

1 Fruiting and flushing phenology in Asian tropical and temperate forests:
2 implications for primate ecology

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18

19 Abstract

20 In order to understand the ecological adaptations of primates to survive in
21 temperate forests, we need to know the general patterns of plant phenology in
22 temperate and tropical forests. Comparative analyses have been employed to
23 investigate general trends in the seasonality and abundance of fruit and young
24 leaves in tropical and temperate forests. Previous studies have shown that 1)
25 fruit fall biomass in temperate forest is lower than in tropical forest, 2) non-fleshy
26 species, in particular acorns, comprise the majority of the fruit biomass in
27 temperate forest, 3) the duration of fruiting season is shorter in temperate forest,
28 and 4) in most temperate forests the fruiting peak occurs in autumn. Through
29 our comparative analyses on the fruiting and flushing phenology between Asian
30 temperate and tropical forests, we revealed that 1) fruiting is more annually
31 periodic (the pattern in one year is similar to the one in the next year) in
32 temperate forest in terms of the number of fruiting species or trees, 2) there is no
33 consistent difference in inter-annual variations in fruiting between temperate and
34 tropical forests, although some oak-dominated temperate forests exhibited
35 extremely large inter-annual variations in fruiting, 3) the timing of the flushing
36 peak is predictable (in spring and early summer) and 4) the duration of the
37 flushing season is shorter. The flushing season in temperate forests (17-28%
38 of that in tropical forests) was quite limited, even compared to the fruiting season
39 (68%). These results imply that temperate primates need to survive a long
40 period of scarcity of the young leaves and fruits, but the timing is predictable.
41 Therefore, dependence on low-quality foods would be indispensable for
42 temperate primates, such as mature leaves, buds, bark and lichens. Due to the
43 high predictability of the timing of fruiting and flushing in temperate forests, fat

44 accumulation during the fruit-abundant period and fat metabolization during the
45 subsequent fruit-scarce period can be an effective strategy to survive the lean
46 period (winter).

47 Keywords: fruit, primates, temperate forest, tropical forest, young leaf

48

49 Introduction

50 Latitude exerts a strong influence on various ecological phenomena: increased
51 species diversity at higher compared to lower latitudes (Eeley and Lawes 1999;
52 Badgley and Fox 2000; Stevens and Willig 2002; Hillebrand 2004; Takyu et al.
53 2005) and variation in animals' dietary strategies (Nakagawa et al. 1996; Zhou et
54 al. 2011) are well-known examples. Since primates are distributed over a large
55 latitudinal range, from 34°S to 41°N (Fleagle 1999), it is important to clarify the
56 latitudinal cline in their habitat to understand the variability with their ecology.
57 As a driving force behind the latitudinal cline of primates' ecological
58 characteristics, climate is sometimes cited, e.g. through its effect on
59 thermoregulation (Iwamoto and Dunbar 1983; Hanya et al. 2007). However,
60 biotic factors, such as food, are often direct causes. For example, within the
61 Japanese archipelago, the availability of mature leaves in winter changes with
62 latitude, and this significantly affects food quality (Nakagawa et al. 1996) and, in
63 turn, the population density of Japanese macaques (Takasaki 1981; Hanya et al.
64 2006).

65 In order to understand the ecology of generalist primary consumers,
66 such as primates, data on forest productivity are indispensable. Moreover,
67 since the essential difference between the temperate and tropical regions lies in
68 seasonality (Martyn 1992), comparisons of plant phenology are particularly
69 important. Global patterns of the variations in plant phenology have typically
70 been discussed separately for tropical and temperate regions (van Schaik et al.
71 1993; Lechowicz 1995; van Schaik and Pfannes 2005). However, a direct
72 comparison of habitat characteristics is needed in order to clarify the selective
73 pressure imposed on animals that had radiated from tropical to temperate

74 regions or vice versa. Primates in temperate regions are particularly interesting
75 for this purpose: they had originated in the tropics and lack special physiological
76 adaptations, such as hibernation, to survive in the cold winter (Fleagle 1999).
77 They eat a wide variety of foods, including the reproductive and vegetative parts
78 of plants as well as animal matter (Clutton-Brock 1977; Hohmann et al. 2006).
79 Therefore, temperate primates need to cope with a stronger seasonality of
80 various foods compared to that in the tropics.

81 Recently, progress has been made in the comparison between tropical
82 and temperate forests with regard to their characteristics as habitats for
83 consumers. In particular, patterns in fruit availability have largely been clarified,
84 at least those patterns occurring in a single year. Here, we summarize the
85 findings of these comparative studies. First, fruit production is generally larger
86 in tropical than in temperate forest, but there is a huge overlap between the two
87 regions (Hanya and Aiba 2010b). Based on a review of 51 temperate and
88 tropical forests throughout the world, Hanya and Aiba (2010b) found that fruit fall
89 in the tropical forests (average \pm SD: 454 ± 258 kg/ha/year, range: 32-1165) is,
90 on average, 1.71 times larger than that in the temperate forests (265 ± 227 ,
91 excluding Australia, range: 10-595). Although mean fruit fall is different
92 between the two regions, the ranges considerably overlap. For example, the
93 highest fruit fall in a temperate region (lowland forest in Yakushima, Japan) is
94 between the 6th and 7th highest levels among the 25 tropical sites.

