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Modeling the Ecological and Phenological Predictors of Fruit Consumption by Gibbons (*Hylobates albibarbis*)

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ABSTRACT

Understanding the ecological interactions between plant reproductive strategies and frugivore feeding behavior can offer insight into the maintenance of tropical forest biodiversity. We examined the role of plant ecological and phenological characteristics in influencing fruit consumption by the White-bearded gibbon (*Hylobates albibarbis*) in Gunung Palung National Park, Indonesian Borneo. Gibbons are widespread across Borneo, highly frugivorous and perform important seed dispersal services. We compare multiple models using information criteria to identify the ecological and phenological predictors that most strongly influence gibbon fruit use of 154 plant genera. The most important predictors of resource use were the overall abundance of a genus and the consistency of fruit availability. Plant genera can maintain constant fruit availability as a result of (1) individual stems fruiting often or (2) stems fruiting out of synchrony with each other (asynchrony). Our results demonstrate that gibbons prefer to feed on plant genera that provide consistent fruit availability due to fruiting asynchrony. Because gibbons feed more often on genera that fruit asynchronously, gibbons are more likely to disperse seeds of plant genera with this reproductive strategy. Research on other frugivorous species is needed to determine whether the results for gibbons are generalizable more broadly. Finally, these results suggest that asynchronously fruiting plant genera may be particularly important for habitat restoration in tropical forests designed for frugivore conservation.

Abstract in Indonesian is available in the online version of this article.

Key words: foraging strategy; frugivory; fruiting asynchrony; Indonesia; phenology; tropical ecology; vertebrate feeding ecology.

MUTUALISTIC INTERACTIONS BETWEEN TREES THAT PRODUCE FLESHY FRUITS AND THE frugivores that disperse their seeds are widespread in forest ecosystems and contribute to the maintenance of biodiversity (McKey 1975, Terborgh *et al.* 2002). Animal-mediated dispersal is the most common means of seed dispersal for angiosperms in tropical forests, comprising 50–75 percent of tropical tree species (Howe & Smallwood 1982, da Silva & Tabarelli 2000). It is therefore unsurprising that there has been a considerable amount of interest in identifying the qualities of fruits and fruiting plants that predict use by frugivores. Research aimed at predicting fruit use has involved both the physiological and morphological traits of the fruits themselves (Janson 1983, Fischer & Chapman 1993, Leighton 1993, McConkey *et al.* 2002) as well as general ecological and phenological characteristics of woody angiosperms (*e.g.,* spatial and temporal abundance (McConkey *et al.* 2003, Walker 2007, Felton *et al.* 2008), crop size (Leighton 1993, Korine *et al.* 2000), and fruiting synchrony (Fredriksson & Wich 2006) or asynchrony (Poulin *et al.* 1999)).

Studies examining the role of fruit morphology and chemistry in determining use by frugivores have determined that commonly eaten fruits are often similar in their macronutrient balance (Conklin-Brittain *et al.* 1998, Felton *et al.* 2009), chemical defenses (Cipollini & Levey 1997, Wrangham *et al.* 1998), and morphological characteristics (*e.g.*, size and color; Fischer & Chapman 1993, Korine *et al.* 2000, Terborgh *et al.* 2002, Stevenson & Link 2010). Indeed a number of studies have hypothesized distinct plant 'dispersal syndromes' based on a correspondence between the morphology and chemistry of fruits and the anatomies and preferences of their putative vertebrate dispersers. Dispersal syndrome patterns have been identified in site-specific field studies (Knight & Siegfried 1983, Gautier-Hion *et al.* 1985, Lomáscolo *et al.* 2010). Broad spatial patterns in plant and animal distributions reflecting dispersal syndromes have also been found (Voigt *et al.* 2004, Almeida-Neto *et al.* 2008, Beaudrot *et al.* 2013).

