Appalachian
STATE UNIVERSITY®
BOONE, NORTH CAROLINA

Responses Of Javan Gibbon (*Hylobates moloch*) Groups In Submontane Forest To Monthly Variation In Food Availability: Evidence For Variation On A Fine Spatial Scale

By: Sanha Kim, **Susan Lappan**, and Jae C. Choe

Abstract

Primates tend to prefer specific plant foods, and primate home ranges may contain only a subset of food species present in an area. Thus, primate feeding strategies should be sensitive to the phenology of specific species encountered within the home range in addition to responding to larger scale phenomena such as seasonal changes in rainfall or temperature. We studied three groups of Javan gibbons (Hylobates moloch) in the Gunung Halimun‐Salak National Park, Indonesia from April 2008 to March 2009 and used general linear mixed models (GLMM) and a model selection procedure to investigate the effects of variation in fruit and flower availability on gibbon behavior. Preferred foods were defined as foods that are overselected relative to their abundance, while important food species were those that comprised >5% of feeding time. All important species were also preferred. Season and measurements of flower and fruit availability affected fruit‐feeding time, daily path lengths (DPL), and dietary breadth. Models that included the availability of preferred foods as independent variables generally showed better explanatory power than models that used overall fruit or flower availability. For one group, fruit and preferred fruit abundance had the strongest effects on diets and DPL in the models selected, while another group was more responsive to changes in flower availability. Temporal variation in plant part consumption was not correlated in neighboring groups. Our results suggest that fine‐scale local factors are important determinants of gibbon foraging strategies.

RESEARCH ARTICLE

Responses of Javan Gibbon (*Hylobates moloch*) Groups in Submontane Forest to Monthly Variation in Food Availability: Evidence for Variation on a Fine Spatial Scale

SANHA KIM[1,2], SUSAN LAPPAN[2,3], AND JAE C. CHOE[2]*
[1]*Seoul National University, Seoul, Republic of Korea*
[2]*Ewha Womans University, Seoul, Republic of Korea*
[3]*Appalachian State University, Boone, North Carolina*

Primates tend to prefer specific plant foods, and primate home ranges may contain only a subset of food species present in an area. Thus, primate feeding strategies should be sensitive to the phenology of specific species encountered within the home range in addition to responding to larger scale phenomena such as seasonal changes in rainfall or temperature. We studied three groups of Javan gibbons (*Hylobates moloch*) in the Gunung Halimun-Salak National Park, Indonesia from April 2008 to March 2009 and used general linear mixed models (GLMM) and a model selection procedure to investigate the effects of variation in fruit and flower availability on gibbon behavior. Preferred foods were defined as foods that are overselected relative to their abundance, while important food species were those that comprised >5% of feeding time. All important species were also preferred. Season and measurements of flower and fruit availability affected fruit-feeding time, daily path lengths (DPL), and dietary breadth. Models that included the availability of preferred foods as independent variables generally showed better explanatory power than models that used overall fruit or flower availability. For one group, fruit and preferred fruit abundance had the strongest effects on diets and DPL in the models selected, while another group was more responsive to changes in flower availability. Temporal variation in plant part consumption was not correlated in neighboring groups. Our results suggest that fine-scale local factors are important determinants of gibbon foraging strategies. Am. J. Primatol. 74:1154–1167, 2012. © 2012 Wiley Periodicals, Inc.

INTRODUCTION

Most primates are physiologically capable of eating foods that they normally do not eat, and primates of many species eat a broader range of food items or lower quality food items when food is scarce than during times of plenty [Marshall & Wrangham, 2007; Oates, 1987], as predicted by foraging theory [MacArthur & Pianka, 1966; Robinson & Wilson, 1998]. Therefore, the actual diet of a given individual or group will be a compromise between their dietary preferences and the diet that can be achieved given current conditions.

Food items can be described in terms of both the quantity eaten and how often the food is selected relative to its availability [Chapman & Chapman, 2002; Lambert, 2007a; Marshall & Wrangham, 2007]. Usually, a food is defined as *preferred* when the percentage of that food item in the diet exceeds the percentage of total food available that is composed of that food item [i.e. when a food is overselected; Marshall & Wrangham, 2007]. Often, primate researchers simply record the percentage of the diet consisting

of each plant food type or species, but the authors of several recent reviews make compelling arguments for distinguishing between preferred foods and *fallback foods* [FBFs; Harrison & Marshall, 2011; Lambert, 2007a; Marshall & Wrangham, 2007; Marshall et al. 2009a]. While preference is normally identified statistically, it is based on physiological realities such as taste [Remis, 2006], as well as other variables such as handling time, fruit size, presentation, and position [Stevenson, 2004]. FBFs are those for which consumption is negatively correlated

with the abundance of preferred foods [Marshall & Wrangham, 2007]. Animals should prefer foods that are nutrient-dense and easy to find and handle [Lambert, 2007a; MacArthur & Pianka, 1966]. Foods that lack these characteristics may function as FBF when high-quality foods are rare. FBF may be *important* [comprising a large component of the diet; Marshall & Wrangham, 2007] despite having low preference ranks.

Animals may adjust their foraging party sizes or change their diets, patterns of home range use, or daily path length (DPL), in months when food is scarce [Itoh & Nishida, 2007] or when preferred foods are scarce, even during periods of high or moderate overall food availability [Simmen et al., 2007]. Food preferences are also important in explaining niche overlap and competition among sympatric species [Yamagiwa & Basabose, 2009].

Most tropical forest tree species occur at low densities and different species often display distinct phenological patterns [Whitten et al., 1996]. Some species flower and fruit synchronously while others are asynchronous, and the intervals between fruiting events vary among species, and even among individuals in a species [van Schaik et al., 1993]. Primates with a preference for specific plants foraging within limited areas should therefore respond to temporal variation in resource abundance on a fine spatial scale. Indeed, neighboring groups of conspecifics may show marked differences in their diets [Chapman et al., 2002; Lappan, 2010; McConkey et al., 2003].

Gibbons (Hylobatidae) eat more fruit than most other primate species [Bartlett, 2011] and most gibbons live in forests that display pronounced temporal fluctuations in food availability [Bartlett, 2009, 2011; McConkey et al., 2003; Raemaekers, 1980]. Gibbon groups usually consist of two to six individuals and defend ~30–40 ha territories [Bartlett, 2011]. Therefore, gibbons living in saturated habitats must adjust their utilization of a given resource base rather than expanding their search area, at least in the short term. Understanding how gibbons respond to variation in food availability may shed light on many aspects of their biology, including the origins of social monogamy [Brockelman, 2009], variation in grouping patterns and mating systems [Savini et al., 2009], and variation in local population dynamics [Marshall, 2009].

Gibbons have a strong preference for ripe fruits [Bartlett, 2011; Chivers, 1984], and the percentage of time that gibbons spend eating fruit generally remains high despite substantial variation in fruit availability [Chivers, 1984]. Small group size enables gibbons to rely on relatively small food patches [Bartlett, 2011]. Perhaps for this reason, gibbons are able to remain selective while exploiting a wide range of food sources that are not typical FBF, in the sense of being common but nutrient-poor or me-

chanically protected foods. Gibbons often increase their consumption of other plant parts and show higher dietary diversity as fruit abundance declines [Bartlett, 1999; Marshall et al., 2009b; McConkey et al., 2003], and movement patterns of some gibbon populations also change in response to variation in resource availability [Bartlett, 2009; Lappan, 2009; Raemaekers, 1980]. However, these patterns are not universal [Bartlett, 1999; Raemaekers, 1980], and gibbons appear to display substantial flexibility in their strategies for coping with variation in fruit availability [Malone & Fuentes, 2009].