95 Second, in temperate forests, the duration of the fruiting season is
96 shorter, but its peak is more predictable than in tropical forests. Using the data
97 taken from 48 sites in a single year, Ting et al. (2008) revealed that the duration
98 of the fruiting season (assessed by the circular standard deviation, see Method

99 for our comparative analysis of flushing) decreases with increasing absolute
100 latitude. When regressed on a Gaussian curve, the duration at the latitude of
101 35°N/S is 68% shorter than at the equator. The peak calendar months of
102 fruiting are variable among different regions of the tropics, but fruiting tends to
103 occur during a more limited time of the year (autumn) in temperate regions.

104 Third, the proportion of animal-dispersed fleshy fruits is larger in
105 tropical than in temperate forests, although there has been no systematic review.
106 For example, on the one hand, in tropical forests, fleshy-fruited species
107 constitute 76-100% in Peru, 65% in Costa Rica, 78-94% in other Neotropical
108 sites and >67% in Malaya (Willson et al. 1989). On the other hand, in 127
109 temperate forests of Japan, the proportion of fleshy-fruited species is 58% (Otani
110 2005). There have been a few studies on the proportion of fleshy fruits in the
111 actual biomass. In Kakachi, southern India, fleshy-fruits account for 36% of the
112 wet weight of fruit fall (Ganesh and Davidar 1999). In Lopé Reserve, Gabon,
113 fleshy fruits account for 54% of the total number of fallen fruits (White 1994).
114 By contrast with these tropical forests, in five warm- and cool-temperate forests
115 in Yakushima, Japan, fleshy fruits constitute only 3-37% of the fruit fall (Hanya
116 and Aiba 2010a). In these temperate forests, there is a common tendency for a
117 few (often only one) particular non-fleshy species, usually large-sized acorns of
118 Fagaceae or cones of conifers, to account for most (42-59%) of the fruit fall.
119 Although data are available from only a few sites, the same tendency is likely to
120 occur in other temperate forests because these species often become dominant
121 in temperate forests (Hendrick 2001).

122 In summary, these previous studies found that in temperate forests, fruit
123 availability is lower with respect to biomass and species composition and that

124 fruiting seasonality is stronger but predictable with respect to timing than in
125 tropical forests. However, we cannot yet draw the whole picture of temperate
126 and tropical forests as primate habitats. In addition to fruits and seeds, leaves
127 provide another major component of primate food, and their availability varies
128 across seasons (Clutton-Brock 1977). However, the global pattern in the
129 variability of young leaf availability has not yet been clarified, as in the case of
130 fruit availability. In addition, although the fruit availability pattern in a single year
131 has largely been clarified, supra-annual patterns remain unknown. This is
132 potentially an important factor in primate feeding ecology (Tsuji and Takatsuki
133 2012).

134 In this paper, we aim to clarify the differences between temperate and
135 tropical forests as food environments for primates, in particular the seasonality of
136 fruiting and flushing, which provide the two most important food resources for
137 primates. As a target region, we examine data from Asia. This is where
138 primates are distributed most extensively in the temperate region. In addition,
139 our data collection (see Method) revealed that virtually no data are available for
140 temperate forests in other primate habitats, such as North and South Africa,
141 Northern Argentina, and Southern Madagascar. Specifically, we compare two
142 aspects of supra-annual patterns of fruiting: the intensity of annual periodicity
143 and inter-annual variations. As for flushing, we examine data on the time of the
144 flushing peak and the duration of the flushing season. Finally, we discuss the
145 implications of the differences in habitat, revealed by this and previous studies,
146 on primate feeding ecology.

147

148 Method

149 In this paper, we regard the border between temperate and tropical Asia as the
150 Tropic of Cancer (23°26'N).

151 Data on community-wide fruiting and flushing phenology for
152 comparative analysis were obtained from the literature (Supplementary Material).
153 We used the ISI Web of Science (<http://apps.isiknowledge.com/>). For fruiting,
154 on December 22, 2011, we conducted our search by inputting the keywords 'fruit
155 AND phenology'. As for flushing, on December 19, 2011, we used the
156 keywords 'phenology AND flushing OR young leaf'. These searches produced
157 1713 and 477 results, respectively. We also examined 348 papers on primate
158 feeding ecology. We read the abstracts of these papers and selected those
159 papers that referred to the community-wide phenology in Asian primate habitat
160 countries. If we judged that the study did not include systematic sampling or
161 the sampling interval was more than a month, we did not use the paper. As for
162 fruiting, we were interested in the supra-annual patterns, so we included only the
163 studies that covered at least two consecutive years. For flushing, we included
164 all of the papers whose studies lasted at least one year in order to increase the
165 sample size. In addition, in the analysis of inter-annual variation of fruiting, we
166 also included data of 10 sites that did not include monthly values of fruit fall but
167 did report the annual values for multiple study years. As for fruiting, data were
168 available from 24 sites with latitudes of 0°S-42°N. Since some authors reported
169 phenology data using multiple indices, we analyzed 31 datasets in total. As for
170 flushing, we examined data from 17 sites (17 datasets), with latitudes of
171 3°N-42°N. The number of sites was 9 in tropical and 15 in temperate forests for
172 fruiting and 8 and 9 for flushing (see Supplementary Materials for details about
173 the study sites).

174 Each study used at least one of the following indices on phenology: (1)
175 number of species, (2) number of plant individuals (whether climbers are
176 included or not depends on the study), (3) sum of basal area of trees, and (4)
177 weight of litter fall. We conducted analysis separately for these four types
178 except for the analysis of flushing peak because peak is expected to coincide
179 with whatever index is used (Hanya and Aiba 2011). Because of data
180 availability, only (1), (2) and (4) were analyzed for fruiting and only (1), (2) and
181 (3) were used in the analysis of flushing. Because data of (3) for flushing were
182 available for tropical regions only and that of (1) were for temperate regions only,
183 these data were used only to compare flushing peak with latitude.