In contrast with the breadth of studies of fruit traits, research on the ecological characteristics of plants important to frugivores has often been confined to a single characteristic or has focused on a single plant taxon. Nevertheless, several areas of research have demonstrated that general ecological characteristics of fruiting plants can strongly influence frugivore diets (van

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Schaik *et al.* 1993, Burns 2004, Thies & Kalko 2004, Hanya 2005). For instance, it is known that taxa with large crop sizes are preferred by several tropical bird and bat species (Korine *et al.* 2000, Blendinger & Villegas 2011). Additionally, spatial abundance of a plant species at multiple scales is known to influence avian frugivore foraging (Garcia & Ortiz-Pulido 2004, Carlo & Morales 2008). Finally, plants that stagger fruiting times across individuals (such as figs [*Ficus*: Moraceae]) play important roles as keystone resources for many tropical frugivores, given their constant availability (Janzen 1979, Terborgh 1983, Lambert & Marshall 1991, van Schaik *et al.* 1993, Marshall & Wrangham 2007).

Despite the importance of specific ecological characteristics of fruiting plants for predicting frugivore use, to date few studies have considered multiple ecological characteristics simultaneously or examined patterns across broad taxonomic groups (Fleming 1992, Leighton 1993). As a result, we know little about the relative importance of ecological characteristics in determining fruit consumption and whether these patterns are consistent across plant taxa in diverse communities. Identification of patterns such as these will inform our understanding of frugivore foraging strategies, as well as their implications for animal-dispersed plant species.

Primates comprise a major proportion of biomass of the frugivorous vertebrates found on the island of Borneo in Southeast Asia (MacKinnon *et al.* 1996, Primack & Corlett 2005). Furthermore, of the 13 primate species found on Borneo, gibbon diets contain the highest percentage of fruit (Gupta & Chivers 1999). Moreover, gibbons have been documented to feed on a wide variety of plant taxa (Marshall *et al.* 2009b). Gibbons therefore provide an excellent taxon in which to investigate the role of ecological plant characteristics in predicting frugivore use. Additionally, the high plant diversity in Southeast Asian forests provides many genera of available fruit resources (Kier *et al.* 2005) encompassing a wide range of phenological patterns (Van Schaik 1986, Marshall & Leighton 2006). Moreover, there are significant temporal fluctuations in fruit availability, with highly productive, aseasonal masting events separated by periods of general fruit scarcity (Wich & van Schaik 2000, Marshall & Leighton 2006, Cannon *et al.* 2007a), which produce a wide range of ecological conditions to which frugivores must adapt.

In this study, we examine the relative importance of multiple ecological and phenological characteristics of plants in influencing consumption by frugivorous White-bearded gibbons (*Hylobates albibarbis*) in Indonesian Borneo. Considering the wide range of plant taxa known to be consumed by co-occurring frugivorous vertebrates in Borneo, we address questions including: (1) does the amount of fruit that a plant produces, as estimated by its diameter at breast height (dbh) and crop size, predict consumption? (2) Does the density of stems of a genus (which reflects the commonness throughout the landscape) or the frequency with which individual stems fruit strongly affect use? (3) Does temporal clustering of fruiting events or timing of reproductive bouts relative to the rest of the forest affect which taxa are more likely to be consumed? We address these questions by quantifying ecological and phenological characteristics of 154 plant genera. We then use an information theoretic approach to identify which predictors most strongly influence gibbon fruit use by comparing multiple models using AICc model selection.

MATERIALS AND METHODS

FIELD SITE.—Our study was conducted at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, West Kalimantan (1°13′ S, 110°7′ E). The study site contains seven distinct forest types that differ due to variations in soil type, drainage, altitude, and underlying geology (Paoli *et al.* 2006, Marshall 2009, 2010, Marshall *et al.* 2014). Phenological patterns in two of the seven forest types, montane and peat swamp forests, differ dramatically from the five other forest types found at the site (Marshall & Leighton 2006, Cannon *et al.* 2007a,b). We therefore restricted our analysis to feeding observations and phenological data from the following five forest types: freshwater swamp, alluvial bench, lowland sandstone, lowland granite, and upland granite. Although there may be interesting differences among these habitats in the ecological characteristics we considered, we did not have a sufficient number of feeding observations in each habitat to permit robust analyses at the level of forest type. We present data on plant phenology and gibbon feeding collected between October 2007 and February 2013.

