



## Seasonality in fruit availability affects frugivorous primate biomass and species richness

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We examine the effect of total annual food abundance and seasonal availability on the biomass and species richness for frugivorous primates on three continents ( $n=16$  sites) by data on fruit fall. We reveal that the best-fit models for predicting primate biomass include total annual fruit fall (positive), seasonality (negative) and biogeography (Old World > New World and mainland > island) and that these factors explain 56–67% of the variation. For the number of species, the best-fit models include seasonality (negative) and biogeography (Old World > New World and mainland > island) but not total annual fruit fall. Annual temperature has additional effects on primate biomass when the effects of fruits and biogeography are controlled, but there is no such effect on species richness. The present results indicate that, measured on local scales, primate biomass and number of species is affected by the seasonal variation in food availability.

What determines the number of species in local communities and the abundance of individuals in each species present? This remains a fundamental question in ecology. Species–energy theory predicts that sites with more food will support more individuals, and thus more species (Connell and Orias 1964), although other factors, such as predation, disease, past catastrophes, and biogeography also play a role (Young 1994, Kay et al. 1997). Supporting the theory, positive correlations between energy availability and species richness have been reported in birds (Evans et al. 2006) and primates (Stevenson 2001). This theory is based on the reasoning that the probability of local extinction of a species or the speciation rate is affected by its population size (Turner 2004). Other various mechanisms are also proposed (Evans et al. 2005). For example, energy availability may affect niche position and diversification rate, and then in turn species richness.

However, food availability is not constant over time and this may affect animal population size, and therefore persistence. For example, in most temperate forests, no fruits are available for several months in the year (Hanya et al. 2004), and the density of frugivorous animals may be negatively affected by strong seasonality. However, animals are known to have evolved a number of adaptations to cope with seasonality (van Schaik et al. 1993), so their number

may not be affected by seasonality. Theoretically, animals having the ability to ‘store’ excess food during the food-abundant period (e.g. fat accumulation or scatter-hoarding) should not be affected by the seasonality in food availability but rather by the annual total (Hanya et al. 2006). On the other hand, animals are predicted to be affected by the lowest level of food availability, if they survive solely by depending on the food available for the current period. van Schaik and Brockman (2005) predicted that large animals would be more tolerant to strong seasonality than would small animals, due to their tolerance of low-quality foods and their ability to accumulate fat.

The effect of seasonality on animal abundance has been tested largely using climatic measures, such as seasonality in rainfall, photosynthetically active radiation, and temperature (Kay et al. 1997, Barcena et al. 2004, van Schaik et al. 2005, Barton and Zalewski 2007, Canavero et al. 2009). These climatic factors either work directly, by imposing thermoregulatory cost or drought stress (Canavero et al. 2009), or indirectly through food (Barton and Zalewski 2007). However, even when food is expected to be the true determinant and climate works only indirectly through food, to our knowledge, no community-level study has examined the direct effect of seasonality in food availability, which is independent of total annual food availability.

Primates are a useful taxon for testing the effect of seasonality independent of total annual food availability. First, they live in a broad array of habitats, ranging from clearly seasonal temperate forest to tropical forest with very little seasonality. Second, data on absolute biomass, which are rare for other taxa, are available for many primate communities. In the case of folivorous primates, they exhibit a remarkably robust pattern in that their abundance is determined by the quality of mature leaves (protein/fiber ratio) available in the habitat. This pattern is consistent among various lineages of primates, including colobines, howler monkeys and lemurs (Milton 1979, Oates et al. 1990, Ganzhorn 1992, Chapman et al. 2004). The folivorous primate example clearly indicates that animals are limited by the food available in their habitat. In the case of frugivorous primates, Stevenson (2001) found that fruit availability, estimated by fruit fall, positively affected the biomass and the number of species among New World primates, but he did not examine the effect of seasonality. Hanya et al. (2004) offer an example examining both total annual food availability and seasonality, and revealed a stronger influence of total annual food availability, although they compared only three sites for one species (*Macaca fuscata yakui*). Kinnaird and O'Brien (2005) compared primate biomass between Sulawesi and Sumatra and clarified that both fruit availability and primate biomass is higher in Sulawesi than in Sumatra, although the fruiting pattern was more seasonal in Sulawesi. At the global scale, Ganzhorn et al. (2009) suggested that a higher species richness of frugivorous in the New World than in Madagascar is explained by the higher protein content of fruits there.