Figs are often considered to be a gibbon FBF [Harrison & Marshall, 2011; Leighton & Leighton, 1983], but some gibbon populations rely heavily on figs [Chivers & Raemaekers, 1986; Palombit, 1997; Ungar, 1995], which has led to the suggestion that gibbons may actively seek out figs [Chivers & Raemaekers, 1986; Ungar, 1995], although most researchers have considered only the importance of figs in gibbon diets, and not food selection. The status of flowers as preferred or FBF is also unclear. Flowers comprise >10% of the diet of some gibbon populations [Lappan, 2009; McConkey et al., 2003], and McConkey et al. [2003] reported that flower abundance was the primary determinant of the diets of hybrid gibbons (*Hylobates muelleri* × *H. agilis/ albibarbis*) at Barito Ulu, but this result has yet to be replicated.

In a previous paper [Kim et al., 2011], we provided ranging, activity, and diet data for Javan gibbons in submontane forest in Gunung Halimun-Salak National Park (GHSNP), and compared the behavior of this high-elevation (950–1150 m asl) population with that of lowland populations in Turalak and Cagar Alam Leuweung Sancang (CALS) [Kappeler, 1984; Malone, 2007]. Gibbon home ranges at the site of our study (mean = 37 ha; Kim et al., 2011) were more than two times the size of those at Turalak and CALS, which may reflect differences in habitat quality. In this article, we expand upon our previous work by examining the relationship between the local abundance of plant reproductive parts (flowers and fruits) and Javan gibbon diets and DPL in GHSNP.

We first identify important and preferred plant foods for three habituated Javan gibbon groups. Following Marshall and Wrangham [2007], we define important foods as foods comprising a substantial component of gibbon diets (>5% of feeding time), and preferred foods as those that are overselected relative to their abundance. Then, we explore the effects of season and food abundance (overall abundance of specific plant parts and abundance of preferred plant species) on gibbon fruit- and fig-eating time, dietary breadth, and DPL. Finally, we examine the extent to which temporal patterns of variation in resource use are similar in neighboring groups.

METHODS

Study Site

The study was conducted in the GHSNP (6°42′S, 106°27′E) in West Java, Indonesia in an area of primary hill and submontane forest (950–1100 m asl) near the village of Citalahab. The research area, which we refer to as "Citalahab," is on a forest edge and has experienced small-scale disturbance (e.g. removal of individual trees, rattan harvesting), but the boundary has remained constant over the last few decades and human activities do not appear to have substantially altered the forest structure in the study area. The research area is crossed by a grid of trails at 200-m intervals and a set of secondary trails on or near common gibbon travel paths.

Rainfall at Citalahab is generally high, with mean monthly rainfall of $316 \pm$ SD 175 mm/month (range = 63–775 mm/month) from June 2007 to March 2009. The five driest months (<200 mm/month) occurred between June and September, and the four wettest months ($\geq$402 mm/month) between October and January. We have previously described Citalahab as having a short dry season from June to September (the "Dry" season), moderate rainfall February–May (the "Wet" season), and high rainfall October–January [the "Very Wet" season; Kim et al., 2011]. However, the addition of data from 2009 to 2010 and reanalysis of existing data showed that rainfall in January (mean = 258 ± 69 mm) was below the mean for the Very Wet season (2007–2010, mean 477 ± 174 mm/mo). Thus, we include January in the Wet, rather than the Very Wet, season here. Mean monthly rainfall differs significantly among seasons (ANOVA with Bonferroni-corrected post-hoc multiple comparisons: $F_{2,11} = 19.175$, $P = 0.001$; Very Wet vs. Wet: $P = 0.019$, Very Wet vs. Dry: $P < 0.001$; Wet vs. Dry: $P = 0.033$).

Study Subjects and Sampling

After a one-year habituation period, we collected behavioral and feeding data from three gibbon groups with adjacent home ranges (groups A, B, and D) from April 2008 to March 2009. Each group contained one adult male, one adult female, and 0–2 immatures. Group A had a 32.3 ha home range (per capita = 8.1 ha/individual), group B had a 43.3 ha home range (14.4 ha/individual), and group D had a 34.3 ha home range (11.4 ha/individual). Group D ranged in an area where the terrain made it especially difficult to follow the animals, resulting in the collection of fewer days of data from group D (group A: 68 days, group B: 74 days, group D: 31 days).

Data Collection

We followed the study groups on a rotating basis, and followed each group from sleeping tree to sleeping tree for three consecutive days whenever possible. We recorded the feeding behavior of a focal individual selected before the daily follow, alternating daily between the adult members of each group whenever possible. The subadult female of group A was habituated much earlier than the adult female. Therefore we substituted the subadult (adult-sized but nonreproductive) female as the focal female for group A. The group D female was the only gibbon that appeared somewhat fearful of humans after an initial process of habituation. Perhaps for this reason, she often did not accompany the male. Thus, most data for group D are from the male.

We recorded each feeding bout for the focal individual throughout the day, noting the start and end times, whether plant parts or insects were consumed, the plant part (fig fruit, non-fig fruit, new leaves, mature leaves, flowers, etc.), and the growth form (tree, liana, epiphyte). Sometimes the focal gibbon would place a food item in its mouth and chew for a few seconds only to promptly move on to the next tree, which appeared to be casual sampling rather than the initiation of a feeding bout. It was often difficult to identify foods consumed during these sampling bouts, so we excluded very brief (<<1 min) feeding bouts from our analyses. We used a rangefinder and compass to estimate the location of food trees within a system of coordinates at 1-m intervals within our trail system. We identified plant species when possible with assistance from local guides and the Herbarium Bogoriense [Kim et al., 2011]. Unidentified species constituted an average of 27% of total-feeding time but most of them were lianas and epiphytes as most (>75%) feeding trees were identified. Unidentified fig species and orchids were grouped into the categories "*Ficus*" and "Orchid." The "*Ficus*" category mainly consists of liana figs that were difficult to see or collect or small trees that were infrequently visited. Most fig feeding was concentrated on 11 identified species, so the "*Ficus*" category refers to a relatively minor portion of fig feeding. The "Orchid" category consists of orchid flowers growing on epiphytes too high in the canopy for sampling. *Callicarpa pentandra* produced small fruits scattered among equally small flowers, making it almost impossible to assign a bout to either fruit or flower feeding, so feeding observations were treated as half fruit and half flower feeding. Dietary breadth was the number of identified species eaten in a month.

We collected information about food abundance from 25 plots (10 × 50 m) set at random junctions within the grid of trails [Kim et al., 2011]. Our plots covered 1.25 ha and contained 364 trees of dbh >10 cm, of which 18 died during the study, leaving 346 in March 2008. Food abundance was measured monthly as the number of trees that bore fruits, flowers, or new leaves. Large woody lianas are rare in submontane forest [Ashton, 2003], and our plots

contained few lianas >10 cm dbh. Thus, we measured plant part production for lianas by randomly selecting one liana of diameter >7 cm/plot. Plots were established before the beginning of the study, and 23 of the plots (covering 1.15 ha) were located within the home ranges of at least one study group (Group A: 7 plots; 28% of total area; Group B: 9 plots, 36%; Group D: 7 plots; 28%).

Data Analysis

We used daily values summed over all feeding events to calculate time spent feeding on each plant part and species on each day. Means are given with SD. We square-root transformed all food availability data after adding one to each count. For fig fruit feeding time, we added 3/8 before the square-root transformation [Zar, 1996]. We used the Kolmogorov–Smirnoff test to verify the assumption of normality before using parametric statistical tests.

We designated important plant foods as species that comprised >5% of the total diet of at least one study group. Following Leighton [1993] we calculated an index of selectivity by dividing the estimated relative feeding frequency for a plant part and species by its relative availability among trees producing that plant part for a given month. The annual preference index (S_i) was the mean of these monthly preference indices. We calculated S_i separately for fruits and flowers. Species with S_i >1 were considered to be preferred. A few species that were frequently eaten were not found in the phenology plots. This was problematic as it resulted in a value of 0 for the relative availability of these species, and division by 0 is impossible. Thus, to derive S_i for these rare but sought-after species, we substituted a value of 1 for the measured value of 0 in our calculation of the total number of food-bearing trees of that species in the plots for the months when the species in question was eaten. We believe that this substitution is reasonable, as the 95% confidence intervals for the estimated density of tree species of which only one tree was found in the phenology plots encompassed zero, and that it is conservative, as it will tend to overestimate the abundance of that food item and therefore to underestimate its preference value.