PLANT DATA COLLECTION AND ANALYSIS.—We used a random number generator to select ten plant phenology plots in each forest type from among the 126 that were randomly placed at the site in the mid 1980s by M. Leighton and colleagues (Cannon & Leighton 2004, Cannon *et al.* 2007b). The locations of the plots in each forest type were determined initially using a random number generator to select co-ordinates and bearings for each (M. Leighton, pers. comm.). Plots were either 0.1 or 0.2 ha in size and sampling area totaled 1.5 ha per forest type. In these plots, trees larger than 14.5 cm dbh, all lianas larger than 3.5 cm dbh, and all hemi-epiphytic figs whose roots reached the ground were identified, measured, and tagged (see Marshall & Leighton 2006, Marshall 2004, 2010 for details). As a result of our dbh cutoff, smaller trees and understory shrubs were excluded from the analysis. We retagged and recorded the locations of all stems in the seventy plots in 2007. Botanical nomenclature followed APGII (Angiosperm Phylogeny Group 2003). We monitored monthly the reproductive behavior of all tagged tree, fig, and liana stems located in the phenology plots (mean stems/mo = 3050; SD = 464). We carefully examined each stem with binoculars and assigned it to one of six reproductive states: reproductively inactive, bearing flower buds, flowers, immature, mature, or ripe fruits. We used changes in fruit size, color, and texture to determine ripeness stages for each plant taxon, following categories developed over the last 20 yr (Cannon *et al.* 2007b, Marshall *et al.* 2009b). If the stem was reproductively active, we assessed the total crop size using a semi-logarithmic scale to avoid compounding errors at large crop sizes (Marshall & Wich 2013).

We conducted all analyses at the generic level. While there are species-specific differences in plant phenology and fruit traits, demonstration of phylogenetic conservatism at the genus level has called into question the appropriateness of broad comparative analyses at the species level, due to statistical non-independence (Harvey & Pagel 1991, Kelly & Purvis 1993, Chazdon *et al.* 2003, Davies *et al.* 2013). In addition, Bornean forests contain some of the highest levels of vascular plant diversity in the world (Kier *et al.* 2005). As a consequence, despite extensive sampling and many voucher specimen collections, a considerable proportion of the flora have yet to receive formal taxonomic treatment in the scientific literature and were therefore only identified to the genus level.

We calculated model predictors for each plant genus (N = 154) that fruited at least once during the 66-mo study period and that was observed to have been fed upon at least once by a vertebrate at CPRS (Blundell 1996, Laman *et al.* 1996, Marshall *et al.* 2009b). In addition to including model predictors for each genus for *growth form* (*i.e.*, tree, liana), *crop size*, and *dbh*, we also calculated several predictors to take into account the commonness of a genus across the landscape and its fruit availability over time. To balance sample sizes among categories and thereby facilitate robust analysis, c*rop size* was organized into four discrete categories: I (1–25 fruits), II (26–100 fruits), III (101500 fruits), IV (>500 fruits). Due to concerns that this categorical approach may have been overly conservative (and insufficient to reveal correlations between crop size and other continuous predictors), we also included *dbh* as a continuous proxy variable for crop size (Chapman *et al.* 1992, Leighton 1993, Marshall & Wich 2013). *Stem density* was defined as the average number of stems of the focal genus per ha. *Fruit frequency* was defined as the average proportion of months in the study that a stem of the focal genus produced fruit. *Productivity* was defined as the average proportion of all plants (focal genus excluded) in fruit during the months in which the focal genus fruited. *Synchrony* was defined as the temporal clustering of fruiting by individuals within the focal genus, calculated as the coefficient of variation of number of individuals in fruit during each month of the study. *Rainfall* was defined as the mean daily rainfall during the months in which the focal genus fruited (Table 1). For clarity, model predictors are indicated by italics throughout.