In this study, we examine the effect of annual fruit availability and its seasonality on frugivorous primate biomass and species richness, using fruit fall data from African, Asian and Central and South American forests. Using part of the data (New World), we examine the difference between large and small species regarding the effect of seasonality on biomass and the number of species. Additionally, we tested the effects of climate (annual precipitation and temperature) and location (absolute latitude and altitude). Climate and location are known to influence primate abundance (Eeley and Lawes 1999), but it was not clear whether they exert their effects through food availability or other mechanisms (e.g. thermoregulation) (Canavero et al. 2009). We examine the possibility that these factors affect abundance even when the effect of food availability is statistically controlled. To our knowledge, this is the first study to demonstrate the effect of both the annual food abundance and seasonality on the animal biomass and species richness, not based on an indirect indicator of seasonality in food availability (e.g. climate), but based on a direct indicator with a statistically robust number of samples.

## Method

### Fruit fall

In order to collect data on fruit fall in primate study sites, we conducted a survey of the literature, but we also used our

own unpublished data. We included data only when they were collected by fruit traps set systematically on the forest floor. In all cases, fruit collection studies covered at least a full continuous year, and fruits were collected at least once a month. If only data on wet mass were available, we estimated dry mass assuming that dry mass is 29.5% of wet mass, which is the average dry/wet mass ratio of fruits in seven temperate sites (Herrera 1985). This value is similar to that in a tropical forest of the Danum Valley, Borneo (29.1%, average of 310 fruits, Hanya unpubl.). We collected data from 16 sites, including Africa (1 site), Asia (6), Central America (2) and South America (7). The range of the traps used was 20–312 (median: 60) and that of the covered area was 0.25–24 ha (median: 1 ha). Yakushima (503 km<sup>2</sup>), Maraca Island (9.2 km<sup>2</sup>), and Barro Colorado Island (15 km<sup>2</sup>) are islands, while the other sites are on continent or large islands (Sumatra and Borneo). See Table 1 for details of the study sites.

As these data were generally drawn from sites of long-term primate studies, there exists a possibility that the data are biased to the places where primatologists are likely to select as study sites. We can expect primatologists to choose areas where primates are abundant or habituated. However, the range of frugivore biomass in our dataset is quite large (5–682 kg km<sup>-2</sup>). Therefore, we consider that we could regard the variations as large as the one by random sampling. Various factors affect habituation, and one of the most significant factors is hunting. It is justified to omit areas with hunting pressure because when hunting is present, primate abundance is kept lower than would be expected by the food availability.

### Primates

We included all of the diurnal primates except for howler monkeys in the New World and colobines in the Old World, which are largely folivorous. Howler monkeys are less affected by fruit fall (Stevenson 2001) and colobines are strongly affected by foliage quality (Chapman et al. 2004). Nocturnal primates were not included because their absolute biomass is difficult to estimate and their diet is typically mostly insectivorous.

Data on primate biomass was calculated (when not reported in the original literature) based on reported population density, group size and composition, and body mass. As for population density, we exclusively used the data taken near the fruit trap site. If there were multiple data sources, we adopted the one based on greater census efforts (e.g. longer transect length). We included only sites where hunting was negligible. We included sites with disturbed habitat only when a decade had passed since logging ended, to ensure that enough time had passed to reach equilibrium between fruit availability and primate biomass. Among our dataset, density does not change over years in the recently disturbed (10–20 yr ago) habitats, such as in the western coniferous forest of Yakushima (Hanya et al. 2005) or Tuanan (van Schaik unpubl.). As for group size, composition, and body mass, if data were not available for the site, we used the average value reported for other populations of the species, using 'All the World's Primates' database (<[www.alltheworldsprimates.com/](http://www.alltheworldsprimates.com/)>),

Table 1. List of study sites.