We calculated DPL by adding the straight-line distances from the first to the last feeding trees. Where a location datum for a feeding tree was missing, we assumed straight-line travel between the two adjacent points.

We used general linear mixed models followed with a model selection procedure to identify the best predictors of gibbon time spent feeding on fruits, dietary breadth, time spent feeding on fig synconia, and DPL. We included group as a random factor, used type III sum of squares, and a variance components covariance structure, with restricted maximum likelihood. Season was a categorical variable

and all food availability variables were continuous. Independent variables considered were season and the availability of fruits (or preferred fruits) and flowers (or preferred flowers). For analyses of fig-feeding time, we included fig synconium availability, non-fig fruit availability, and flower availability, but only included a single variable in each model. Some food plants are present in the study area at fairly high density (e.g. *Altingia excelsa:* 29.6 individual/ha), whereas others are rare (e.g. *Polyalthia lateriflora:* ∼0.09 individual/ha). Vegetation plots inside a gibbon group home range should be more sensitive to variation in the local density or phenology of abundant plants than plots outside of the group's home range. However, plots covering a larger area may more accurately measure the abundance of rare plants with synchronous fruiting and flowering schedules. Thus, we estimated plant part availability using data only from the plots in a group's home range [resulting in the variables "fruit (gp)," "preferred fruit (gp)," "flowers (gp)," and "preferred flowers (gp)"], but we also estimated plant part availability using data from all of the phenology plots ["fruit (all)," "preferred fruit (all)," "flowers (all)," or "preferred flowers (all)"] and used model selection to identify the variables with the strongest predictive value. Only one fruit- or flower-availability measure was included in each model as some measurements within each category were correlated, but models using each possible combination of fruit- and flower-availability measurements were considered.

For fruit-feeding time, DPL, dietary breadth, and fig-feeding time, there was no significant autocorrelation among days in any season for any group (Box–Ljung statistic >0.05 for every lag). Thus, data days were treated as independent. We calculated Akaike information criterion [AIC; Akaike, 1974] values to identify the variables with the greatest explanatory power, and used Δ_i (|AIC for variable i − the lowest AIC value in the set|) to identify the simplest models with good explanatory power, selecting models with $\Delta_i \leq 2$. We used log likelihood ratio tests to check for the effect of groups on the models. The GLMM models used to identify candidate variables for feeding behavior and DPL were all significantly improved by including group as a random factor (log likelihood ratio test; Δ values range from 6.7 to 20.0, df = 1, $P < 0.01$), which suggests heterogeneity in the group responses. Thus, model selection procedure was also conducted for each group separately. All statistical analyses were conducted using IBM© SPSS v. 17 or 20.

This research was conducted in adherence to protocols approved by the Animal Behavior Research Committee of Ewha University, the Indonesian Ministry of Research and Technology, the Indonesian Ministry of Forestry, and GHSNP and was conducted in full compliance with Indonesian law and the American Society of Primatologists (ASP)

TABLE I. Mean Percentage of Daily Feeding Time for the Top 15 Food Plant Species

Species	Group A	Group B	Group D	Preferred
Ficus sinuata	15	15	4.5	Yes
Ficus punctata	7.1	7.6	7.8	Yes
Ficus group (see text)	7	5.8	7.8	Yes
Callicarpa pentandra	8.5	1.3	9.4	Yes
Ficus recurva	3.7	12	0.3	Yes
Sandorium koetjapi	3.9	0.2	11.6	Yes
Mussaenda frondosa		0.6	8.7	Yes
Ficus sundaica		4.1	4.4	No
Dysoxylum parasiticum	3.9	3.4	3.4	Yes
Bruinsmia styracoides	3	2	2.1	Yes
Orchid group (see text)	1	0.6	5.4	Yes
Nyssa javanica	0.1	2.1	4	Yes
Scindapsus marantaefolius	2.6	2.3	0	No
Knema cinerea	2.4	0.9	0.2	Yes
Artocarpus nitidus	0.3	0	3.1	No
Total percentage (%)	58.6	58	72.5	

Important species (those that comprise >5% of mean feeding time for the three groups) are in bold.

TABLE II. Selectivity Indices (S_i) for Preferred Fruit and Flower Species

Plant part	Species	S_i
Fruits	*Ficus* group (see text)	27.59
	Antidesma tetrandum	9.38
	Callicarpa pentandra	7.55
	Ficus punctata	5.83
	Ficus sagitata	5.40
	Ficus padana	4.92
	Sandorium koetjapi	4.22
	Knema cinerea	3.23
	Mussaenda frondosa	3.17
	Ficus sinuata	3.02
	Polyalthia lateriflora	2.85
	Pongong (local name)	2.42
	Ficus kuning (local name)	2.40
	Ficus recurva	2.07
	Symplocos cochichinensis	1.89
	Daemonorops melannochages	1.66
	Bom (local name)	1.50
	Vaccinium korthalsii	1.46
	Nyssa javanica	1.24
	Bruinsmia styracoides	1.02
Flowers	Orchid group (see text)	13.25
	Kurai (local name)	9.43
	Sandorium koetjapi	9.43
	Callicarpa pentandra	5.15
	Schefflera elliptica	3.84
	Ficus group (see text)	1.57
	Dysoxylum parasiticum	1.05

Principles for the Ethical Treatment of Non-Human Primates.

RESULTS

Javan Gibbon Diets at Citalahab

Gibbons at Citalahab spent most of their feeding time eating fruit (59 ± SD 3%), while also feeding on flowers (12 ± 6%), leaves (27 ± 1%), insects, and other plant parts (2 ± 1%). All groups spent >50% of feeding time eating fruit (Group A: 58 ± 19% fruit, 12 ± 12% flowers, 28 ± 17% leaves, and 2 ± 4% other foods; group B: 62 ± 22% fruit, 7 ± 10% flowers, 27 ± 19% leaves, 3 ± 8% other foods; group D: 56 ± 29% fruit, 18 ± 26% flowers, 26 ± 24% leaves, 0.8 ± 3.0% other foods). We identified 68 plant food species, including 48 fruit species, 17 flower species, and 39 leaf species. Gibbons ate parts of trees (45 ± 23% of feeding time), lianas (46 ± 23%), and epiphytes (8 ± 12%). The three groups fed in 1,730 individual trees. Including the "*Ficus*" and "orchid" groups, eight food species were important for at least one group (Table I) and 20 fruit and seven flower species were preferred (Table II). All important food species were also preferred (Table I), but eight preferred fruit species were not important.

Temporal and Spatial Variation in Plant Food Availability and Diets

Fruit availability was highest from December to March, whereas flower availability peaked in March–June. and October–December (Fig. 1). Monthly numbers of fruiting and flowering trees were not correlated in the study area ($r = -0.463$, $N = 12$, $P = 0.130$) or in the home ranges of any group after Bonferroni correction (group A: $r = -0.244$, $N = 12$, $P = 0.444$; group B: $r = -0.403$, $N = 12$, $P = 0.194$; group D $r = -0.637$, $N = 12$, $P = 0.026$). Therefore, fruit and flower availability were treated as independent. Preferred fruit and flower species both increased in abundance from April until September, after which preferred flower abundance decreased while preferred fruit abundance increased (Fig. 1). Preferred fruit and preferred flower abundance were not correlated ($r = -0.282$, $N = 12$, $P = 0.370$).