TABLE 1. *Description of predictors used in models of* Hylobates albibarbis *foraging behavior.*

Predictor	Description
Form	Plant growth form: tree or liana (*Ficus* categorized as a liana)
Crop Size	Average # of fruits per crop of genus *i* in four ordered categories: I(1–25 fruits), II(26–100 fruits), III(101–500 fruits), IV(>500 fruits)
Dbh	Average stem diameter at breast height of genus *i*
Stem density	Stems per hectare of genus *i*
Fruit Frequency	Proportion of months in fruit for an average stem of genus *i*
Synchrony	Temporal overlap of fruiting stems of genus *i* (calculated as the coefficient of variation of the vector of # fruiting stems per month)
Productivity	Average proportion of all stems in forest in fruit during months in which genus *i* fruited
Rainfall	Average daily rainfall (cm) during months in which genus *i* fruited

GIBBON FEEDING OBSERVATIONS.—We observed the feeding behavior of *H. albibarbis* along standardized vertebrate survey transects and during focal follows (see Marshall 2010, Marshall *et al.* 2009b for details). Mean monthly survey effort across the five forest types sampled was 61.45 km/mo (SD = 2.73 km). In addition to gathering standard line-transect data (Buckland *et al.* 2001, 2010), whenever we encountered a group of *H. albibarbis* feeding, the following data on the plant fed upon by the first primate individual sighted were collected: the identification (to the lowest taxonomic level possible), location (using a GPS unit or detailed address from the trail), *dbh*, and *growth form* (*e.g.*, tree, liana, hemi-epiphytic fig) of the plant; the part being eaten (*e.g.*, fruit pulp, seeds, young leaves); the maturity stage, if applicable (*e.g.*, immature, ripe); the number of animals feeding; and an estimate of the total *crop size* (Marshall 2004, Marshall & Leighton 2006). Following collection of these data, we continued observations along the vertebrate survey route, so multiple feeding observations were not made from the same group on the same day. Therefore, we considered all feeding observations recorded along transects as independent measures of intake. The probability of observing feeding on a particular genus was proportional to the proportion of time that gibbons spent feeding on it, therefore these independent measures gathered along survey routes reflect overall diet composition (*i.e.*, proportions of feeding time spent eating each genus).

We collected additional feeding data during the course of targeted focal observations. Target groups were selected at random from among the known groups at the site (during the research period N = 20–28 groups, located across the full range of forest types). After contacting the target group, we randomly selected a focal individual and followed until it began feeding. The same feeding data were gathered as were collected on census routes and data collection continued for 30 min, at which point a new focal individual was randomly chosen. Feeding by the new focal animal was not recorded until it had travelled to a different tree or liana to ensure that multiple feeding observations were not recorded from the same individual plant.

We gathered one feeding observation every 3.6 d (duration between successive feeding observations varied from 0 to 68 d, SD = 6.3). We found no significant difference in use of plant genera between data gathered on follows and those gathered on census routes (N = 154, Mann Whitney U = 11,857, P = 0.99), and therefore they were lumped in order to increase sample size.

ECOLOGICAL PREDICTORS OF FRUIT CONSUMPTION.—We created 20 models (including an intercept model) predicting use (number of feeding observations for each genus) of a given plant genus based on a set of candidate predictor variables, reflecting hypotheses about which variables influenced gibbon fruit consumption

(Table S1). We compared these models using an information theoretic approach based on Akaike's Information Criterion (AICc, corrected for small sample sizes; Burnham & Anderson 2002). All models were fit using a negative-binomial distribution, which incorporates an additional parameter (θ) to account for over-dispersed count data. They were therefore generalized linear regression models, using a log link function. Because raw values of the continuous predictor variables were on scales that differed by orders of magnitude, they were log-transformed in order to facilitate compatible scaling, variance stabilization, and use of a GLM with a log-link. Models were evaluated using AICc model comparison and averaging (Johnson & Omland 2004) using the MuMIn package (Bartoń 2012) in R (R Development Core Team 2012) to produce estimates of predictors within an averaged model. Estimates of predictors were considered reliable if 95% confidence intervals did not overlap zero.