Site	Country	Latitude	Longitude	Altitude	Annual fruitfall (kg ha <sup>-1</sup> )	CV	Annual temperature (°C)	Annual precipitation (mm)	No. frugivorous primate species \$	Biomass of frugivorous primates (kg km <sup>-2</sup> )	Data source (fruits)	Data source (primates)	Data source (climates)
Barrero Rico	Brazil	-22.7	-47.5	870	400	0.50	20	1340	4 (1)	123	1	2	1
Cocha Cashu BS	Peru	-11.9	-71.4	400	796	0.56	24	2080	9 (4)	286	3	3	3
Tinigua NP	Colombia	-2.6	-74.0	350	770	0.70	25	2622	5	305	4	5	4
Caparu BS	Colombia	-1.1	-69.5	200	726	0.60	26	2688	6 (1)	103	6	7*	database
Maraca island	Brazil	3.3	-61.7	100	300	0.70	31	1840	4 (1)	62	8	9	database
Nouragues	French Guyana	4.8	-53.0	250	292	0.84	26	3000	3 (1)	65	10	11*	10
Hato Masaguaral	Venezuela	8.6	-67.7	70	330	1.00	28	920	1	38	12	13	12
Barro Colorado Island	Panama	9.2	-79.8	40	650	0.95	26	2637	3 (1)	21	14	15*	14
Los Tuxtlas	Mexico	18.3	-95.3	120	250	0.85	22	4639	1	5	16	17*	16
Kanyawara	Uganda	0.8	32.4	1500	746	0.46	23	1700	6	682	18	19	18
Tuanan	Indonesia	-2.1	114.4	5	480	0.42	27	2672	3	200	this study	this study	this study
Suaq	Indonesia	3.1	97.9	5	330	0.60	27	3400	5	640	this study	this study	this study
Danum Valley	Malaysia	5.4	116.8	300	59	1.25	27	2825	4	254	this study	this study	this study
Yakushima, eastern coniferous	Japan	30.3	130.6	1200	320	0.68	11	8945	1	92	this study	20*	this study
Yakushima, western coniferous	Japan	30.3	130.5	1050	231	1.40	12	5770	1	115	this study	21*	this study
Yakushima, western lowland	Japan	30.4	130.4	280	595	0.79	17	2620	1	407	this study	21*	this study

Data sources. 1: Morellato 1992, 2: Torres de Assupcao 1983, 3: Terborgh 1983, 4: Stevenson et al. 2000, 5: Stevenson 2007, 6: Vargas and Stevenson 2009, 7: Palacois and Peres 2005, 8: Villela and Proctor 1999, 9: Pontes 1999, 10: Zhang and Wang 1995, 11: Kessler 1998, 12: Colonnello 1991, 13: Eisenberg 1978, 14: Foster 1982, 15: Glanz 1990, 16: Sanchez and Alvarez-Sanchez 1995, 17: Estrada and Coates-Estrada 1985, 18: Chapman et al. 1994, 19: Chapman et al. 1999, 20: Yoshihiro et al. 1998, 21: Yoshihiro et al. 1999.

\* Biomass calculated from the population density data.

\$ Numbers in the parentheses indicate the number of species with body mass <1 kg.

which provides information on basic morphology and ecology of all species of primates written by specialists of each species. If data were available for multiple sites in the database, we used the data for the one corresponding to where we took the population density data. When group composition was not known, we assumed that half of the groups were immatures whose body mass is half that of adults. This assumption is consistent with previous studies of primate biomass in the both Old and New Worlds (White 1994, Stevenson 2001).

