology*, 47, 2-39.
- 490 Rothman, J. M., Chapman C. A. & Pell A. N. (2008). Fiber-bound nitrogen in
491 gorilla diets: Implications for estimating dietary protein intake of primates.
492 *American Journal of Primatology*, 70, 690-694.
- 493 Sakai, S. (2002). General flowering in lowland mixed dipterocarp forests of
494 South-east Asia. *Biological Journal of the Linnean Society*, 75, 233-247.
- 495 Soxhlet, F. (1879). Die gewichtsanalytische Bestimmung des Milchfettes.

- 496 *Polytechnisches J*, 232, 461-465.
- 497 van Schaik, C. P. & Pfannes K. (2005). Tropical climates and phenology: a
498 primate perspective. In D. K. Brockman & C. P. van Schaik (eds), *Seasonality in*
499 *Primates: Studies of Living and Extinct Human and Non-Human Primates* (pp.
500 23-54). Cambridge: Cambridge University Press.
- 501 van Soest, P. J., Robertson J. B. & Lewis B. A. (1991). Methods for dietary fiber,
502 neutral detergent fiber, and nonstarch polysaccharides in relation to animal
503 nutrition. *Journal of Dairy Science*, 74, 3583-3597.
- 504 Vogel, E. R., Haag L., Mitra-Setia T., van Schaik C. P. & Dominy N. J. (2009).
505 Foraging and ranging behavior during a fallback episode: *Hylobates albibarbis*
506 and *Pongo pygmaeus wurmbii* compared. *American Journal of Physical*
507 *Anthropology*, 140, 716-726.
- 508 Wich, S. A. & van Schaik C. P. (2000). The impact of El Niño on mast fruiting in
509 Sumatra and elsewhere in Malesia. *Journal of Tropical Ecology*, 16, 563-577.
- 510 Wich, S. A., Utami-Atmoko S. S., Setia T. M., Djoyosudharmo S. & Geurts M. L.
511 (2006). Dietary and energetic responses of *Pongo abelii* to fruit availability
512 fluctuations. *International Journal of Primatology*, 27, 1535-1550.
- 513 Wong, S. T., Servheen C., Ambu L. & Norhayati A. (2005). Impacts of fruit
514 production cycles on Malayan sun bears and bearded pigs in lowland tropical
515 forest of Sabah, Malaysian Borneo. *Journal of Tropical Ecology*, 21, 627-639.
- 516 Yasuda, M., Matsumoto J., Osada N., Ichikawa S., Kachi N., Tani M., Okuda T.,
517 Furukawa A., Nik A. R. & Manokaran N. (1999). The mechanism of general
518 flowering in Dipterocarpaceae in the Malay Peninsula. *Journal of Tropical*
519 *Ecology*, 15, 437-449.
- 520 Yeager, C. P., Silver S. C. & Dierenfeld E. S. (1997). Mineral and phytochemical

- 521 influences on foliage selection by the proboscis monkey (*Nasalis larvatus*).
522 *American Journal of Primatology*, 41, 117-128.
- 523 Zhou, Q. H., Huang Z. H., Wei X. S., Wei F. W. & Huang C. M. (2009). Factors
524 influencing interannual and intersite variability in the diet of *Trachypithecus*
525 *francoisi*. *International Journal of Primatology*, 30, 583-599.
- 526
527
528

Table 1. Number of species consumed by the red leaf monkeys

| Food category | No. Species | No. Species | No. Species | No. Species |
|--------------------|-------------|-------------|-------------|-------------|
| | Total | Tree | Liana | Epiphyte |
| Young leaf | 68 | 50 | 14 | 4 |
| Seed | 54 | 40 | 14 | 0 |
| Whole fruit | 27 | 21 | 6 | 0 |
| Flower, flower bud | 11 | 8 | 3 | 0 |
| Pith | 4 | 2 | 2 | 0 |
| Bark | 5 | 5 | 0 | 0 |
| Mature leaf | 1 | 1 | 0 | 0 |