RESULTS

Variability in plant ecological and phenological characteristics.—We examined the correlation among variables prior to model fitting to determine whether any were highly correlated, which may have produced inaccurate model results. There were no strong correlations between continuous predictors (maximum $r = -0.44$; Table S2).

There was a large amount of variation in ecological and phenological predictor values (Table 2) across the 154 plant genera included in this study (Table S3). For instance, spatial and temporal abundance varied by orders of magnitude, as did average crop sizes. There was also a large range of stem sizes within both trees (mean = 30.4 ± SD = 15.7 cm) and lianas (mean = 5.5 ± SD = 0.5 cm). *Stem density* ranged from 0.1 to 27.1 stems per ha (mean = 2.5 ± SD = 3.6 stems per ha). *Fruit frequency* ranged from 0.0005 to 0.33 (mean = 0.05 ± SD = 0.06). *Productivity* ranged from 0.02 to 0.09 (mean = 0.05 ± SD = 0.01), while *synchrony* ranged from 46.4 to 806.2 (mean = 273.6 ± SD = 189.4). The distributions of these values were similar between plant genera that were consumed versus those that were unused by gibbons, with the exception of the shape of the distributions for *synchrony* and *stem density* (Fig. 1). Gibbons fed on genera with higher stem densities and lower synchrony values.

TABLE 2. *Mean and standard deviation of predictors for all genera (column 2), and subset of those genera unused (column 3) and used (column 4) by gibbons.*

Predictors	All genera	Unused genera	Used genera
Fruit frequency	0.05 ± 0.06	0.05 ± 0.06	0.06 ± 0.06
Stem density	2.48 ± 3.57	1.94 ± 2.97	4.32 ± 4.72
Mean productivity	0.05 ± 0.01	0.05 ± 0.01	0.05 ± 0.01
Synchrony	277.05 ± 191.94	303.00 ± 195.50	188.83 ± 150.86
DBH	24.84 ± 16.37	24.48 ± 15.55	26.05 ± 19.10
Mean rainfall	11.63 ± 2.45	11.60 ± 2.46	11.72 ± 2.45
Mean richness	52.81 ± 8.70	53.09 ± 9.23	51.85 ± 6.59