## Climate

Data on annual average temperature and annual precipitation were derived from original literature whenever possible. When not available, data were cited from the nearest meteorological station, using the database 'World Climate' <[www.climate-charts.com/](http://www.climate-charts.com/)>.

## Analysis

We calculated two parameters for fruit fall. 1) Annual fruit fall ( $\text{kg ha}^{-1} \text{ yr}^{-1}$ ): sum of the fruit fall of 12 consecutive months. When data were available for more than one year, data were averaged for all of the years. 2) Coefficient of variation (CV): standard deviation of the 12 consecutive months/average of the 12 months. When data were available for more than one year, CV was calculated for each year, and then averaged over the years.

We examined data using generalized least squares (GLS) regression. GLS models are similar to general linear models (GLM), except that their estimates of standard errors and type-I errors are more realistic in the presence of spatially correlated residuals (Dormann et al. 2007). GLS models also prevent clusters of sites from exerting undue (pseudo-replicated) influence on estimates of beta coefficients, which may be an important consideration if study sites are not uniformly distributed in space (Ting et al. 2008). In applying GLS, three common variogram models are available, but we used only the 'Gaussian' functions, which always fitted the data best among the three. GLS models were fit using the 'gls' command of the 'nlme' package in R (The R Foundation for Statistical Computing). It is possible to apply generalized linear mixed models (GLMM), examining different sources of literature as a random factor (Dormann et al. 2007), which is often used for meta-analysis. In this way, we can only control the spatial autocorrelation within each source of data. However, we chose GLS rather than GLMM because we considered it necessary to control the spatial autocorrelation not only within the same study but also among the study sites derived from different source of data. Collinearity (correlations between independent factors) was not severe in this dataset: the maximum variance inflation factor (VIF) between factors was smaller (1.32) than the cut-off value (5) recommended in Neter et al. (2004). Therefore, we can examine the independent effects of both annual fruit fall and its seasonality, in spite of the partial correlation between them. We do not discuss on the relative importance of these two variables.

First, we examined the GLS models for the effects of 1) annual fruit fall, 2) CV, 3) region (Old World or New

World) and 4) small island or not, on frugivorous primate biomass and species richness. We examined all possible combinations of these independent variables and searched for the best-fit model having the smallest AIC (Akaike's information criterion). To clarify the additional effect of climates, we added annual precipitation, annual average temperature, and both on the full models (adding all three of the above factors) and checked whether model fitness increased. We also did the same for location factors (absolute latitude and altitude). Analyses using a finer scale of biogeographic region (such as Central America, South America, Asia and Africa) produced almost identical results but with lower explanatory power, so we used a broader scale (Old World vs New World) which corresponds to infraorder level of taxonomy (Platyrrhini vs Catarrhini). It should be noted that results from the Old World in this study are largely driven by Asian forests, due to the biased distribution of our data points. However, the biomasses of the folivorous primates of both Africa and Asia seem to follow the same rule (Chapman et al. 2002), suggesting that variations within the same subfamily does not pose serious problems. Therefore, we consider it acceptable to assume that predictors of frugivorous primates are also consistent between Africa and Asia. Our dataset included three sites in Yakushima, Japan. We included each of them as an independent point in the analysis of biomass because it is known that the altitudinal variation of fruit availability within this island explains much of the variations in the density of the only primate in Japan, Japanese macaques (Hanya et al. 2004). However, in the analysis of the number of species, we included only one of them (having the medium of fruit fall) because they are not independent of each other.

To assess the difference in the effect of seasonality between large and small species, we examined Pearson's regression between CV and biomass or species richness between the large and small species. Following van Schaik et al. (2005) in the New World, we defined small species as having a body mass of less than or equal to 1 kg, and large species > 1 kg. This roughly corresponds to the distinction between Callitrichids and the others. There is also a large variation within Old World primate communities and the largest difference in body mass occurs between great apes and others. However, the distribution of great apes, particularly in Asia, is quite limited, so the result could be confused with biogeography. Therefore, we confined this analysis to the New World.