184 These different indices are expected to correlate with each other, and
185 thus any difference between the regions in at least one of the indices suggests
186 there is a difference in food availability in a broad sense. However, these
187 indices represent different aspects of food availability, and thus the discrepancy
188 in the results among indices may explain the situation that the primates are
189 facing. The number of fruiting/flushing species indicates the diversity available
190 to primates for a given period. The number of fruiting/flushing plant individuals
191 represents the number of patches, thus it is likely to correlate with the searching
192 cost for primates (Hanya 2009). The sum of basal areas or the weight of litter
193 would be more strongly correlated with the actual food biomass than with other
194 indices. Therefore, we treat all of the indices separately in the analysis.
195 However, caution needs to be taken in the interpretation of the results because
196 the data sources are different for different indices.

197 For each study site, we collected the following information: (1) latitude,
198 (2) longitude, (3) annual average temperature, and (4) annual precipitation.

199 The direct effect of longitude on phenology was not assessed but used only to
200 calculate the inter-site distance in order to correct the spatial autocorrelation.
201 We used the absolute values of latitude in the analysis of its effect on phenology;
202 therefore, northern and southern hemispheres were treated equally. Data on
203 annual average temperature and annual precipitation were derived from original
204 publications whenever possible. When not available, data from the nearest
205 meteorological station were used, using the database 'World Climate'
206 <http://www.climate-charts.com/>. In cases where the altitude of the
207 meteorological station differed from the study site by more than 200 m, we
208 corrected the temperature value by assuming that the temperature lapse rate is
209 0.6°C/100 m (Martyn 1992). This database is reliable because the temperature
210 and precipitation values from the original literature significantly positively
211 correlated with the values obtained through this database (temperature: $r=0.93$,
212 $p=2.59 \times 10^{-9}$; precipitation: $r=0.84$, $p=1.66 \times 10^{-6}$).

213 We defined the index on phenology as follows:

214 *Annual periodicity of fruiting*: In order to control the length of the study period, we
215 used the data of the first 24 months only. We performed a series of (12)
216 generalized linear models (GLM) using cosine wave functions (Anderson et al.
217 2005) with periodicities of 12 months having maximum values in either of the 12
218 months. We used the R^2 value of the best-fit model (with lowest Akaike
219 Information Criterion AIC) as an index of the degree of annual periodicity
220 (Hanya and Aiba 2011).

221 *Inter-annual variation of fruiting*: We examined the data of the first 24 months
222 only. We quantified its intensity as (sum of the 12 months, year of larger
223 value)/(sum of the 12 months, year of the smaller value).

224 *Peak of flushing*: Following Ting et al. (2008), we defined the peak as the circular
 225 average of the value of the first 12 months. The arithmetic average of February
 226 (month 2) and December (month 12) is July (month 7), but in reality, it should be
 227 January. Therefore, we need to apply ‘circular’ statistics when examining
 228 annual cycles. Each month i (=Jan, Feb, ...) was converted to an angle series
 229 a_i (=15°, 45°, ...). Using the corresponding number of flushing index (e.g.
 230 number of species), f_i (normalized by dividing by average), the mean angle
 231 (0°-360°, roughly equivalent to the day of the year) of flushing, μ_f , was calculated
 232 as follows:

$$\mu_f = \begin{cases} \text{If } C > 0, S \geq 0 & \mu_f = \arctan (S/C) \\ \text{If } C = 0, S > 0 & \pi/2 \\ \text{If } C < 0 & \arctan (S/C) + \pi \\ \text{If } C \geq 0, S < 0 & \arctan (S/C) + 2\pi \\ \text{Undefined if } C = 0, S = 0 & \end{cases}$$

238 whereas

$$239 \quad C = \frac{\sum_{i=1}^{12} f_i \cos a_i}{12}$$

$$240 \quad S = \frac{\sum_{i=1}^{12} f_i \sin a_i}{12}$$

241 *Flushing duration*: Following Ting et al. (2008), we defined the duration as the
 242 circular standard deviation of the value of the first 12 months. Circular standard
 243 deviation s was calculated as:

$$244 \quad s = \frac{180\sqrt{-2 \ln r}}{\pi}$$

245 whereas

246 $r = 1 - \sqrt{C^2 + S^2}$

247 r is the relative length of the mean vector, ranging from 0 to 1.

248 Following a similar analysis of fruiting (Ting et al. 2008), we examined
249 the peak of flushing only graphically because the obtained results are circular
250 values and thus not suitable for conventional statistics, such as the t-test. For
251 this parameter, we are interested only in whether the peak month is
252 concentrated in a particular season. As for the other parameters of phenology,
253 we examined the effects of environmental factors in three ways: (1) a simple
254 t-test between the temperate and tropical Asia, (2) generalized least squares
255 (GLS) regression on the effect of location (absolute latitude), and (3) GLS
256 regression on the effect of climate (annual average temperature and
257 precipitation). We separated location and climate models because these two
258 factors affect phenology at different causal levels: In principle, location
259 determines climate and climate in turn determines phenology. GLS models are
260 similar to general linear models (GLM), except that their estimates of standard
261 errors and type-I errors are more realistic in the presence of spatially correlated
262 residuals (Dormann et al. 2007). GLS models also prevent clusters of sites
263 from exerting undue (pseudo-replicated) influence on estimates of beta
264 coefficients, which may be an important consideration if study sites are not
265 uniformly distributed in space (Ting et al. 2008). Among the three common
266 variogram models, we used 'Gaussian' because it always fit the data most. For
267 both location and climate models, we ran the full models and examined the effect
268 of the independent variables. All of the statistical analyses were conducted
269 using R 2.13. 2. (© 2011 The R Foundation for Statistical Computing), and GLS
270 models were fit using the 'gls' command of the 'nlme' package.