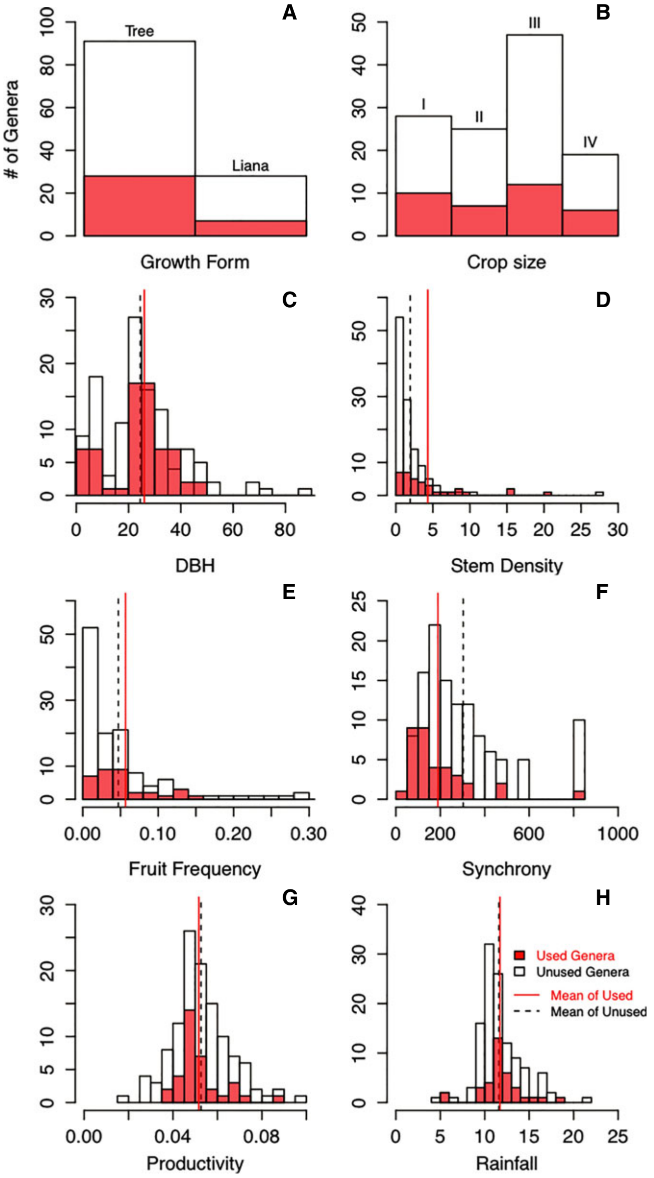

FIGURE 1. Histograms of model predictors, divided into genera used (shown in red) and unused (shown in white) by gibbons. Vertical lines depict means of continuous predictor variables for used (solid red) and unused (dashed black) genera.

There was significant temporal variation in the overall availability of fruiting stems (Fig. 2A). There were also differences among genera in *synchrony* and *fruit frequency* of individual stems, resulting in distinct phenological patterns (Figs. 2B, C and D). Stems of some genera, such as *Ochanostachys* (Olacaceae) produced fruit as often as the overall average (*Ochanostachys* fruit frequency = 0.04, overall genera mean *fruit frequency* = 0.05), while confining fruiting to only several months, resulting in a high *synchrony* value (CV = 295.8; Fig. 2B). In contrast, other genera such as *Girroniera* (Ulmaceae, Fig. 2C) and *Artabotrys* (Annonaceae, Fig. 2D) produced fruit in almost every month. Unlike *Girroniera*

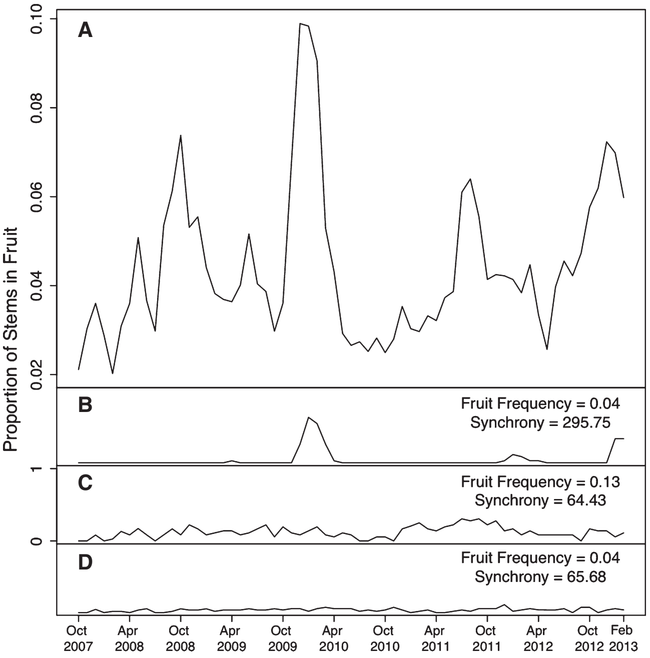

FIGURE 2. Plot of general forest productivity illustrating the proportion of the overall number of stems in the forest bearing fruit over time (A), as well as fruiting profiles of three genera representing prototypical phenological patterns. Stems of some genera, such as *Ochanostachys* (B) produced fruit as often as the overall average (*Ochanostachys* fruit frequency = 0.04, overall genera mean *fruit frequency* = 0.05), yet were highly synchronous (CV = 295.8). In contrast, other genera such as *Girroniera* (C) and *Artabotrys* (D) produced fruit in almost every month, either by fruiting often (*Girroniera*; *fruit frequency* = 0.13) or exhibiting low *synchrony* among stems (*Artabotrys*; CV = 65.7).