529

530

Table 2. Best-fit generalized linear models for the effect of phenology on the seasonal variations of diet

a. Feeding time of fruits and seeds

QAIC=6.88, R²=0.35, P=0.00043

| | Coefficient | SE | t | p |
|----------------|-------------|------|------|-------|
| (Intercept) | 0.35 | 0.06 | 6.22 | 0.000 |
| %Fruiting tree | 6.90 | 1.96 | 3.52 | 0.002 |

b. Feeding time of young leaves

QAIC=6.78, R²=0.33, P=0.00073

| | Coefficient | SE | t | p |
|----------------|-------------|------|-------|-------|
| (Intercept) | 0.59 | 0.05 | 11.20 | 0.000 |
| %Fruiting tree | -6.21 | 1.84 | -3.38 | 0.003 |

531 %Fruiting tree: Percentage of trees bearing food fruits or seeds

532

Table 4. Best-fit models for the effect of leaf chemistry and abundance on young leaf sele

a. Food (1) vs. non-food (0)

AIC=17.6, R²=0.54, P=0.0001

| | Coefficient | SE | t | p |
|---------------|-------------|-------|-------|-------|
| (Intercept) | -9.24 | 3.80 | -2.43 | 0.015 |
| Crude protein | 56.20 | 23.93 | 2.35 | 0.019 |

b. Feeding time of young leaves

AIC=-79.3, R²=0.99, P<0.00001

| | Coefficient | SE | t | p |
|------------------|-------------|------|--------|-------|
| (Intercept) | -0.16 | 0.02 | -8.23 | 0.077 |
| NDF | -0.82 | 0.05 | -16.55 | 0.04 |
| Crude ash | 7.99 | 0.58 | 13.75 | 0.046 |
| Crude lipid | 2.29 | 0.22 | 10.31 | 0.062 |
| Condensed tannin | 0.07 | 0.01 | 9.75 | 0.065 |
| Abundance | 0.00 | 0.00 | 18.57 | 0.034 |

536

537 Legends for figures

538 Fig. 1. Climate data from the Danum Valley Field Centre for December

539 2006-December 2008.

540 Fig. 2. Fruiting (a) and flushing (b) phenology between July 2004 and December

541 2008. Values are percentage of total trees in the sample plot bearing fruit

542 at a given time. Closed diamonds: all trees; open squares: red leaf

543 monkey food species only.

544 Fig. 3. Seasonal changes in the diet composition of red leaf monkeys; values are

545 percent of monthly feeding time spent on each food category.

546 Fig. 4. Relationships between fruiting phenology (proportion of trees bearing

547 fruits in the phenology plot) and time spent feeding on (a) fruits and seeds

548 and (b) young leaves.

549 Fig. 5. Relationships between flushing phenology (proportion of trees having

550 young leaves in the phenology plot) and time spent feeding on (a) fruits

551 and seeds and (b) young leaves.

