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1   Fruiting and flushing phenology in Asian tropical and temperate forests:

2   implications for primate ecology

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14   Running title: Fruiting and flushing phenology

15

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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

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   <u>Tropic of Cancer</u> (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*10^{-9}; precipitation: r=0.84, p=1.66*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:

233   $\qquad\qquad$ If $C > 0$, $S \geq 0$ $\mu_f = arctan\ (S/C)$

234   $\qquad\qquad$ If $C = 0$, $S > 0$ $\pi/2$

235   $\mu_f\ =$ $\qquad$ If $C < 0$ $\qquad\qquad$ $arctan\ (S/C) + \pi$

236   $\qquad\qquad$ If $C \geq 0$, $S < 0$ $arctan\ (S/C) + 2\pi$

237   $\qquad\qquad$ Undefined if $C = 0$, $S = 0$

238   whereas

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

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

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   $s = \dfrac{180\sqrt{-2\ln r}}{\pi}$

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 $>20^{\circ}$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 $>30^{\circ}$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.

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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-annul 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
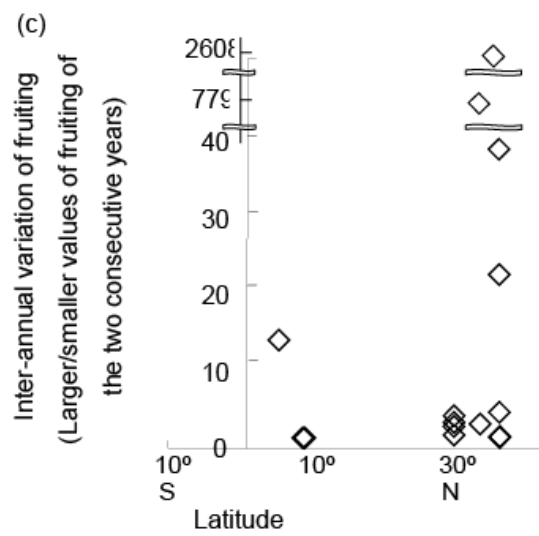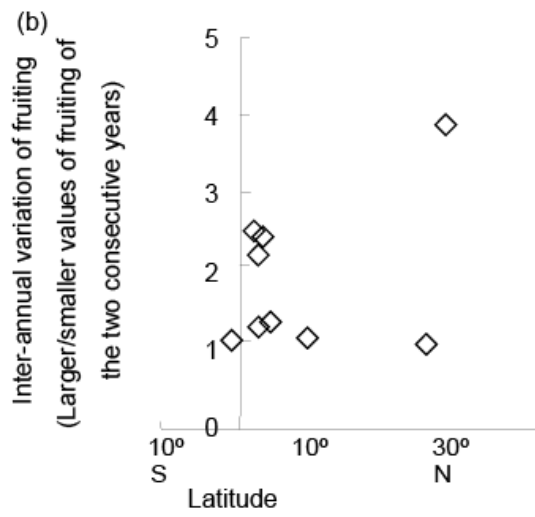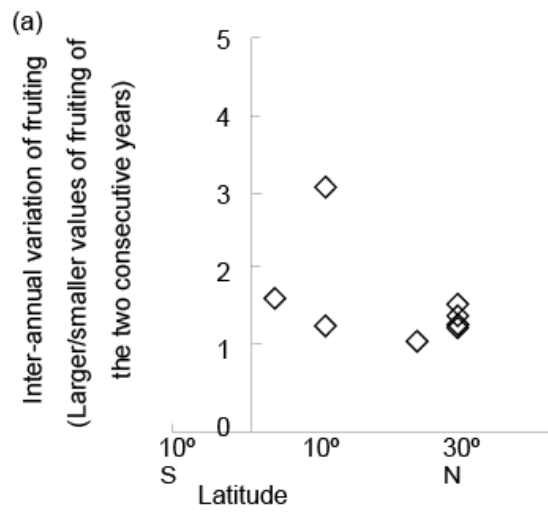
631   number of plant individuals.

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(a)

(b)
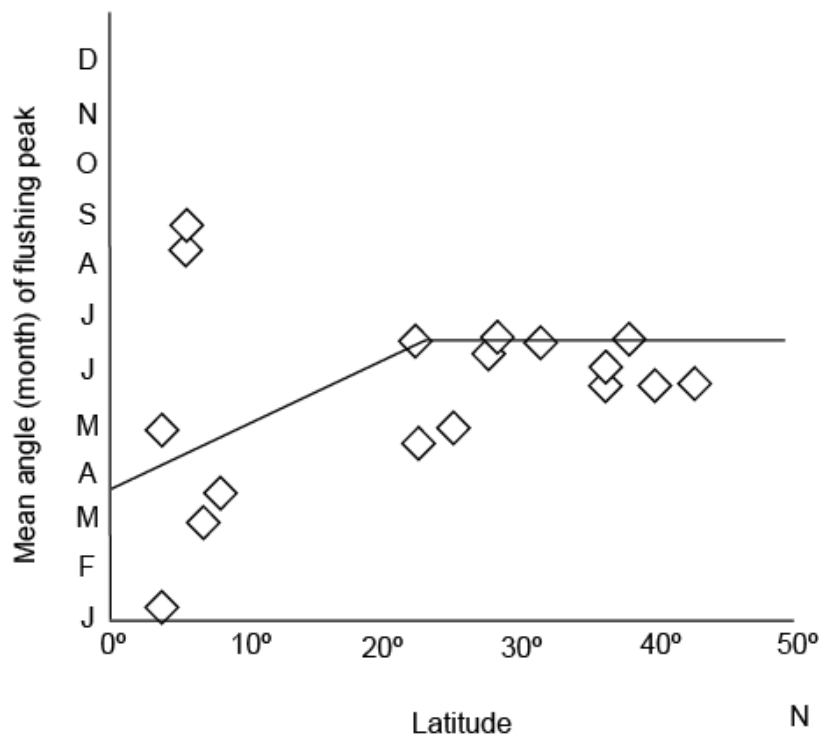
(c)