Dietary and Behavioral Responses to Variation in Food Availability

For fruit-feeding time, the models selected included three variables for all analyses (Table III). For
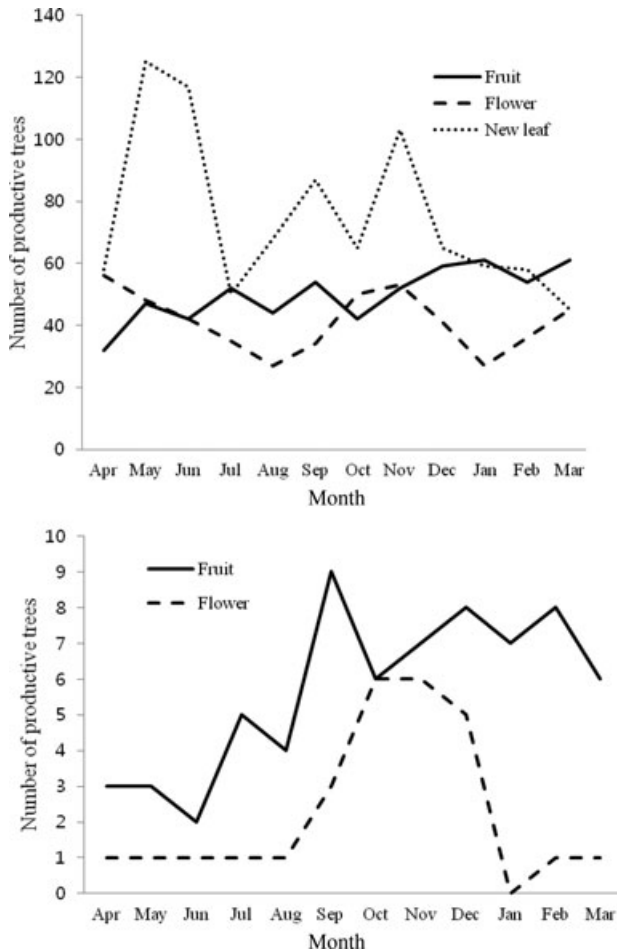
Fig. 1. Monthly food availability (above) and preferred food availability (below).

the models built using data from all three groups, flower availability was negatively related to fruit-feeding time, whereas fruit availability was positively related to fruit-feeding time, and the absolute value of β were generally higher for measurements of flower availability than fruit availability. However, for group A, β values were higher for measures of fruit availability for every model selected (Table III). For group B, β values for preferred fruit (gp) and flowers (gp) were similar, but the relationship with both variables was negative (Table III). The models selected for group D were more variable (Table III). All of the models showed positive relationships between both food availability variables and fruit-feeding time, and most showed a stronger effect of flower availability than fruit availability, but one model had higher β for fruit availability than for flower availability. For group D, almost every model selected included only measurements of preferred plant part availability rather than overall plant part availability (Table III).

For DPL, β for measures of fruit and flower availability were similar in absolute value, but the relationship was positive for fruit and negative for flowers. The availability of preferred plant parts was more important than overall food availability. Measures of preferred fruit availability had a stronger effect on DPL than measures of flower availability in most models selected for group A (Table IV(A)), whereas both variables were equally important for group B (Table IV(B)), and for group D, flower availability had a stronger effect than fruit availability in each model selected, and the relationship was positive for both variables (Table IV(D)).

For dietary breadth, β values for preferred fruit and flower availability were similar in absolute value, although the relationship between dietary breadth and food availability was positive for preferred fruit, but negative for preferred flowers (Table V). For group A, the absolute values of β were higher for preferred fruit availability than for preferred flower or flower availability in all models, whereas for group B, the model selected had a somewhat higher absolute β value for preferred flower availability.

The Role of Figs

Flower availability was the best predictor of fig-feeding time for all groups and for groups B and D (Table VI). AIC for models including non-fig fruit availability were much higher and non-fig fruit feeding time was not a significant predictor of fig-feeding time for all groups, or for group B or D (Table VI). Non-fig fruit feeding time was the best predictor of fig-feeding time for group A, but the relationship was positive, not the negative relationship predicted if group A used figs as an FBF during periods of low non-fig fruit availability.

Relationships between Temporal Patterns of Resource Use in Neighboring Groups

There was a significant positive correlation between the monthly percentages of feeding time spent feeding on non-fig fruit for groups B and D ($r = 0.673$, $N = 12$, $P = 0.017$), but not for any other pair of groups (A and B: $r = 0.176$, $N = 12$, $P = 0.584$; A and D: $r = 0.436$, $P = 0.157$). Monthly flower-feeding was not correlated for any pair of neighboring groups (A and B: $r = -0.122$, $P = 0.706$; A and D: $r = 0.551$, $P = 0.063$; B and D: $r = 0.019$, $P = 0.953$). Fig fruit feeding time were significantly positively correlated for groups A and B ($r = 0.678$, $N = 12$, $P = 0.015$), but not for any other pair of groups (A and D: $r = -0.009$, $P = 0.977$; B and D: $r = 0.400$, $P = 0.197$).

TABLE III. GLMM Models of the Relationship between Season, Flower, and Fruit Availability (Four Measures) and Fruit-Feeding Time (min/day)

Group(s)	Variable names	AIC	Δ_i	β	95% CI
All	Season[a]	1768.4	0	Dry = 5.8	− 23.8 to 35.5
				Wet = −39.6	− 71.2 to −8.0
	Preferred flowers (gp)[a]			− 51.3	− 88.8 to −13.6
	Preferred fruit (all)[a]			23.7	2.4 to 45.0
	Season[a]	1770.5	2.1	Dry = 1.4	− 27.7 to 30.6
				Wet = −44.1	− 75.2 to −13.0
	Preferred flowers (gp)[a]			− 45.0	− 82.9 to −7.1
	Fruit (all)			12.9	− 0.6 to 26.5
A	Season	666.9	0	Dry = 13.3	− 50.9 to 77.5
				Wet = −19.9	− 90.7 to 51.0
	Preferred fruit (gp)[a]			80.8	− 0.1 to 161.7
	Preferred flowers (gp)			− 37.4	− 111.8 to 37.0
	Season	667.3	0.4	Dry = −15.5	− 57.5 to 26.4
				Wet = 34.7	− 90.9 to 21.5
	Fruit (all)[a]			35.0	5.7 to 64.3
	Preferred flowers (gp)			− 4.3	− 91.1 to 82.5
	Season	667.6	0.7	Dry = 7.4	− 81.5 to 96.4
				Wet = −22.8	− 121.5 to 76.0
	Preferred fruit (gp)[a]			100.3	30.5 to 170.0
	Preferred flowers (all)			− 24.0	− 92.1 to 44.1
	Season	667.7	0.8	Dry = −7.4	− 89.5 to 74.6
				Wet = −24.0	− 119.7 to 71.7
	Fruit (all)[a]			36.7	14.3 to 59.1
	Preferred flowers (all)			6.5	− 63.9 to 76.9
	Season	667.8	0.9	Dry = −12.1	− 90.2 to 66.0
				Wet = −19.5	− 75.6 to 36.7
	Preferred fruit (gp)			59.3	− 29.5 to 148.1
	Flowers (all)			− 19.2	− 44.5 to 6.2
	Season	668.7	1.8	Dry = −31.8	− 81.4 to 17.7
				Wet = −39.9	− 74.8 to −5.0
	Fruit (all)			26.0	− 3.5 to 55.5
	Flowers (all)			− 13.2	− 40.3 to 13.9
	Season	668.8	1.9	Dry = −13.8	− 65.7 to 38.0
				Wet = −32.0	− 73.1 to 9.0
	Fruit (all)[a]			36.2	8.9 to 63.6
	Flowers (gp)			0.5	− 39.2 to 40.3
	Season	668.9	2.0	Dry = 15.3	− 60.1 to 90.7
				Wet = −4.7	− 64.3 to 54.9
	Preferred fruit (gp)[a]			88.1	6.5 to 169.7
	Flowers (gp)			− 11.8	− 48.7 to 25.0
B	Season	720.1	0	Dry = 18.5	− 18.5 to 55.6
				Wet = −10.4	− 43.3 to 22.5
	Preferred fruit (gp)[a]			− 61.0	− 117.3 to −4.7
	Flowers (gp)[a]			− 53.4	− 90.7 to −16.2
D	Season[a]	269.6	0	Dry = 123.2	38.2 to 208.1
				Wet = 43.9	− 39.9 to 127.6
	Preferred fruit (all)			52.2	− 7.8 to 112.2
	Preferred flowers (gp)			159.5	− 36.0 to 355.0
	Season[a]	269.7	0.1	Dry = 107.9	44.8 to 171.1
				Wet = 32.1	− 30.1 to 94.3
	Preferred fruit (all)			80.3	15.6 to 145.1
	Flowers (gp)[a]			55.9	8.4 to 103.5

TABLE III. Continued.