552 Fig. 6. Comparison of chemical properties and abundance between consumed

553 and non-consumed young leaves (mean+SD) Values are proportion of

554 dry weight for (a)-(d). Consumed species include *Spatholobus*

555 *macropterus* (Leguminosae; 27.9% of feeding time), *Ziziphus angustifolia*

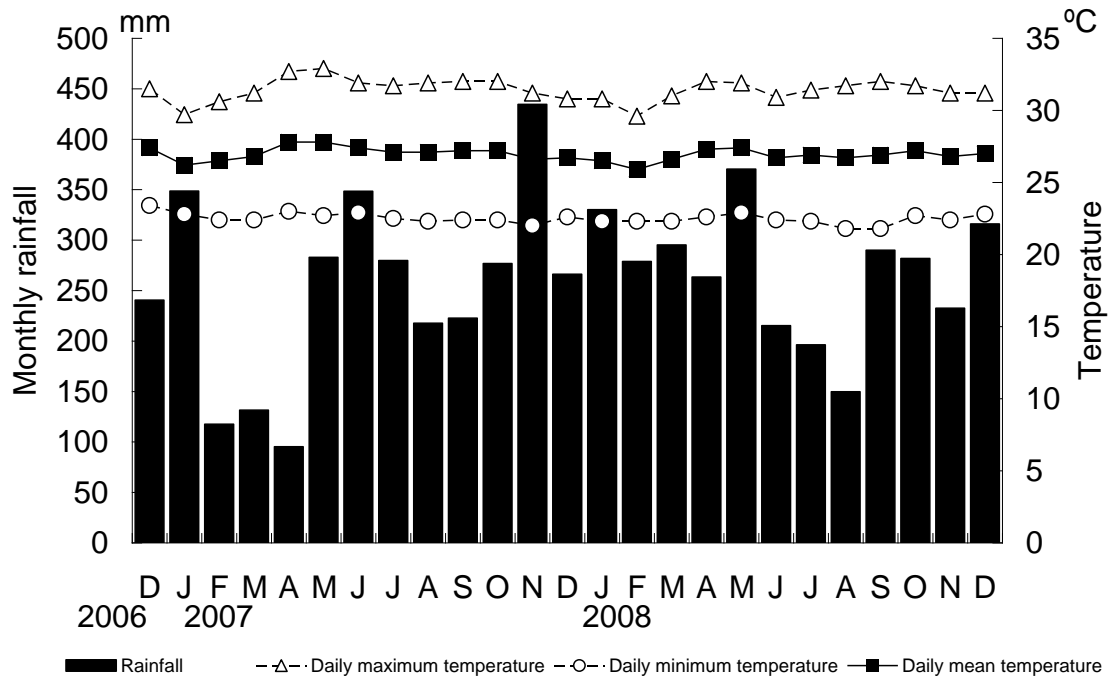
556 (Rhamnaceae; 1.5%), *Xanthophyllum affine* (Polygalaceae; 1.1%),

557 *Ryparosa hullettii* (Flacourtiaceae; 0.5%), *Parashorea malaanonan*

558 (Dipterocarpaceae; 0.2%), *Koompassia excelsa* (Leguminosae; 0.1%),

559 and *Nothaphoebe umbelliflora* (Lauraceae; 0.1%).