271

272 Results

273 Fruiting

274 Annual periodicity in fruiting was larger in temperate than in tropical forests.

275 The difference was significant when assessed by the number of species ($t=2.71$,

276 $p=0.030$) and by the number of plant individuals ($t=2.83$, $p=0.025$), but not when

277 assessed by fruit litter ($t=0.13$, $p=0.90$; Fig. 1). According to the GLS location

278 models, the effect of absolute latitude was significant when assessed by the

279 number of species and plant individuals, but was not significant when assessed

280 by fruit litter (Table 1abc). Climate models indicated that temperature

281 significantly negatively affected the annual periodicity when assessed by the

282 number of plant individuals or fruit litter but not when assessed by the number of

283 species (Table 1def). There was also a tendency for annual periodicity to be

284 higher in drier areas when assessed by the number of plant individuals (Table

285 1e) but not when assessed by other indices (Table 1df).

286 There was no significant difference in inter-annual variation of fruiting

287 between temperate and tropical forests when assessed by the number of

288 species ($t=1.92$, $p=0.096$) or plant individuals ($t=0.98$, $p=0.36$) or by fruit litter

289 ($t=0.48$, $p=0.64$) (Fig. 2). None of the GLS models included absolute latitude as

290 a significant variable (Table 2abc). Among the climate models, the only

291 significant independent factor was precipitation (positive) when assessed by the

292 number of plant individuals (Table 2def). Inter-annual variation in some

293 temperate forests (Uji and Chichibu in Japan) was quite large (779 and 2608,

294 respectively). Fruit fall in these forests was dominated by acorns (*Quercus* or

295 *Fagus*).

296

297 Flushing

298 The flushing peak in tropical Asia occurred in various periods of a year, but in
299 temperate Asia, the peak occurred only in spring and early summer (April
300 through June, Fig. 3).

301 Length of flushing season was longer in tropical than in temperate Asia
302 when assessed by the number of plant individuals ($t=2.59$, $p=0.032$) (Fig. 4).
303 GLS location also included absolute latitude as a significant factor (Table 3a).
304 The circular standard deviation of flushing season in tropical Asia (mean+SD:
305 $65+51$ when assessed by the number of plant individuals) was 2.7 times longer
306 than in temperate Asia ($24.5+4.4$). Data with the number of species was
307 available only for temperate Asia, but it was also very short ($18.7+6.4$). None of
308 the factor was significant in the climate model (Table 3b).

309

310 Discussion

311 Overall, the difference between temperate and tropical Asia was made clear
312 both in the t-test and the GLS analyses. Since the vegetation in the Japanese
313 archipelago is diverse and shares many similarities with continental temperate
314 East Asia (Hendrick 2001; Takyu et al. 2005), we believe that Japan can be used
315 as a representative in East Asian temperate primate habitat. So far, data from
316 other temperate regions are deficient to examine the validity of our conclusion,
317 and our conclusions should be reexamined in the future when data are
318 accumulated for other temperate regions.

319

320 Fruit availability

321 Our comparative study revealed that fruiting is more annually periodic in
322 temperate than in tropical Asia but that there is no consistent difference in
323 inter-annual variations.

324 There are two aspects of predictability in the timing of fruiting. One is
325 the inter-site predictability shown by Ting et al. (2008). They indicated that the
326 timing of fruiting peak is more or less the same period of a year (autumn) in any
327 temperate forest. The other aspect is inter-annual predictability, or annual
328 periodicity, shown by our analysis. We have shown that the fruiting phenology
329 in one year is similar to that in another year in the same area. However, this is
330 true only at the plant species or individual level, not at the level of fruit biomass.
331 Hanya and Aiba (2011) pointed out that when assessed by the fruit biomass,
332 community-level annual periodicity can be disturbed by the heavy fruiting of a
333 few species that bear fruits out of the fruiting peak. Therefore, primates in
334 temperate forests are likely to experience the same degree of species diversity
335 and patch density for fruit resources in the same calendar month of different
336 years. However, the season when fruits are most abundant (in terms of
337 biomass) may be different over years, as in tropical forests. Analyses of
338 climate models indicated that not only colder habitats but also drier habitats
339 tended to show an annual periodic pattern of fruiting. In these areas, plant
340 fruiting behavior is constrained by seasonal climatic stress, such as drought or
341 winter coldness, which comes at a predictable period each year. However,
342 again, with regard to fruit biomass, no such tendency was found.