(*fruit frequency* = 0.13, CV = 64.4) however, genera such as *Artabotrys*, only remained constantly available due to low *synchrony* among stems (CV = 65.7), rather than by stems fruiting often (*fruit frequency* = 0.04). All three genera had comparable *stem density* (~3–5 stems per ha).

Ecological characteristics of gibbon fruit use.—The AICc comparisons gave the top model 89 percent of the model weight (Table 3), which performed substantially better than the intercept only null model (ΔAICc = 38; 0% model weight). This top model consisted of three predictors: *synchrony*, *stem density*, and *fruit frequency*. The next highest-ranking model included only *synchrony* (ΔAICc = 6; 4% of model weight). Effect estimates of *synchrony*, *stem density*, and *fruit frequency* were produced in an averaged model, based on AICc weighting of all 20 models, which was heavily biased toward the top two models (comprising over 90% of model weight).

TABLE 3. *Akaike's information criterion (AICc) model comparison results, showing the top two models and the null model.*

Model components	df	Log-likelihood	AICc	ΔAICc	Weight
Stem density, fruit frequency, synchrony	5	−121.98	254.36	0.00	0.89
Synchrony	3	−127.10	260.36	6.00	0.04
Intercept (Null Model)	2	−144.16	292.41	38.04	0.00

Stem density (estimate = 0.32, SE = 0.32; Fig. 3A) and *fruit frequency* (estimate = −0.50, SE = 0.38; Fig. 3B) had only weak reliability as predictors of use of a given genus by *H. albibarbis*. In contrast, *synchrony* had a reliably negative effect on the amount of predicted use (estimate = −2.14, SE = 0.71; Fig. 3C). There was one other reliable predictor in the averaged model (Fig. 4): *dbh* (estimate = 1.75, SE = 0.80); although our AICc model comparison indicated that it was of low relative importance (receiving only 2% model weight when occurring with the top two predictors, *stem density* and *fruit frequency,* and ranked lower than the null model when occurring as a lone predictor). This likely reflects the small effect size of *dbh*.

To establish whether *Ficus* was solely responsible for the strong negative effect of *synchrony* on *H. albibarbis* food use, we re-ran the analysis with *Ficus* excluded. The order of models favored by AICc comparison did not change (additionally, the model with *synchrony* alone increased from 4% weight to 9% weight) and the averaged model estimate for *synchrony* was still well supported (estimate = −1.76, SE = 0.68).

We were also concerned that genera that only fruited once may have had a high *synchrony* value as an artifact, erroneously driving this result. We therefore re-ran our analysis using only genera that fruited at least three times and found no qualitative difference in our results from the full analyses presented here.

DISCUSSION

The central objective of this study was to identify the ecological and phenological predictors of fruit consumption by White-bearded gibbons inhabiting a highly variable Southeast Asian forest. We used a model selection approach to identify key characteristics of gibbon fruit use. The results of model comparison based on AICc suggested that only three ecological characteristics were important predictors of resource use: the overall abundance of a genus (*stem density*), the proportion of time that a genus produced fruit (*fruiting frequency*), and the extent to which stems within a genus fruited at the same time (*synchrony*). Further analysis revealed that, of the three most important predictors, only *synchrony* had a reliable (negative) effect, indicating that gibbons feed more often on genera whose stems fruit out of phase with each other (*i.e.*, low *synchrony*). *Dbh* was also found to have a reliable effect estimate, but was a far less useful predictor than *synchrony*. Although low fruiting *synchrony* is a well-known characteristic of the most frequently consumed genus (*Ficus*), we found the same result when *Ficus* was excluded from the analysis, which suggests that the importance of low fruiting *synchrony* for gibbons is not due solely to figs.