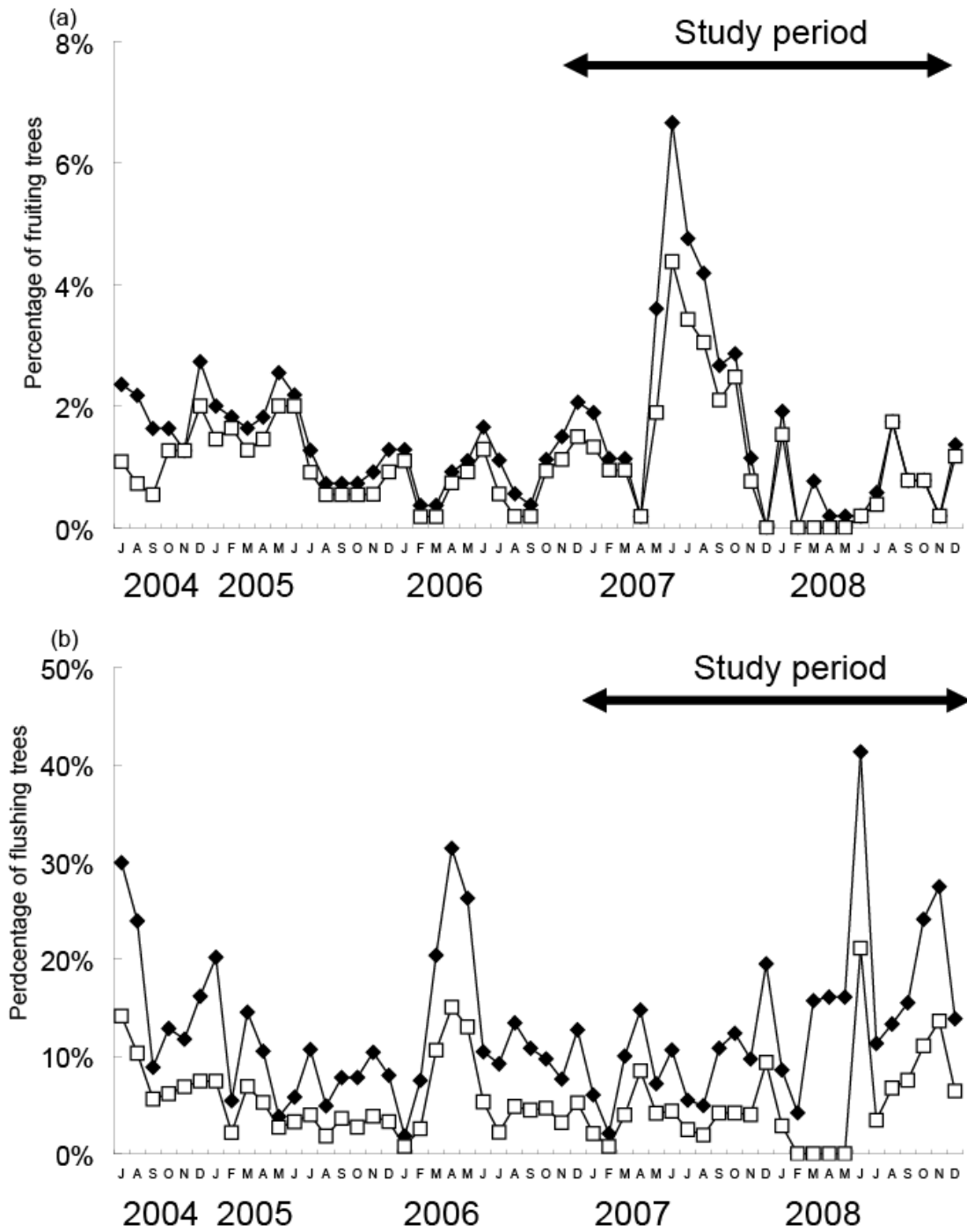
560



561

562 Fig. 1

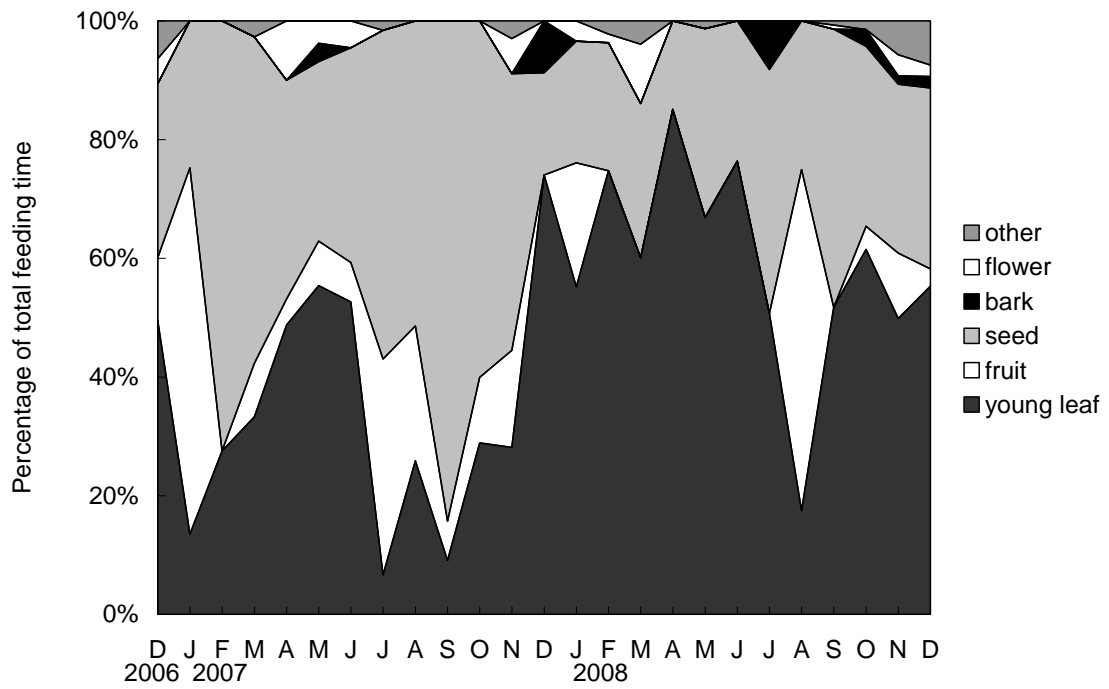