343 We could not find any consistent differences in the inter-annual
344 variations between the temperate and tropical Asia. It is already known that
345 inter-annual variations in fruiting can be large in lowland dipterocarp forests in

346 Southeast Asia, where mast fruiting occurs (Sakai 2002); however, the degree of
347 variability seems even larger in some temperate forests when assessed by fruit
348 litter. Since we could not detect any such huge inter-annual variations when
349 assessed by the number of species or plant individuals, this large variation is
350 caused mainly by the heavy fruiting of individual plants, not by the within- or
351 between-species synchronization of fruiting. Four temperate sites exhibited
352 larger inter-annual variations than the maximum value in tropical forests (14.1 in
353 Danum Valley, Borneo). In all four of these forests, almost 100% of the fruit fall
354 was occupied by acorns, such as *Quercus* and *Fagus*. Masting of acorns
355 seems to occur at a much larger scale than any other plants, and thus the
356 dominance of Fagaceae in many temperate forests seems to result in extreme
357 community-level inter-annual variability in some temperate forests. The
358 extreme variability in temperate regions in our dataset probably arose because
359 we assessed inter-annual variability using data of only two years. In our
360 method, intensified inter-annual variation would be detected only when either
361 one of the two years included mast years. In the future, we need to assess
362 inter-annual variability with phenology data of many years, which are currently
363 not available. We found a significant effect of precipitation on inter-annual
364 variability when assessed by the number of plant individuals, but we are not
365 aware of any biological explanation for it.

366

367 Young leaf availability

368 The characteristics of flushing phenology in temperate and tropical Asia are
369 summarized as follows: 1) peak timing (spring or early summer) is similar among
370 different sites in temperate regions but that in the tropics is variable, and 2) the

371 duration of young leaf availability is shorter in temperate than in tropical regions.

372 The duration of flushing season in temperate Asia was only 17-28% of
373 that in tropical Asia, and the difference between the two regions was even
374 greater than in the case of fruiting (68%) (Ting et al. 2008). Since the circular
375 standard deviation of fruiting season at 30°N/S is 80 (Ting et al. 2008), the small
376 value of flushing in temperate forest (18.7-24.5) indicates that, in temperate
377 forests, young leaf is a temporarily more limited resource than fruit. In fact, in
378 many temperate forests analyzed in this study, flushing was observed for only 2
379 months in a year.

380 The flushing peak was observed only during a limited period of a year
381 in temperate forests. At >20°N in the Asia, the flushing peak occurred only in
382 April, May and June. Fruiting also tends to have a peak in a limited season
383 (autumn) (Ting et al. 2008); however, the actual peak month was more variable
384 than in the case of flushing: at >30°N, fruiting peak occurred in September
385 through January and, in one case, in June (Ting et al. 2008).

386 The highly predictable peak months and the short duration of flushing
387 season is probably the result of cold stress in winter, which is shared by all of the
388 temperate plants. Cold stress should inhibit plant photosynthetic activity, and
389 once plants are released from this stress after winter, it is important for them to
390 flush young leaves immediately in order to increase net annual productivity. It
391 may be possible for even tropical plants to increase photosynthetic activity by
392 synchronizing flushing with abiotic climatic events, such as solar maxima (van
393 Schaik et al. 1993). However, in our current data set, there was no
394 circular-circular correlation between the time of solar maxima and the flushing
395 peak ($r=0.12$, $p=0.54$). Thus, the selection pressure to make tropical plants

396 synchronize flushing to solar maxima is not so large as the cold stress in
397 temperate regions.

398

399 Implications for primate ecology

400 The temperate region harbors approximately 20 genera of primates, including
401 *Microcebus*, *Cheirogaleus*, *Hapalemur*, *Lemur*, *Eulemur*, *Lepilemur*, *Avahi*,
402 *Propithecus*, *Nycticebus*, *Leontopithecus*, *Alouatta*, *Aotus*, *Brachyteles*, *Cebus*,
403 *Chlorocebus*, *Cercopithecus*, *Papio*, *Macaca*, *Trachypithecus*, *Presbytis*,
404 *Semnopithecus*, *Rhinopithecus*, and *Hylobates* living in East Asia, North and
405 South Africa, South America and Madagascar (Fleagle 1999). Our analyses on
406 habitat included only Asia, thus our discussion on implications for primate
407 ecology is primarily applicable to Asian primates. However, it may lead the way
408 for future investigations into adaptations of temperate primates of various taxa
409 living in other regions.

410 First, we found that fruit and young leaf availability is smaller than in
411 tropical forest in terms of biomass (smaller fruit fall), seasonality (shorter fruiting
412 and flushing season), and species composition (smaller proportion of fleshy
413 fruits). Therefore, it is predicted that temperate primates need to survive a long
414 period of scarcity of young leaves and fruits. In accordance with this the
415 prediction, both Hanya (2004) and Grueter et al. (2009), who proposed fallback
416 strategies of Japanese macaques and Chinese snub-nosed monkeys,
417 respectively, pointed out that during the lean period (winter), primates fall back to
418 lower-quality foods than fruits and young leaves, such as mature leaves, lichens,
419 bark and buds. We also found that the flushing season in temperate forest
420 (17-28% of that in tropical forest) was quite limited even compared with the

421 fruiting season (68%). Fruits and seeds sometimes become the main food
422 even for temperate primates (Hanya et al. 2011a), but young leaf is never
423 reported to be so (Grueter et al. 2009). When fruit availability is low, young leaf
424 is often an option as a fallback food for tropical primates (Kanamori et al. 2010;
425 Hanya and Bernard 2012), but it is impossible for temperate primates to rely on
426 young leaves, in particular in winter, when fruit scarcity is likely to occur in
427 temperate forests.