Group(s)	Variable names	AIC	Δ_i	β	95% CI
	Season[a]	270.0	0.4	Dry = 183.0	48.9 to 317.0
				Wet = 127.5	− 30.1 to 285.8
	Preferred fruit (all)			32.3	− 25.8 to 90.4
	Preferred flowers (all)			111.6	− 11.2 to 234.5
	Season[a]	270.4	0.8	Dry = 185.5	39.6 to 331.0
				Wet = 127.6	− 39.0 to 294.2
	Preferred fruit (gp)			3.7	− 85.6 to 93.0
	Preferred flowers (all)			123.9	− 8.5 to 256.2
	Season[a]	271.2	1.6	Dry = 105.0	2.9 to 207.0
				Wet = 13.9	− 69.6 to 97.4
	Preferred fruit (gp)			20.6	− 99.9 to 141.1
	Preferred flowers (gp)			150.2	− 125.2 to 425.6

Group was a random factor. Separate models were conducted for groups A, B, and D. Group identity was included as a random factor. Only models with $\Delta_i < 2$ are shown.
[a]$P < 0.05$

DISCUSSION

Javan Gibbons at Citalahab Subsist Largely on Preferred Foods

All food species that comprised >5% of Javan gibbon diets at Citalahab (i.e. that were important) were also preferred (Table I). Indeed, 77–87% of the diets of each group consisted of preferred plant species. Thus, Javan gibbons appear to include a sufficiently broad range of species in their diets to allow them to eat mostly preferred fruit species even when overall fruit availability is relatively low.

Bornean white-bearded gibbons (*H. albibarbis*) at Gunung Palung are also selective, yet they eat fruits from more plant families than sympatric frugivores [Marshall et al., 2009b]. Marshall and colleagues (2009b) suggested four explanations for this pattern: First, gibbons lack a specialized digestive tract such as that possessed by colobine monkeys [Chivers, 1994; Lambert, 2007b], which may limit their ability to rely heavily on abundant foods such as leaves. Second, brachiation may permit gibbons to exploit foods found in small patches more efficiently than most other frugivores. In our study, >50% of feeding time was spent feeding on lianas and epiphytes, which is consistent with the idea that gibbons heavily exploit relatively small food patches. Third, while gibbons prefer fruits with specific features [McConkey et al., 2003], many plant families may have converged on an appropriate morphology and chemistry. Javan gibbons at Ujung Kulon [Kappeler, 1984] ate fruits from 40 families, but gibbons at Citalahab fed on fruits from 25 families, suggesting that a narrower range of foods may be available in the submontane forest at Citalahab. A fourth possibility is that gibbons may become more generalized feeders during periods of resource scarcity [Marshall et al., 2009b]. Gibbons may also select only the ripest food from each tree, but we have observed gibbons eating both ripe and unripe fruit from several highly preferred species.

Optimal foraging theory predicts that when food is abundant, animals should consume only preferred, high-quality foods, leading to low dietary breadth, whereas during periods of food scarcity, animals must eat more different types of food to obtain sufficient nutrients [MacArthur & Pianka, 1966; Robinson & Wilson, 1998]. Accordingly, several researchers have reported a negative relationship between fruit abundance and dietary breadth or diversity in gibbons [Bartlett, 1999; Marshall et al., 2009b; McConkey et al., 2003]. However, in our study, measures of overall fruit and flower abundance were not the best predictors of dietary breadth, and preferred fruit abundance was positively associated with the number of food species in the diet (Table IV). If gibbons are generally selecting among preferred fruits and flowers, rather than moving from preferred species to non-preferred FBF, then the abundance of specific fruit and flower species, rather than overall food abundance, should be the primary determinant of gibbon dietary breadth. The low densities of many preferred tree and liana species in the submontane habitat at Citalahab may also force gibbons to feed on a fairly broad set of species even in months with relatively high fruit availability.

Figs are Not Fallback Fruits for Javan Gibbons at Citalahab

The importance of figs for gibbons has long been recognized, but some researchers report that figs are actively sought out [Chivers & Raemaekers, 1986; Ungar, 1995], while others describe them as FBF [Harrison & Marshall, 2011; Leighton & Leighton, 1983]. At Citalahab, gibbons overselected four fig species and the "*Ficus*" group (Table II), and fig consumption was not generally negatively related to

TABLE IV. GLMM Models of the Relationship between Season, Flower, and Fruit Availability (four Measures) and DPL (m)

Group(s)	Variable names	AIC	Δ_i	β	95% CI
All	Season	2326.5	0	Dry = 12.0	−181.3 to 205.2
				Wet = −141.4	−348.2 to 65.5
	Preferred fruit (all)[a]			239.0	99.9 to 378.1
	Preferred flowers (gp)[a]			−250.8	−495.6 to −6.0
	Season	2328.2	1.7	Dry = −73.2	−405.4 to 259.0
				Wet = −245.7	−642.3 to 150.8
	Preferred fruit (all)[a]			240.1	99.4 to 380.7
	Preferred flowers (all)			−204.8	−495.1 to 85.5
A	Season	870.5	0	Dry = −120.0	−513.5 to 273.6
				Wet = −229.1	−540.3 to 82.2
	Preferred fruit (gp)			259.8	−166.5 to 686.0
	Flowers (gp)			−185.9	−378.4 to 6.7
	Season[a]	871.3	0.8	Dry = −86.8	−559.4 to 385.7
				Wet = −321.6	−846.2 to 202.9
	Preferred fruit (gp)[a]			460.0	89.4 to 830.5
	Preferred flowers (all)			−230.9	−592.7 to 130.8
	Season	871.6	1.1	Dry = 50.4	−293.4 to 394.2
				Wet = −177.9	−557.5 to 201.6
	Preferred fruit (gp)			357.7	−75.7 to 791.1
	Preferred flowers (gp)			−207.8	−606.4 to 190.8
	Season[a]	871.8	1.3	Dry = −205.8	−493.5 to 81.9
				Wet = −290.3	−529.4 to −51.3
	Preferred fruit (all)			130.0	−73.6 to 333.7
	Flowers (gp)			−184.5	−375.6 to 6.6
	Season	871.8	1.3	Dry = −291.7	−710.2 to 126.6
				Wet = −495.4	−986.1 to −4.6
	Preferred fruit (all)[a]			237.8	61.0 to 414.7
	Preferred flowers (all)			−282.6	−641.3 to 76.2
	Season	871.9	1.4	Dry = −41.5	−288.5 to 205.5
				Wet = −126.0	−516.1 to 264.1
	Fruit (gp)			227.3	−10.5 to 465.1
	Preferred flowers (gp)			−8.3	−522.2 to 505.6
	Season	872.0	1.5	Dry = −192.7	−521.8 to 136.3
				Wet = −257.4	−558.6 to 43.7
	Fruit (gp)			125.7	−115.6 to 366.9
	Flowers (gp)			−144.9	−401.0 to 111.1
	Season	872.2	1.7	Dry = 15.3	−493.5 to 524.0
				Wet = −52.2	−674.7 to 570.3
	Fruit (gp)[a]			242.1	53.7 to 430.4
	Preferred flowers (all)			49.5	−382.6 to 481.6
	Season	872.4	1.9	Dry = −92.7	−510.8 to 325.4
				Wet = −176.8	−477.6 to 123.9
	Preferred fruit (gp)			236.2	−238.9 to 711.4
	Flowers (all)			−107.3	−243.1 to 28.6
B	Season	987.7	0	Dry = 85.0	−440.0 to 609.9
				Wet = 9.5	−522.8 to 541.7
	Preferred flowers (gp)			−373.7	−1016.0 to 268.6
	Preferred fruit (all)[a]			372.4	74.0 to 670.9
	Season	988.5	0.8	Dry = −140.3	−720.8 to 440.2
				Wet = −149.6	−826.0 to 526.7
	Preferred fruit (gp)[a]			383.5	36.1 to 730.9
	Preferred flowers (all)			−373.8	−882.3 to 134.7
	Season	988.8	1.1	Dry = 114.8	−437.3 to 666.9
				Wet = −15.6	−684.2 to 653.0
	Preferred fruit (all)[a]			267.6	38.8 to 496.3
	Preferred flowers (all)			−233.2	−714.4 to 247.9

TABLE IV. Continued.