563



564

565 Fig. 2

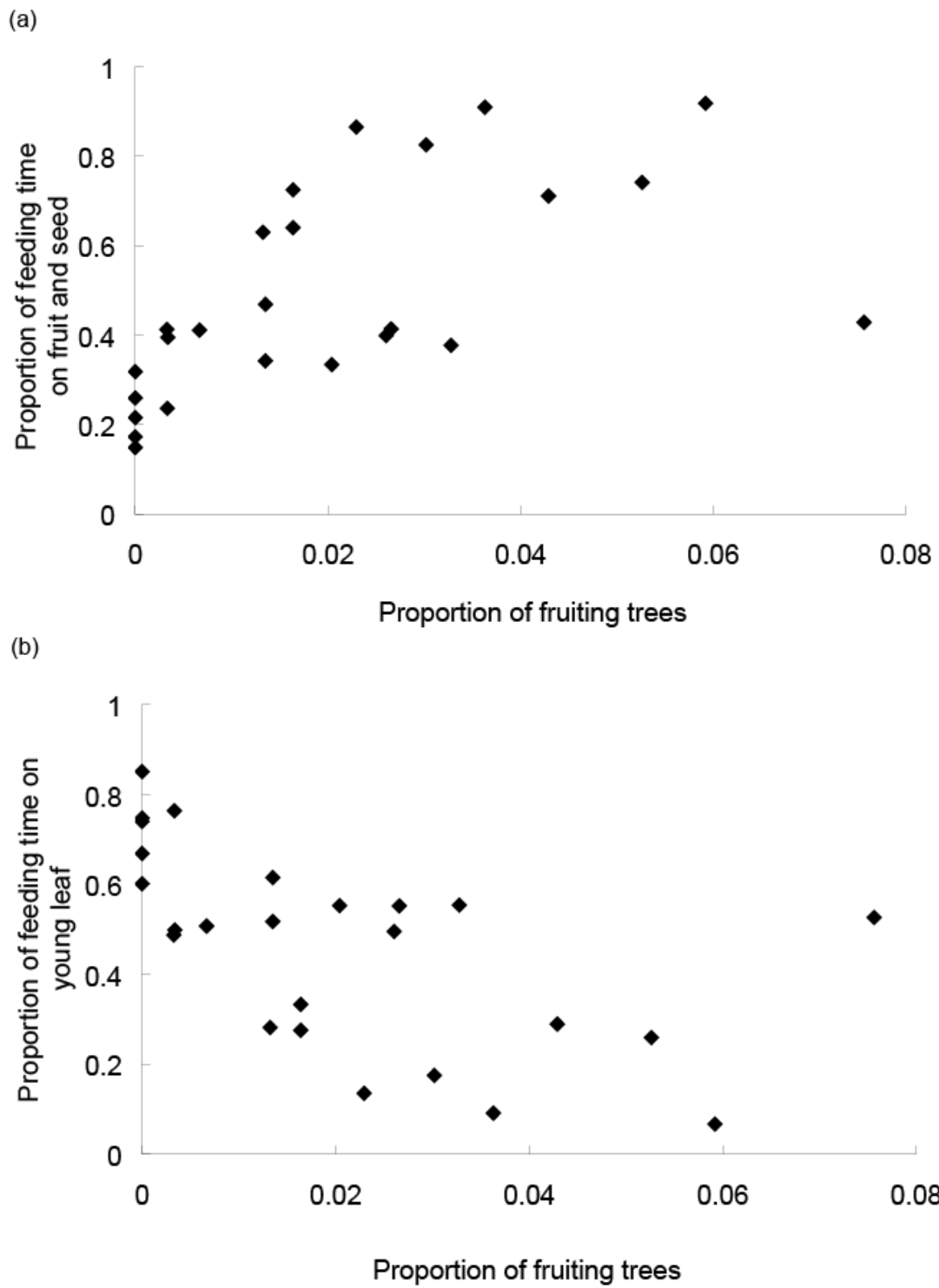