## Results

### Predictors of frugivorous primate biomass

Frugivorous primate biomass became higher as annual fruit fall increased and seasonality decreased (Fig. 1). According to the GLS analysis, the best-fit model included annual fruit fall, CV, region, and island, while the second-best-fit model included CV, region and island. The third-best-fit and other models had considerably larger values of AIC ( $\Delta\text{AIC} > 9.8$ ), so we did not examine these models. There was only a small difference in the AIC ( $\Delta\text{AIC} = 0.0375$ ) between the best- and second-best-fit models. The same set

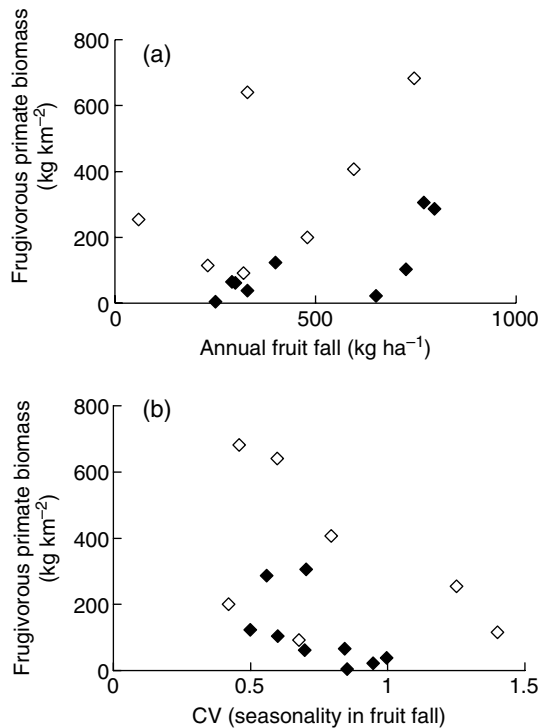


Figure 1. Effect of (a) annual fruit fall and (b) seasonality of fruit fall (assessed by CV) on frugivorous primate biomass. Closed symbols indicate New World, and open symbols indicate Old World. See Table 2 for statistical results.

of variables was selected for the best- and second-best-fit models even if we used only one of the three sets of Japanese data. The effect of CV was not significant in the second-best-fit model, but omitting CV from this model considerably increased AIC ( $\Delta\text{AIC} = 10.2$ ), so the effect of seasonality should be taken into account. Therefore, we assume that all four variables contribute to primate biomass independently. GLS analysis revealed that the biomass in the Old World was consistently higher (ca 300 kg km<sup>-2</sup> in the current data set, Table 3) than in the New World when the effect of fruit fall was controlled. The biomass at island sites was, according to the best-fit model, 127 kg km<sup>-2</sup> lower than at other sites. In the New World, the biomass of small species was more strongly negatively correlated with CV ( $r = -0.43$ ) than that of large species ( $r = -0.15$ ), although neither regression was significant ( $p > 0.1$ ).

Annual temperature had additional effects on frugivorous primate biomass. When adding climate factors to the full model (including annual fruit fall, CV region and island), AIC decreased when adding annual temperature (168.5, in the original model AIC = 173.7) but not when adding precipitation (179.0) and when both temperature and precipitation were added (174.4). Addition of annual temperature decreased AIC, even when we discard the three Japanese data, near the northernmost extreme of non-human primate distribution (AIC = 135.2 without temperature, AIC = 129.4 with temperature). Addition of location factors increased AIC (latitude: AIC = 176.1; altitude: 184.3; latitude+altitude: 181.3). These analyses indicated that biomass of frugivorous primates increased when the annual

temperature was high, even when the effects of fruit availability and biogeography are controlled.