Group(s)	Variable names	AIC	Δ_i	β	95% CI
D	Season	310.5	0	Dry = 375.8	− 215.5 to 967.1
				Wet = −10.4	− 486.6 to 465.8
	Preferred flowers (gp)[a]			1925.4	312.2 to 3538.6
	Preferred fruit (gp)			461.1	− 262.9 to 1185.1
	Season	311.8	1.3	Dry = 255.7	− 230.7 to 742.2
				Wet = −98.5	− 543.7 to 346.7
	Preferred flowers (gp)[a]			1658.5	368.8 to 2948.2
	Fruit (gp)			198.4	− 62.1 to 458.8
	Season	312.1	1.6	Dry = 266.9	− 253.3 to 787.2
				Wet = 24.8	− 485.7 to 535.4
	Preferred flowers (gp)[a]			1388.0	168.5 to 2607.4
	Preferred fruit (all)			214.6	− 164.4 to 593.6
	Season	312.5	2	Dry = 277.3	− 234.0 to 788.6
				Wet = −2.7	− 480.6 to 475.1
	Preferred flowers (gp)[a]			1640.7	304.8 to 2976.6
	Fruit (all)			163.1	− 86.4 to 412.5

Group was a random factor. Separate models were conducted for groups A, B, and D. Only models with $\Delta_i < 2$ are shown.
[a]$P < 0.05$.

non-fig fruit availability (Table VI). Individual figs may produce massive fruit crops, which makes measurements of dietary preference highly sensitive to the methods used to assess food availability. For example, figs are preferred foods for siamangs in southern Sumatra when food availability is measured as the number of fruiting individuals, but not when food availability is measured as the number of fruits available [Lappan, 2010]. However, at Citalahab, estimated crop sizes in the phenology plots were not significantly larger for figs than for non-fig species [Kim, unpublished data]. Thus, our analyses indicate that figs as a species group are not FBF among fruits eaten by gibbons at Citalahab, although some species may be FBF, and several fig species are preferred.

There are at least two possible explanations for the variation in the importance of figs for gibbons between sites. First, fig species almost certainly vary at least somewhat in their characteristics (nutrient contents, food patch sizes, phonological patterns, etc.). Thus, the overall importance of figs for frugivores may vary because of differences among sites in the availability of high-quality fig resources. Alternatively, the relative abundance of other high-quality food resources at a site may affect the relative preference rank of figs, even if the actual quality of figs as food resources is identical. Thus, gibbons at sites where other high-quality foods are abundant may use figs as FBF, while figs may be preferred at sites where foods of superior quality are rare.

Gibbon Groups Differ in Their Responses to Variation in Fruit and Flower Availability

Several previous studies have shown differences in the diets of neighboring primate groups [Chap-

man et al., 2002; Lappan, 2010; McConkey et al., 2003], suggesting that local factors are important determinants of primate foraging strategies. Fruit typically comprises >50% of gibbon diets, making it the most important gibbon food [Bartlett, 2009]. However, in our study, some groups were more sensitive to variation in fruit availability than others, and flower availability was an equally or more important driver of gibbon diets (Tables III and VI)

Home range quality may affect gibbon responses to variation in fruit availability. Group B had the largest home range, and their home range had a higher density of food trees than the other two home ranges [Kim et al., 2011]. Thus, group B probably had access to more fruit and more preferred fruit in most months. Accordingly, group B ate more fruit than the other groups, and group B's diet included ≥50% fruit on more days (group A: 63.6%; group B: 77.5%; group D: 62.1%). Thus, group B may have had access to sufficient fruit on most days, which may explain why they appear to have been less affected by variation in fruit availability.

Our vegetation plots did not sample every fruit or flower species that the gibbons ate. However, previous studies in west Javan forests of similar elevation suggest that most tree species except those present at very low densities will be sampled in plots covering an area of 1 ha [Simbolon, 2001]. Tree species diversity in lowland tropical forests is often very high, but wet forests in Southeast Asia display distinct altitudinal floristic zones [Ashton, 2003; Whitten et al., 1996], with tree species diversity declining with increasing altitude, and different sets of species at different altitudes [Whitten et al., 1996]. In addition, many Sundaic plant families are poorly represented on Java, and Java is relatively poor in endemic plant species and has no endemic genera

TABLE V. GLMM Models of the Relationship between Season, Flower, and Fruit Availability (Four Measures) and Dietary Breadth

Group(s)	Variable names	AIC	ΔAIC	β	95% CI
All	Season	629.7	0	Dry = −0.1	− 2.6 to 2.4
				Wet = −1.4	− 4.4 to 1.6
	Preferred fruit (all)[a]			2.3	1.3 to 3.4
	Preferred flowers (all)			− 2.0	− 4.1 to 0.2
A	Season[a]	299.2	0	Dry = 2.3	0.1 to 4.4
				Wet = 0.7	− 2.0 to 3.5
	Preferred fruit (all)[a]			2.1	0.3 to 4.0
	Preferred flowers (gp)			0.0	− 3.5 to 3.5
	Season	299.2	0	Dry = 1.6	− 2.2 to 5.5
				Wet = −0.0	− 4.5 to 4.5
	Preferred fruit (all)[a]			2.1	0.5 to 3.8
	Preferred flowers (all)			− 0.6	− 3.9 to 2.7
	Season[a]	300.2	1	Dry = 3.1	− 0.1 to 6.3
				Wet = 1.2	− 2.3 to 4.7
	Preferred fruit (gp)			3.3	− 0.7 to 7.3
	Preferred flowers (gp)			− 0.3	− 4.0 to 4.0
	Season[a]	300.4	1.2	Dry = 3.1	− 1.3 to 7.5
				Wet = 1.2	− 3.6 to 6.1
	Preferred fruit (gp)[a]			3.5	0.0 to 6.9
	Preferred flowers (all)			− 0.2	− 3.5 to 3.2
	Season	300.6	1.4	Dry = 2.1	− 0.5 to 4.8
				Wet = 0.6	− 1.6 to 2.8
	Preferred fruit (all)[a]			2.1	0.2 to 4.0
	Flowers (gp)			− 0.1	− 1.9 to 1.7
B	Season	314.8	0	Dry = −1.5	− 4.8 to 1.8
				Wet = −2.5	− 6.6 to 1.6
	Preferred flowers (all)[a]			− 3.0	− 5.9 to −0.1
	Preferred fruit (all)[a]			2.5	1.1 to 3.9

Group was a random factors. Separate models were conducted for groups A and B. Only models with $\Delta_i < 2$ are shown.
[a]$P < 0.05$.