566



567

568 Fig. 3

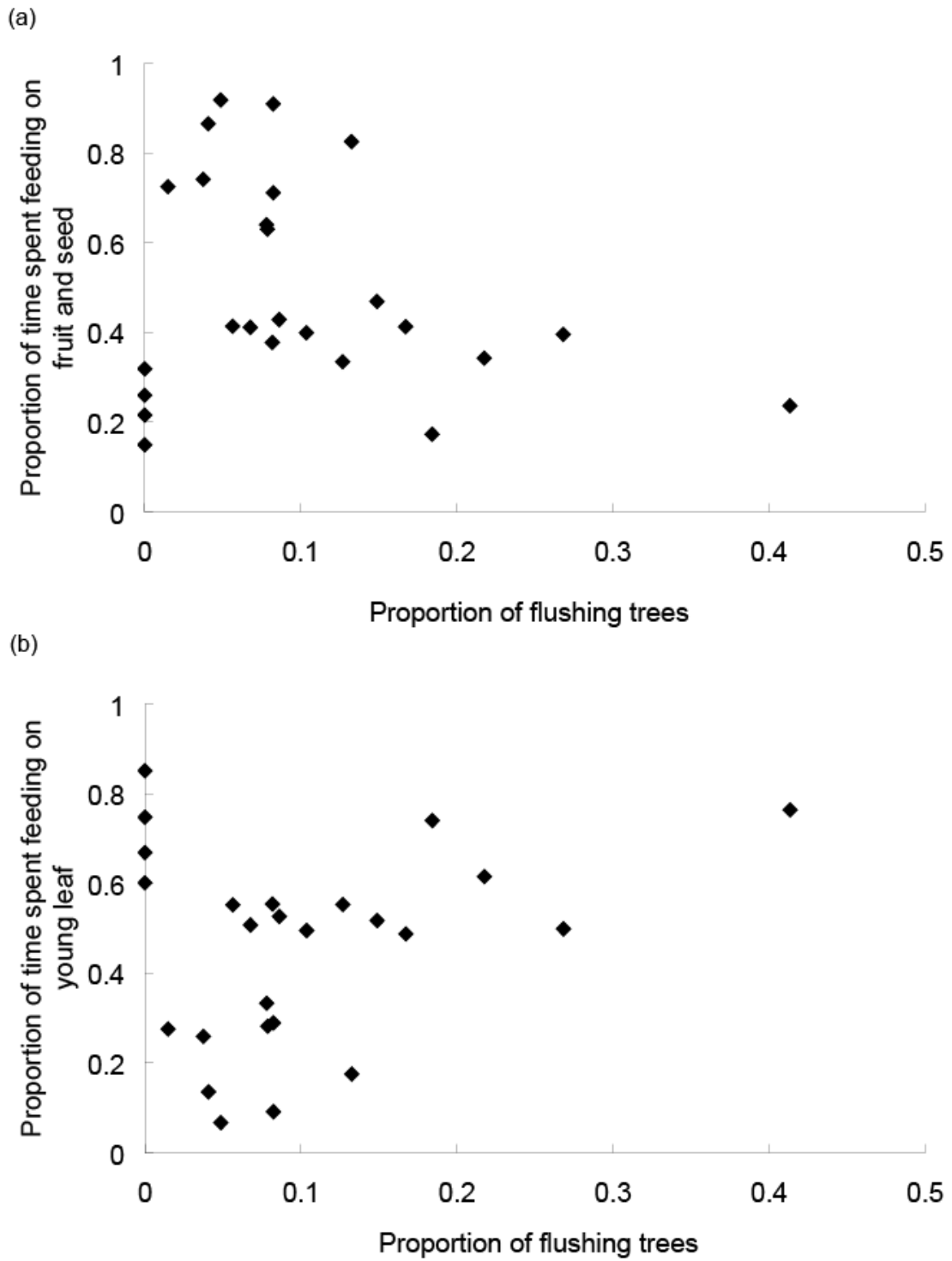
569



570

571 Fig. 4