428 Another finding of our analysis was the high predictability of fruiting
429 phenology in temperate forest. Concerning this, Hanya (2004) pointed out the
430 effectiveness of fat accumulation as another fallback strategy for temperate
431 primates. Accumulation of fat during the fruit-abundant period and
432 consumption during the subsequent fruit-scarce period can be an effective
433 strategy if the timing of the end of the lean season is predictable. If not, animals
434 cannot predict the amount of fat necessary to survive the lean period, and thus
435 heavy reliance on accumulated fat is a risky strategy. Fat accumulation has
436 been widely reported among temperate macaques (Wada 1975; Zhao 1994;
437 Muroyama et al. 2006) and other endotherms (Pond 1978). However, there
438 has been no reported evidence for other temperate primates, such as colobines.
439 Temperate colobus monkeys, as well as temperate macaques, increase fruit- or
440 seed-eating in autumn (Guo et al. 2007; Sayers and Norconk 2008; Grueter et al.
441 2009). It is not clear whether the nutritional condition of colobus monkeys
442 actually improves so much as to accumulate fat by the consumption of fleshy
443 fruits. Consumption of a large amount of carbohydrates or fleshy fruits abruptly
444 changes the pH of the forestomach of colobines, which is believed to cause fatal
445 affliction (acidosis) (Kay and Davies 1994). However, fleshy ripe fruit is known

446 to become a main food, at least in a particular season for two species of
447 colobines (Sayers and Norconk 2008; Grueter et al. 2009). Future studies on
448 the digestive physiology of colobines, in particular the digestion of fleshy fruits,
449 and their ability of fat accumulation are necessary in order to understand their
450 fallback strategy in temperate regions.

451 In addition to feeding strategy, the strong seasonality and high
452 predictability in food availability in temperate forests may also affect other
453 aspects of primate ecology. Temperate primates may exhibit seasonal
454 breeding (Valdespino 2007), larger home range size (Li et al. 2000; Hanya et al.
455 2006; Grueter et al. 2008), lower species diversity (Eeley and Lawes 1999) and
456 lower biomass (Hanya et al. 2011b). Systematic comparisons are necessary to
457 confirm whether primates show dichotomy between temperate and tropical
458 regions with respect to these characteristics and how it relates to the
459 characteristics of temperate forests revealed by this study.

460

461 In conclusion, we have shown that in temperate forests, fruit and young leaf
462 availability is smaller than in tropical forest in terms of biomass (smaller fruit fall),
463 seasonality (shorter duration fruiting and flushing season), and species
464 composition (smaller proportion of fleshy fruits). Both fruiting and flushing tend
465 to occur in a limited period of a year, that is, autumn and spring, respectively.
466 Predictability of fruiting season, both in terms of space and over time, was higher
467 in temperate than in tropical forest. In response to this variation, we predict that
468 temperate primates rely on more low-quality food, such as mature leaves,
469 lichens, bark and buds. High predictability of fruiting seasonality enables the
470 temperate primates to rely on fat which was accumulated during the

471 fruit-abundant period to survive the fruit-scarce winter.

472

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481

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616 Legends of figures

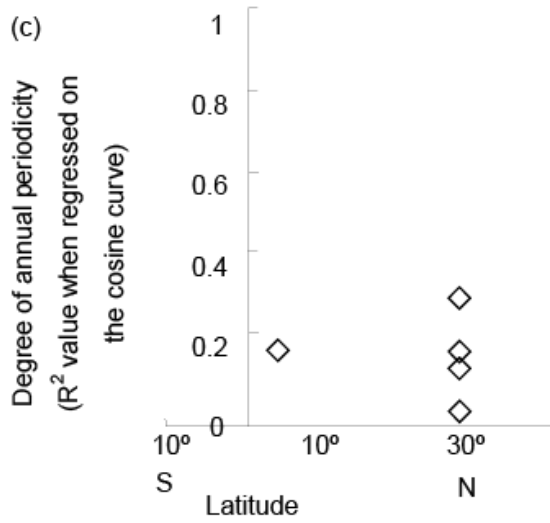
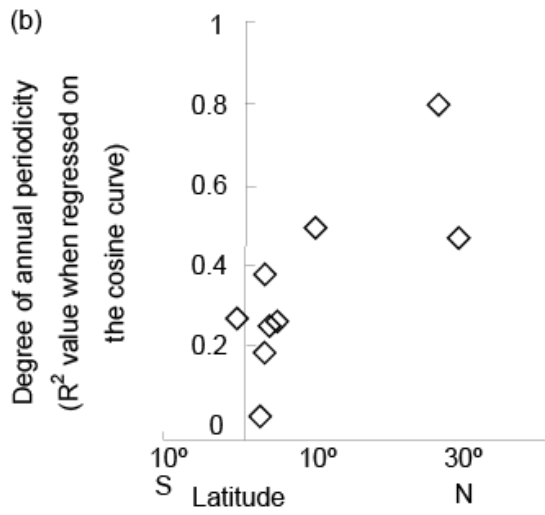
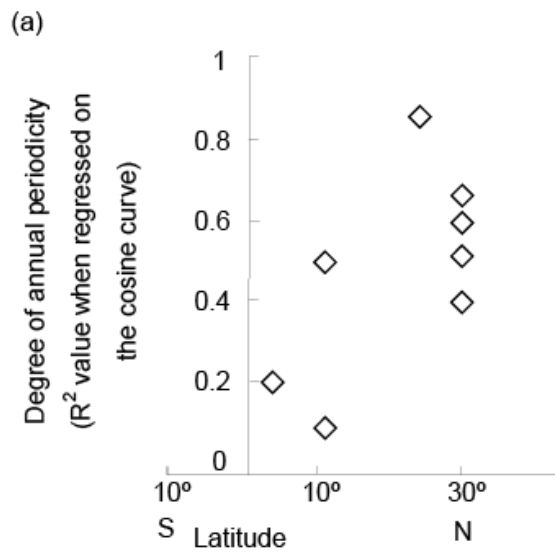
617 Fig. 1. Latitudinal variations in the degree of annual periodicity in fruiting. Index
618 of annual periodicity was the R^2 value of the correlation model of monthly
619 phenology for two years on a cosine wave function having periodicity of 12
620 months. (a) When fruiting phenology is assessed by the number of species,
621 (b) number of plant individuals, and (c) fruit biomass.