[Whitten et al., 1996]. About 700 plant species grow in the GHSNP [Mirmanto et al., 2008; Priyadi et al., 2010], but fewer than half of the species identified in the GHSNP in a recent survey were large tree species growing outside of areas of human cultivation [Priyadi et al., 2010], and only a fraction of those should be expected to occur in the altitudes represented at Citalahab. Researchers have consistently found only 57–116 tree species in west Javan submontane forests, including GHSNP, with a few species dominating the canopy, and most species represented at low densities [Ashton, 2003; Mirmanto et al., 2008; Whitten et al., 1996]. We identified 92 species in our plots, including 36 of the 48 identified fruit species that Javan gibbons ate. To confirm that the species not included in the plots were rare, we identified each individual tree of three of the 12 unsampled species that gibbons ate most frequently, *Garcinia dioica*, *Mussaenda frondosa*, and *P. lateriflora*. These species occurred at very low densities (*G. dioica* 0.04 individuals/ha, *M. frondosa* 0.06 individuals/ha, *P. lateriflora* 0.09 individuals/ha). Thus, the species not sampled in our vegetation plots likely represent very little of the available food supply, and our method should have produced a reasonable approximation of total fruit production from trees and large lianas in the study area. Our inability to identify and sample small-bore liana species probably represents a more serious limitation to our data set, since feeding from lianas and epiphytes comprises >50% of gibbon feeding time, including some component of fruit- and flower-feeding time.

The ultimate causes of variation in gibbon responses to food availability in this population may relate to the ecology of the study area. Microhabitat variation, stochastic processes, and interactions among individuals of the same or different species may lead to an uneven distribution of individuals in a landscape [Condit et al., 2000], and ecological context can have powerful effects on frugivore–fruit interactions [Prasad & Sukumar, 2010]. Variation in the local densities of preferred species may result in differences in the availability of specific foods in the home ranges of neighboring groups, especially for species with asynchronous fruiting and flowering schedules. Gibbon behavioral differences resulting

TABLE VI. GLMM Models of the Relationship between Fruit Availability (Two Measures), Flower Availability, and Fig Fruit Feeding Time (min/day)

Group	Variable names	AIC	ΔAIC	β	95% CI
All	Flowers (all)[a]	864.6	0	−0.9	−1.6 to −0.3
A	Non-fig fruit[a]	336.8	0	1.5	0.1 to 2.8
B	Flowers (all)[a]	359.6	0	−1.1	−2.0 to −0.2
D	Flowers (all)[a]	148.5	0	−2.3	−3.9 to −0.6
	Fig fruit[a]	150.0	1.5	4.5	0.1 to 8.8

Group was a random factor. Separate models were conducted for groups A, B, and D. Only models with $\Delta_i < 2$ are shown.
[a]$P < 0.05$.

from variation in food abundance in their home ranges may in turn tend to increase ecological differentiation between gibbon territories over generations due to the role of gibbons as seed dispersers [McConkey, 2009]. It is also possible that differences in local ecology may be caused by or reinforced by differences in behavioral traditions among groups [Chapman & Fedigan, 1990; Boesch et al., 2006], especially among long-lived animals with relatively stable group compositions, such as hominoids, but this intriguing possibility is difficult to rigorously evaluate given available data.

Seasonal variation in rainfall and food availability is often less pronounced than supraannual variation caused by El Niño-Southern Oscillation and mast fruiting events at multiyear intervals in insular Southeast Asia. Our results here confirm that seasonal variation in rainfall has a subtle but significant effect on gibbon diets and ranging behavior, but patterns of seasonal variation vary among groups [Kim et al., 2011], and group B, the group for which fruit-feeding time, dietary breadth, and DPL were most affected by flower availability, does not show significant seasonal variation in flower-feeding time [Kim et al., 2011]. Thus, temporal variation in gibbon diets and DPL for this population is affected by both seasonal and aseasonal factors, and local ecological factors appear to be more important than areawide weather patterns in determining the behavior of each gibbon group.

Flowers are Important Gibbon Foods, and May Drive Gibbon Foraging Strategies

Gibbons at Citalahab spent 12% of feeding time eating flowers, which is higher than rates reported from most gibbon populations [mean = 4.2% of feeding time, $N = 24$ populations; Bartlett, 2011]. Measurements of flower availability had a more pronounced effect on gibbon behavior than measurements of fruit availability in most models selected for fruit-feeding time, fig-feeding time, and DPL for the three groups combined (Tables III, IV, and VI). Flower availability was also the strongest predictor of diets for hybrid gibbons (*H. muelleri* ×

H. agilis/albibarbis) at Barito Ulu that spent 13% of feeding time eating flowers (McConkey et al., 2003), and high flower consumption was associated with reduced DPL in siamangs (*Symphalangus syndactylus*) at Way Canguk [Lappan, 2009], the other site at which flower-feeding >10% of gibbon feeding time. Our results confirm that flowers are important drivers of gibbon diets and ranging patterns for some gibbon groups, despite the greater overall importance of fruit in gibbon diets.

Flowers are FBF for some primate species [Terborgh, 1983], but the negative relationship between preferred flower abundance and fruit-feeding time (Table III), as well as fig-feeding time (Table VI) suggests that fruit consumption increased during periods of low availability of preferred flowers, which is consistent with the interpretation that some flowers are highly preferred foods. We did not detect a significant negative correlation between flower and fruit abundance, so a reduction in fruit-feeding time when flowers are abundant cannot be interpreted simply as a response to reduced fruit abundance. The apparent preference for at least some species of flowers over ripe fruit, even in highly frugivorous gibbons, may indicate that preferred flowers offer important nutritional benefits that other foods lack. Flowers of some species contain high levels of sugars, such as ripe fruits, but also contain moderate levels of protein [McConkey et al., 2003], and may provide essential amino acids, which are particularly important for reproducing females [Simmen et al., 2007; White, 2011]. Thus, females, in particular, might prefer flowers over fruits, at least until their needs for these key nutrients are met. If flowers as a class are preferred over fruits, though, it is difficult to explain why group B ate fewer flowers than group A or D, given group B's higher home range size and quality and greater responsiveness to variation in flower abundance. This seemingly counterintuitive result may be explained by temporal or spatial variation in the preference rank of flowers. Animals should prefer foods that are easy to find [Lambert, 2007a; MacArthur & Pianka, 1966], and search time may depend on abundance [Werner & Hall, 1974]. Thus, a nutritionally superior food may be nonpreferred when rare, but highly preferred when abundant [Werner & Hall, 1974]. Mean monthly flower feeding ranged from 0 to 242 min. in our study groups. Ultimately, the effects of flowers on gibbon behavior should depend on the qualities of the flowers eaten, not just the quantities consumed. The availability of specific nutrients in other locally abundant foods may also affect the importance and preference ranks of primate foods. A finer grained analysis considering spatial and temporal variation in the abundance of specific food species might reveal considerable variation in primate responses to changes in the food availability within broad classes such as "fruits" and "flowers."

ACKNOWLEDGMENTS

REFERENCES

Akaike H. 1974. A new look at statistical model identification. IEEE Trans Automat Contr 19:716–723.

Ashton PS. 2003. Floristic zonation of tree communities on wet tropical mountains revisited. Perspect Plant Ecol Evol Syst 6:87–104.

Bartlett TQ. 1999. Feeding and ranging behavior of the white-handed gibbon (*Hylobates lar*) in Khao Yai National Park, Thailand [PhD Dissertation]. St. Louis, MO: Washington University-St. Louis. 193 p.

Bartlett TQ. 2009. Seasonal home range use and defendability in white-handed gibbons (*Hylobates lar*) in Khao Yai National Park, Thailand. In: Lappan S, Whittaker DJ, editors. The gibbons: new perspectives on small ape socioecology and population biology. New York: Springer. p 265–275.

Bartlett TQ. 2011. The Hylobatidae: small apes of Asia. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. 2nd edition. New York: Oxford University Press. p 300–312.

Boesch C, Bi C, Anderson D, Stahl D. 2006. Food choice in Taï chimpanzees: are cultural differences present? In: Hohmann G, Robbins MM, Boesch C, editors. Feeding ecology in apes and other primates. Cambridge: Cambridge University Press. p 183–201.

Brockelman WY. 2009. Ecology and the social system of gibbons. In: Lappan S, Whittaker DJ, editors. The gibbons: new perspectives on small ape socioecology and population biology. New York: Springer. p 211–240.

Chapman CA, Chapman LJ. 2002. Foraging challenges of red colobus monkeys: influence of nutrients and secondary compounds. Comp Biochem Physiol A 133:861–875.