### Predictors of species richness of frugivorous primates

Frugivorous primate species richness increased as seasonality of fruit fall decreased (Fig. 2), but no effect on the annual fruit fall was detected when the effect of seasonality was controlled. The explanatory power of the best-fit models was smaller for species richness (34%) than for biomass (67–56%, Table 2, 3). According to the GLS analysis, best- and fourth-best-fit models had similar AIC ( $\Delta\text{AIC} < 0.70$ ) while other models had large AIC ( $\Delta\text{AIC} > 4.9$ ), so we considered only the four best-fit models. CV was included in all of them, and region or island was included in some of them. The number of frugivorous primate species tended to be slightly smaller in the Old World than in the New World, or in mainland than in islands when the effect of fruit was controlled. Although fruit fall had positive relations with the number of species when analyzed without CV, region or island (coefficient = 0.0061,  $p = 0.0135$ ), AIC was considerably larger than the best-fit model ( $\Delta\text{AIC} = 12.7$ ), indicating their explanatory power was less than that of CV. In the New World, the number of large species was more strongly negatively correlated with CV ( $r = -0.76$ ,  $p = 0.015$ ) than was that of small species ( $r = -0.51$ ,  $p = 0.169$ ).

Addition of climate or location factors to the above best fit-model did not better explained the species richness. Compared with the AIC of the original model (70.1), AIC increased after adding annual temperature (74.1), annual

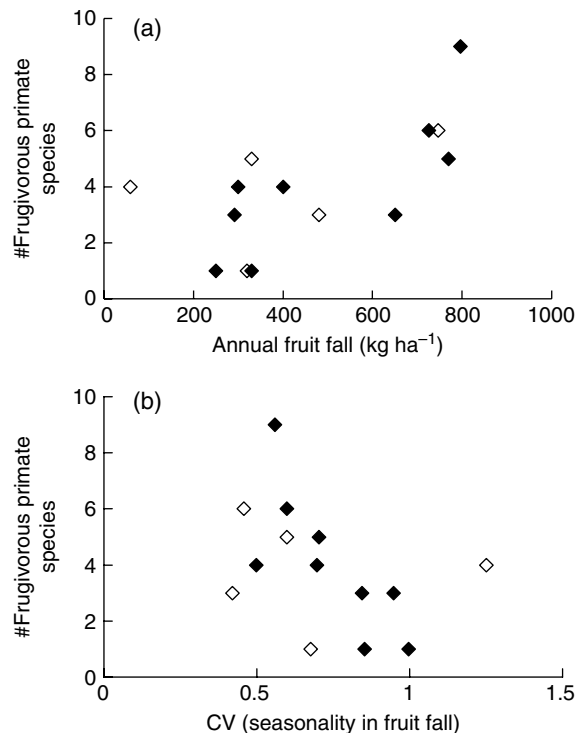


Figure 2. Effect of (a) annual fruit fall and (b) seasonality of fruit fall (assessed by CV) on the number of frugivorous primate species. Closed symbols indicate New World, and open symbols indicate Old World. See Table 3 for statistical results.

Table 2. Best- and second best-fit models in the generalized least square regression on the effect on frugivorous primate biomass.

a. Best-fit model

AIC = 173.7, DF = 16,  $R^2 = 0.67$ ,  $p < 0.0001$

Independent factors	Coefficient	SE	t	p
(Intercept)	-5.73	184.21	-0.03	0.976
Annual fruit fall	0.41	0.20	2.08	0.062
CV	-82.91	121.72	-0.68	0.510
Region (Old World)	316.44	80.30	3.94	0.002
Island	-126.50	86.47	-1.46	0.171

b. Second best-fit model

AIC = 174.1, DF = 16,  $R^2 = 0.56$ ,  $p < 0.0001$

Independent factors	Coefficient	SE	t	p
(Intercept)	344.58	101.53	3.39	0.005
CV	-278.28	115.57	-2.41	0.033
Region (Old World)	268.98	84.65	3.18	0.008
Island	-114.52	94.49	-1.21	0.249

precipitation (85.2), or both (88.9) to the model, and after adding absolute latitude (75.5), altitude (83.5) or both (88.3).