622 Fig. 2. Latitudinal variations in the intensity of inter-annual variations of fruiting.
623 The intensity was calculated by dividing the sum of one year (the one with the
624 larger value) by the sum of the other year (smaller value). (a) When fruiting
625 phenology is assessed by the number of species, (b) number of plant
626 individuals, and (c) fruit biomass.

627 Fig. 3. Latitudinal variations in peak flushing months. Lines indicate the time of
628 solar maxima.

629 Fig. 4. Latitudinal variations in the length of flushing seasons, assessed by
630 circular standard deviation, when the flushing phenology is assessed by the
631 number of plant individuals.

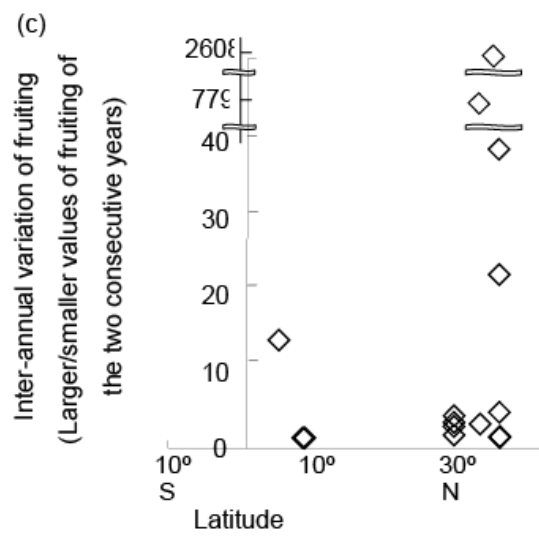
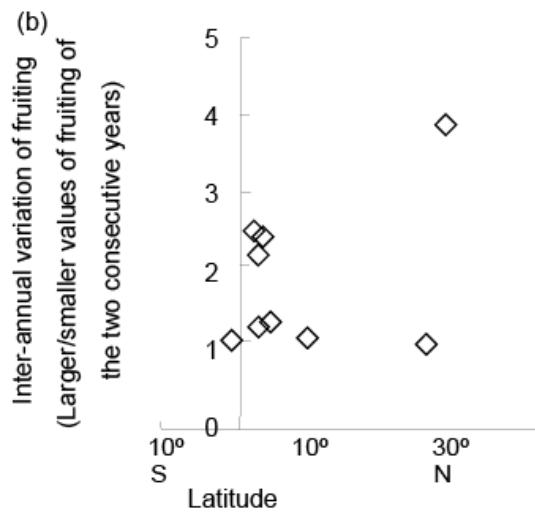
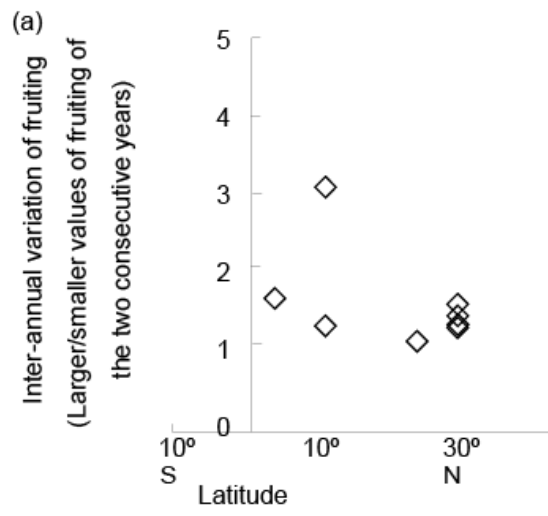
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634 Fig. 1

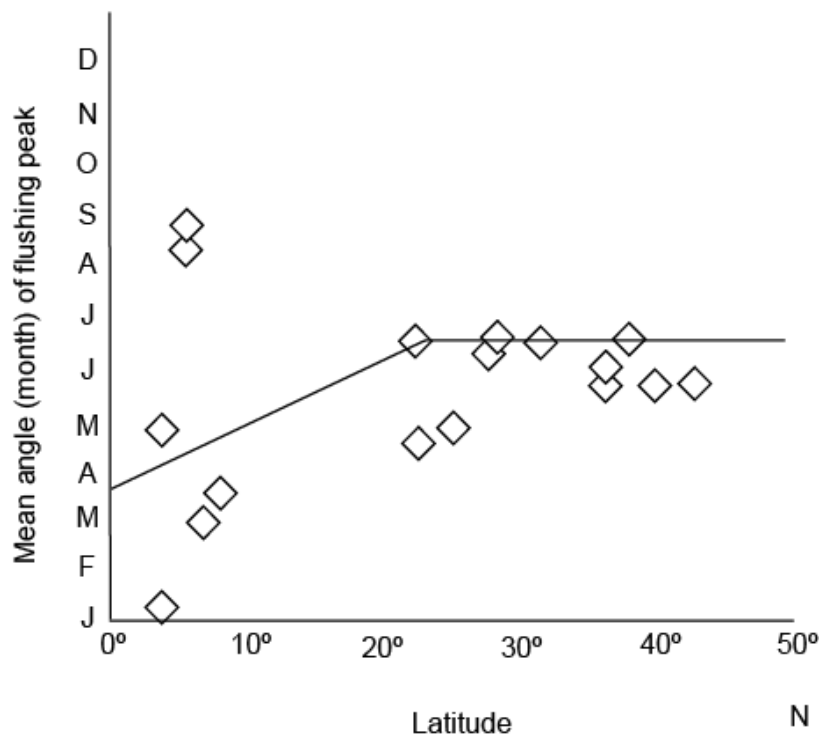
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637 Fig. 2