Chapman CA, Chapman LJ, Gillespie TR. 2002. Scale issues in the study of primate foraging: red colobus of Kibale National Park. Am J Phys Anthropol 117:849–868.

Chapman C, Fedigan L. 1990. Dietary differences between neighboring Cebus capucinus groups: local traditions, food availability or responses to food profitability? Folia Primatol 54:177–186.

Chivers DJ. 1984. Feeding and ranging in gibbons: a summary. In: Preuschoft H, Chivers D, Brockelman W, Creel N, editors. The lesser apes: evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 267–284.

Chivers DJ. 1994. Functional anatomy of the gastrointestinal tract. In: Davies AG, Oates JF, editors. Colobine monkeys. their ecology, behaviour, and evolution. Cambridge: Cambridge University Press p 205–228.

Chivers DJ, Raemaekers JJ. 1986. Natural and synthetic diets of Malayan gibbons. In: Else JG, Lee PC, editors. Primate ecology and conservation. Cambridge: Cambridge University Press. p 39–56.

Condit R, Ashton PS, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell SP, Foster RB, Itoh A, LaFrankie JV. 2000. Spatial patterns in the distribution of tropical tree species. Science 288:1414–1418.

Harrison ME, Marshall AJ. 2011. Strategies for the use of fallback foods in apes. Int J Primatol 32:531–565.

Itoh A, Nishida T. 2007. Chimpanzee grouping patterns and food availability in Mahale Mountains National Park, Tanzania. Primates 48:87–96.

Kappeler M. 1984. Diet and feeding behaviour of the moloch gibbon. In: Preuschoft H, Chivers DJ, Brockelman WY, Creel N, editors. The lesser apes: evolutionary and behavioural biology. Edinburgh: Edinburgh University Press. p 228–241.

Kim S, Lappan S, Choe JC. 2011. Diet and ranging behavior of the endangered Javan gibbon (*Hylobates moloch*) in a submontane tropical rainforest. Am J Primatol 73:270–280.

Lambert JE. 2007a. Seasonality, fallback strategies, and natural selection: a chimpanzee and cercopithecoid model for interpreting the evolution of hominin diet. In: Ungar PS, editor. Evolution of the human diet: the known, the unknown, and the unknowable. Oxford: Oxford University Press. p 324–343.

Lambert JE. 2007b. Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In: Campbell C, Fuentes A, MacKinnon KC, Panger M, Bearder SK, editors. Primates in perspective. New York: Oxford University Press. p 482–495.

Lappan S. 2009. Flowers are an important plant food for small apes in southern Sumatra. Am J Primatol 71:624–635.

Lappan S. 2010. Siamang socioecology in spatiotemporally heterogenous landscapes: do 'typical' groups exist? In: Gursky S, Supriatna J, editors. Indonesian primates. New York: Springer. p 73–96.

Leighton M. 1993. Modeling dietary selectivity by Bornean orangutans: evidence for integration of multiple criteria in fruit selection. Int J Primatol 14:257–313.

Leighton M, Leighton DR. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. In: Sutton SL, Whitmore TC, Chadwick AC, editors. Tropical rain forest: ecology and management. Oxford: Blackwell Scientific. p 181–196.

MacArthur R, Pianka E. 1966. On optimal use of a patchy environment. Am Nat 100:603–609.

Malone NM. 2007. The socioecology of the critically endangered Javan gibbon (*Hylobates moloch*): assessing the impact of anthropogenic disturbance on primate social systems [PhD Dissertation]. Eugene, OR: University of Oregon. 180 p.

Malone N, Fuentes A. 2009. The ecology and evolution of hylobatid communities: causal and contextual factors underlying inter- and intraspecific variation. In: Lappan S, Whittaker DJ, editors. The gibbons: new perspectives on small ape socioecology and population biology. New York: Springer Publishing. p 241–264.

Marshall AJ. 2009. Are montane forests demographic sinks for Bornean white-bearded gibbons? Biotropica 41:257–267.

Marshall AJ, Boyko CM, Feilen KL, Boyko RH, Leighton M. 2009a. Defining fallback foods and assessing their importance in primate ecology and evolution. Am J Phys Anthropol 140:603–614.

Marshall AJ, Cannon CH, Leighton M. 2009b. Competition and niche overlap between gibbons (*Hylobates albibarbis*) and other frugivorous vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia. In: Lappan S, Whittaker DJ, editors. The gibbons: new perspectives on small ape socioecology and population biology. New York: Springer. p 161–188.

Marshall AJ, Wrangham RW. 2007. The ecological significance of fallback foods. Int J Primatol 28:1219–1235.

McConkey KR. 2009. The seed dispersal niche of gibbons in Bornean dipterocarp forests. In: Lappan S, Whittaker DJ, editors. The gibbons: new perspectives on small ape socioecology and population biology. New York: Springer. p 189–210.

McConkey KR, Ario A, Aldy F, Chivers DJ. 2003. Influence of forest seasonality on gibbon food choice in the rain forests of Barito Ulu, central Kalimantan. Int J Primatol 24:19–32.

Mirmanto E, Wiriadinata H, Royyani MF, Ichikawa S, Ismirza. 2008. Merajut Pesona Flora Hutan Pegunungan Tropis di Gunung Salak. Bogor: LIPI-TNGHS-JICA.

Oates JF. 1987. Food distribution and foraging behavior. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 197–209.

Palombit RA. 1997. Inter- and intra-specific variation in the diets of sympatric siamang (*Hylobates syndactylus*) and lar gibbons (*Hylobates lar*). Folia Primatol 68:321–337.

Prasad S, Sukumar R. 2010. Context-dependency of a complex fruit–frugivore mutualism: temporal variation in crop size and neighborhood effects. Oikos 119:514–523.

Priyadi H, Takao G, Rahmawati I, Supriyanto B, Nursal WI, Rahman I. 2010. Five hundred plant species in Gunung Halimun Salak National Park, west Java: a checklist including Sundanese names, distribution and use. Bogor, Indonesia: CIFOR.

Raemaekers J. 1980. Causes of variation between months in the distance traveled daily by gibbons. Folia Primatol 34:46–60.

Remis MJ. 2006. The role of taste in food selection by African apes: implications for niche separation and overlap in tropical forests. Primates 47:56–64.

Robinson BW, Wilson DS. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. Am Nat 151:223–235.

Savini T, Boesch C, Reichard U. 2009. Varying ecological quality influences the probability of polyandry in white-handed gibbons (*Hylobates lar*) in Thailand. Biotropica 41:503–513.

Simbolon H. 2001. The growth dynamics on tree species of Fagaceae family in a tropical montane rain forest of west Java, Indonesia. Berita Biologi, LIPI-PHPA-JICA Bogor 5:659–666.

Simmen B, Bayart F, Marez A, Hladik A. 2007. Diet, nutritional ecology, and birth season of *Eulemur macaco* in an anthropogenic forest in Madagascar. Int J Primatol 28:1253–1266.

Stevenson PR. 2004. Fruit choice by woolly monkeys in Tinigua National Park, Colombia. Int J Primatol 25:367–381.

Terborgh J. 1983. Five new world primates: a study in comparative ecology. Princeton: Princeton University Press.

Ungar P. 1995. Fruit preferences of four sympatric primate species at Ketambe, northern Sumatra, Indonesia. Int J Primatol 16:221–245.

van Schaik CP, Terborgh JW, Wright SJ. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. Annu Rev Ecol Syst 24:353–377.

Werner EE, Hall DJ. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology 55:1042–1052.

White TCR. 2011. The significance of unripe seeds and animal tissues in the protein nutrition of herbivores. Biol Rev 86:217–224.

Whitten AJ, Soeriaatmaja RE, Afiff SA. 1996. The ecology of Java and Bali. Hong Kong: Periplus.

Yamagiwa J, Basabose AK. 2009. Fallback foods and dietary partitioning among *Pan* and *Gorilla*. Am J Phys Anthropol 140:739–750.

Zar JH. 1996. Biostatistical analysis. Upper Saddle River, NJ: Prentice Hall.