## Discussion

### Effects on frugivorous primate biomass

We showed that the biomass of frugivorous primates increased with increasing total annual fruit availability and

with decreasing seasonality. This finding provides further evidence for the species–energy theory (Connell and Orias 1964), which assumes that sites with more available energy support more individuals, but also reveals the importance of seasonality in the energy availability. Not only the total available food but also the temporal variation affects the animal biomass. In habitats with higher fruit availability (whatever the temporal scale), animals require smaller home ranges, and thus reach higher density and biomass (Hanya et al. 2006). When food availability varies seasonally, however, animals have access to less food or lower-quality

Table 3. Best- to fourth best-fit models in the generalized least square regression on the effect on the number of species of frugivorous primates.

a. Best-fit model

AIC = 61.4, DF = 14,  $R^2 = 0.34$ ,  $p = 0.014$

Independent factors	Coefficient	SE	t	p
(Intercept)	7.23	1.67	4.34	0.002
CV	-4.25	2.20	-1.93	0.083
Region (Old World)	0.14	1.17	0.12	0.908
Island	-0.30	1.51	-0.20	0.849

b. Second best-fit model

AIC = 61.6, DF = 14,  $R^2 = 0.34$ ,  $p = 0.013$

Independent factors	Coefficient	SE	t	p
(Intercept)	7.25	1.58	4.58	0.001
CV	-4.20	2.07	-2.03	0.068
Island	-0.31	1.43	-0.22	0.831

c. Third best-fit model

AIC = 62.11, DF = 14,  $R^2 = 0.34$ ,  $p = 0.012$

Independent factors	Coefficient	SE	t	p
(Intercept)	7.31	1.54	4.73	0.001
CV	-4.44	1.88	-2.37	0.037
Region (Old World)	0.16	1.11	0.15	0.887

d. Fourth best-fit model

AIC = 62.11, DF = 14,  $R^2 = 0.34$ ,  $p = 0.012$

Independent factors	Coefficient	SE	t	p
(Intercept)	7.33	1.47	5.00	0.000
CV	-4.41	1.78	-2.47	0.029

food during the food-scarce season than when food is equally available throughout the year. Primates adapt to seasonality in various ways: they are known to store excess food intake obtained during the food-rich period as fat reserves (Knott 1998, Muroyama et al. 2006, Kanamori et al. 2010), to switch their diet to abundant but less preferred food items (fallback foods) (Marshall et al. 2009), or to shift ranging patterns or use different habitats (Buij et al. 2002). For example, both Japanese macaques and orangutans switch their diet from fruits to leaves or bark in response to decreased fruit availability, and they mobilize their fat reserves during the fruit-scarce season (Knott 1998, Hanya 2004, Muroyama et al. 2006). However, these adaptations have limits and inevitably entail cost. For example, animals cannot indefinitely increase the amount of fat they store. Due to the limitations of digestive features, frugivorous primates typically cannot extract enough energy to satisfy their daily requirements by digesting foliage (Mori 1979). Because of these limitations, the biomass of frugivorous primates remains low when the seasonality in fruit supply is high. The fact that biomass of small New World species was more strongly negatively correlated with seasonality than large species also supported this reasoning. Small species are expected to have less ability of accumulate fat and require more energy relative to their body size (Kleiber 1987), and thus they are more vulnerable to seasonal shortages of foods.

We also showed that annual temperature had additional positive effects on the biomass of frugivorous primates, even when the effect of food was controlled. This tendency remained even when the three Japanese sites were excluded; therefore, even a moderate degree of temperature variation imposes thermoregulatory cost on primate communities. When the temperature is low, animals need more energy for thermoregulation (Dunbar 1992) and require a larger home range to secure the excess energy demands, which leads to reduced density and biomass (Hanya et al. 2006).