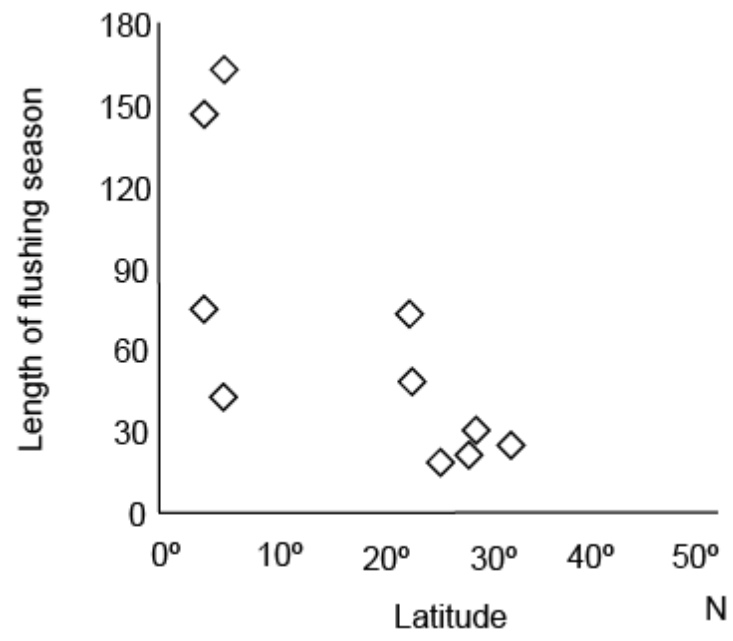
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640 Fig. 3

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643 Fig. 4

644

Table 1. GLS models on the effect of location or climate on annual periodicity in fruiting

a. Effect of location, assessed by the number of species

	Coefficient	SE	t	p
(Intercept)	0.12	0.16	0.73	0.49
Absolute latitude	0.02	0.01	2.90	0.02

b. Effect of location, assessed by the number of plant individuals

	Coefficient	SE	t	p
(Intercept)	0.22	0.08	2.88	0.02
Absolute latitude	0.01	0.00	2.96	0.02

c. Effect of location, assessed by the fruit litter

	Coefficient	SE	t	p
(Intercept)	0.19	0.16	1.20	0.32
Absolute latitude	0.00	0.01	-0.09	0.93

d. Effect of climate, assessed by the number of species

	Coefficient	SE	t	p
(Intercept)	1.37	0.57	2.41	0.05
Rainfall	0.00	0.00	-1.24	0.26
Temperature	-0.04	0.03	-1.41	0.21

e. Effect of climate, assessed by the number of plant individuals

	Coefficient	SE	t	p
(Intercept)	1.16	0.16	7.22	0.00
Rainfall	0.00	0.00	-2.56	0.04
Temperature	-0.03	0.01	-4.63	0.004

f. Effect of climate, assessed by the fruit litter

	Coefficient	SE	t	p
(Intercept)	0.78	0.22	3.59	0.07
Rainfall	0.00	0.00	0.56	0.63
Temperature	-0.03	0.00	-8.03	0.02

646

647

Table 2. GLS models on the effect of location or climate on intensity of inter-annual variations in fruiting

a. Effect of location, assessed by the number of species

	Coefficient	SE	t	p
(Intercept)	2.18	0.43	5.09	0.00
Absolute latitude	-0.03	0.02	-1.66	0.14

b. Effect of location, assessed by the number of plant individuals

	Coefficient	SE	t	p
(Intercept)	1.45	0.51	2.88	0.02
Absolute latitude	0.03	0.03	1.07	0.32

c. Effect of location, assessed by the fruit litter

	Coefficient	SE	t	p
(Intercept)	-291.15	779.31	-0.37	0.71
Absolute latitude	30.88	26.74	1.15	0.27

d. Effect of climate, assessed by the number of species

	Coefficient	SE	t	p
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	nt			
(Intercept)	1.05	1.36	0.77	0.47
Rainfall	0.00	0.00	-0.40	0.70
Temperature	0.03	0.06	0.56	0.60

e. Effect of climate, assessed by the number of plant individuals

	Coefficie nt	SE	t	p
(Intercept)	0.91	0.97	0.93	0.39
Rainfall	0.00	0.00	3.19	0.02
Temperature	-0.03	0.03	-0.91	0.40

f. Effect of climate, assessed by the fruit

litter

	Coefficie nt	SE	t	p
(Intercept)	476.96	371.4 8	1.28	0.22
Rainfall	0.00	0.01	-0.06	0.95
Temperature	0.07	3.19	0.02	0.98

649

650

Table 3. GLS models on the effect of location or climate on the length of flushing season

a. Effect of location, assessed by the number of plant individuals

	Coefficient	SE	t	p
(Intercept)	123.07	22.23	5.54	0.00
Absolute latitude	-3.32	1.08	-3.07	0.02

b. Effect of climate, assessed by the number of plant individuals

	Coefficient	SE	t	p
(Intercept)	-19.83	48.19	-0.41	0.69
Rainfall	0.02	0.02	0.66	0.53
Temperature	2.66	2.91	0.91	0.39