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634   Fig. 1
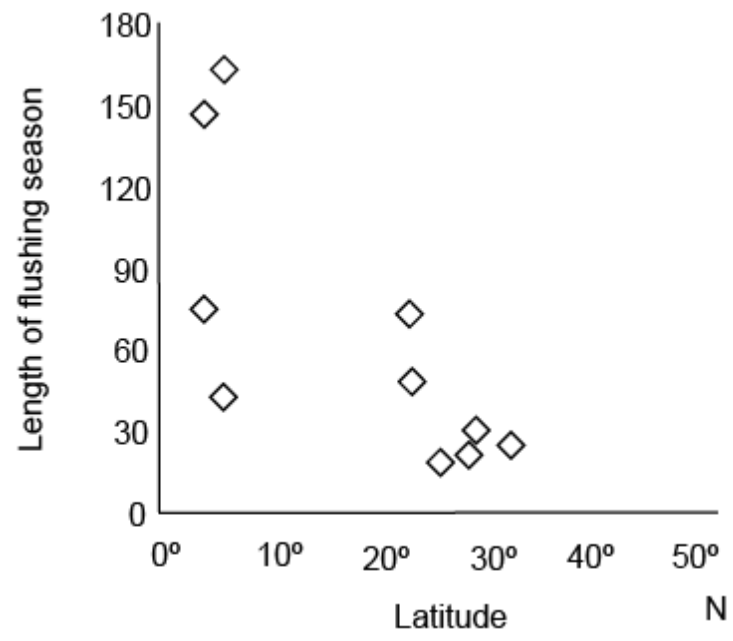
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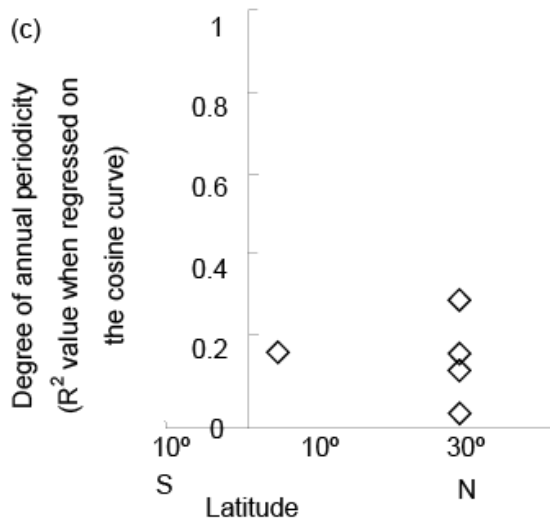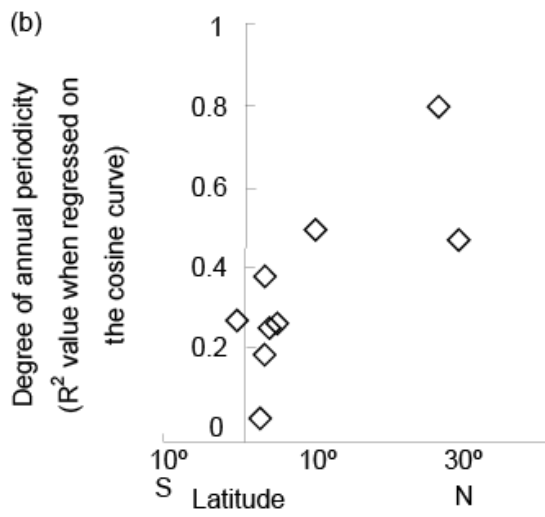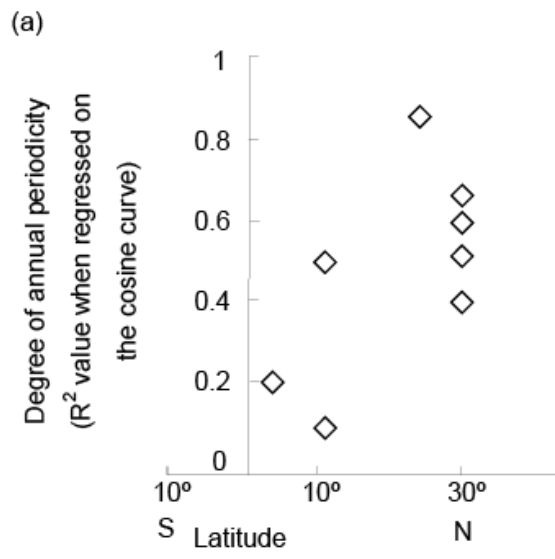
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637   Fig. 2

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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

	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

	Coefficient	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

	Coefficient	SE	t	p
(Intercept)	476.96	371.48	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