Although we could not directly show the importance of seasonality, the availability of fallback foods during the food-scarce season is also suggested as a determinant of primate abundance. For example, variations in gibbon density over the seven vegetation types are best explained by the density of figs, which provide fallback food during the fruit-scarce season (Marshall and Leighton 2006). Based on inter-community comparisons, the biomass of frugivores is shown to become larger when the interval between the peaks of fruiting and flushing is longer, since the opportunities for dietary switching increase during the fruit-scarce season (van Schaik et al. 2005). Hanya et al. (2006) explained the interaction between total annual food abundance and fallback foods as follows: when the quality of fallback foods is low, animals suffer from increasingly severe food shortage and need to accumulate more fat, thus requiring a large area, and density becomes lower. This study further supported the importance of the food-scarce period: if the seasonality is strong, food shortage becomes more severe during the food-scarce season and animals need a larger home range during the food-abundant period. It is usually difficult to detect the direct effect of fallback foods (e.g. figs, palms) on primate abundance by inter-community comparisons (Stevenson 2001, 2005) because different species use different fallback foods. In future studies, it will be necessary to show the

integral effect of total annual food abundance, availability of fallback foods, and degree of seasonality based on inter-population comparisons of a single species.

Biogeographic factors also affected frugivorous primate biomass. It is already known that primate biomass (both frugivores and folivores) is smaller in the New World than in the Old World (Janson and Chapman 1999). Smaller body mass, lack of terrestrial species, and the competition with sloths are discussed as the cause of the smaller primate biomass of the New World (Reed and Bidner 2004). To our knowledge, no study has demonstrated island has a smaller primate biomass than mainland, as we found in this study, and thus this tendency needs to be tested with a more extensive dataset. Following island biogeography theory, islands may have fewer species of food plants, and this may limit primate abundance negatively. Unlike annual temperature, addition of absolute latitude did not decrease AIC. This was not expected considering the strong correlations between the absolute latitude and annual temperature ( $r = -0.89$ ,  $p < 0.0001$ ). Latitudinal environmental gradient includes not only gradient of temperature but also that of fruit abundance and its seasonality (Ting et al. 2008, Hanya and Aiba 2010). Therefore, when examined simultaneously with fruit availability factors, the effect of latitude may have been difficult to detect. Effect of latitude needs to be examined with a larger number of data.

### **Effects on the number of frugivorous primate species**

We showed that the number of frugivorous primate species decreased with increasing seasonality of fruit availability. Again, this finding revealed the importance of temporal variations of energy availability in the energy-species hypothesis. The effects of biogeographic factors, if any, were small. The degree of adaptation to seasonality is expected to vary among species, so the seasonality-sensitive species cannot survive in very seasonal habitats. Contrary to the results on biomass, and contrary to the prediction that small species are more vulnerable to seasonality, the number of species was affected by seasonality more for large species than for small species. In our dataset, the number of small species was 0 or 1, except for one site having 4 species. Because of the low variance, it may be more difficult to detect the effect statistically than with large species.

We detected only weaker explanatory power for the total annual fruit availability, compared to that of seasonality, either because a qualitative measure such as presence/absence is less sensitive than the quantitative measure of abundance, or because of the rather small sample size ( $n = 14$  sites). Since we also detected a significant effect of annual fruit availability on the number of species when analyzed separately from seasonality, further analysis with a larger sample size might detect an influence of both. Neither climate nor location factors had additional effects on the number of species when the effect of fruit was controlled, suggesting these factors work by way of fruit availability. Hanya and Aiba (2010) showed that the smaller number of frugivorous primate species in temperate than in tropical forests can only partially be explained by total annual fruit fall. The present analysis suggests that stronger seasonality in food availability should be taken into consideration when

explaining the smaller number of species in temperate forest. Since we could include only one temperate site in this analysis, much more data in other temperate regions are necessary.

In conclusion, this study demonstrated that seasonality in food availability has a negative effect on animal biomass and species richness, using frugivorous primates as an example, whereas total annual food availability had a positive impact on the consumers' biomass. Annual temperature also had an additional positive effect on the biomass. Future study is required on the integrative effect of food and non-food factors, such as historical factors, competition with other animals, predation and disease (Oates et al. 1990).

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