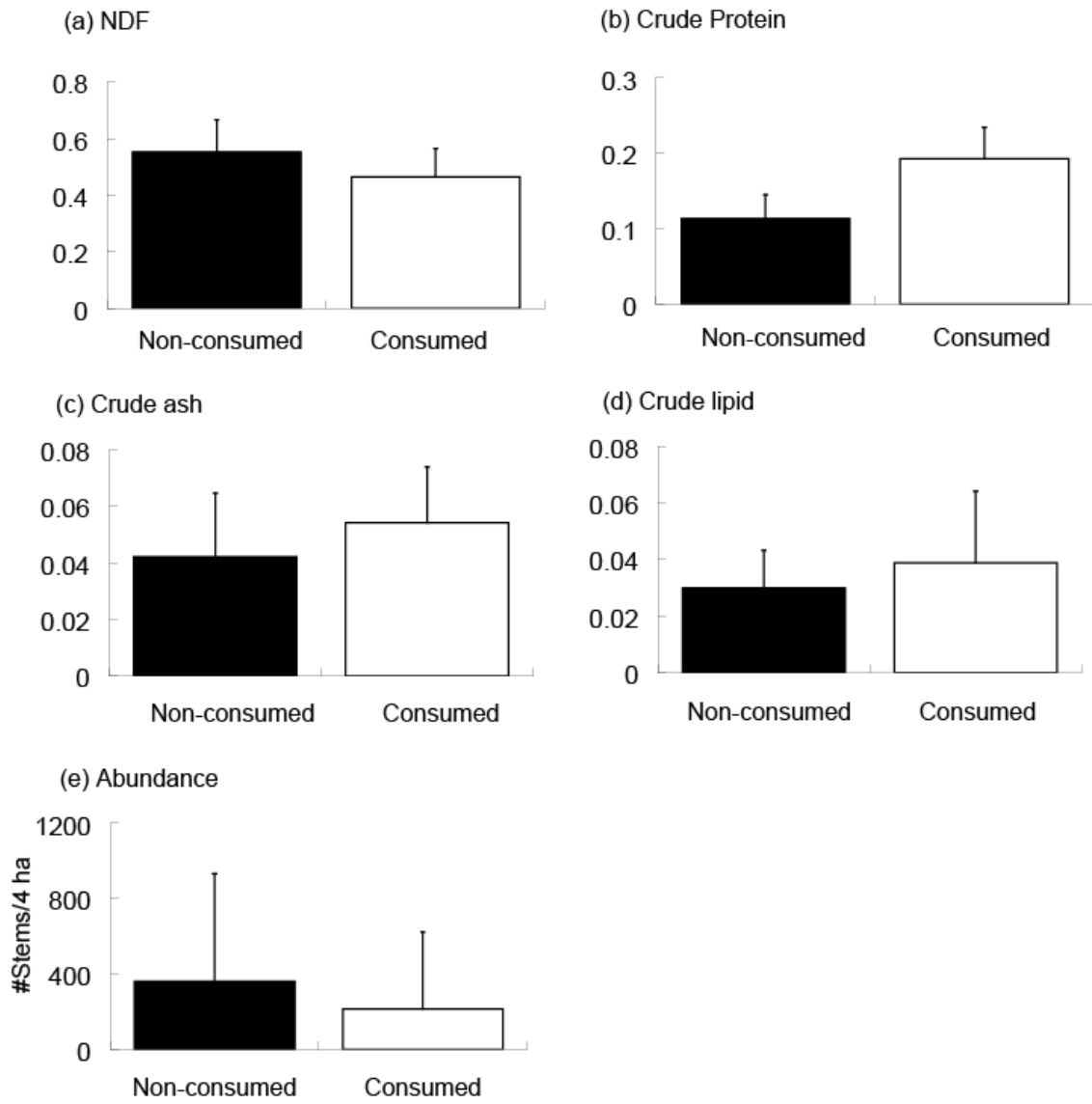
572



573

574 Fig. 5

575



576

577 Fig. 6