Importance of fruiting asynchrony for frugivores.—*Ficus* spp. have long been known for their asynchronous phenology, as

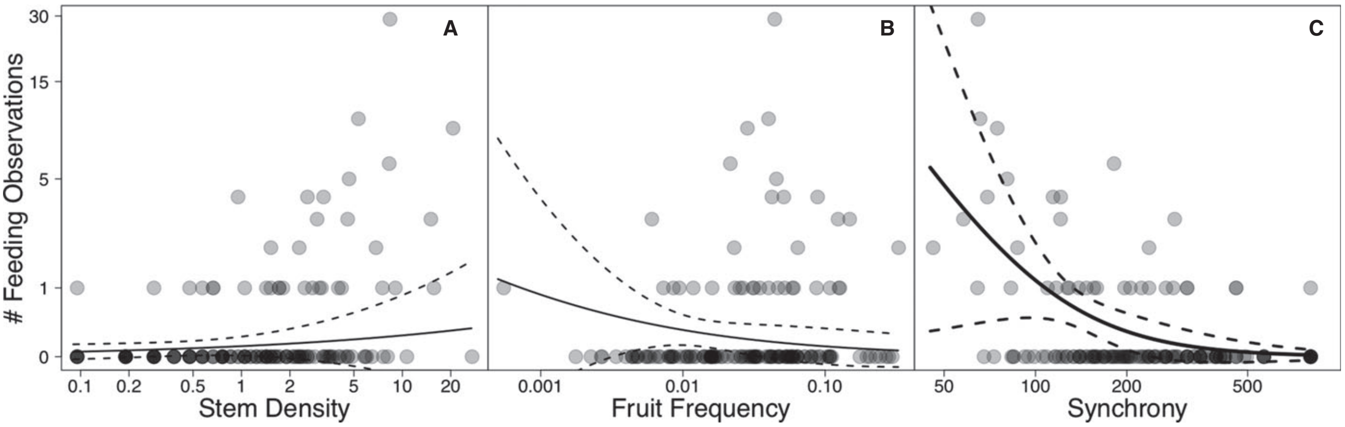

FIGURE 3. Estimated trends for key ecological variables. Number of feeding observations per genus by *Hylobates albibarbis* as a function of the per genus *stem density* (A), *fruit frequency* (B) and *synchrony* (C). Axes are displayed in natural log scaling to match the scale used for model fitting. Gray dots are the raw observations and solid curves depict estimated means. Dashed and dotted curves depict 95 percent confidence bands for the mean. Heavy line in C indicates that the model-averaged confidence intervals for this variable do not include zero. Neither stem density nor fruit frequency had reliable effects on fruit use. In contrast, genera with low synchrony values (high asynchrony) were reliably consumed more often.

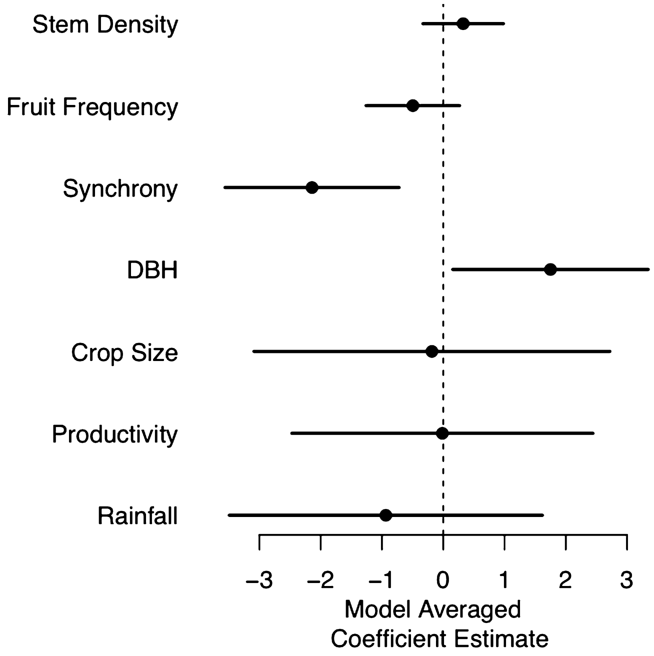

FIGURE 4. Model-averaged coefficient estimates (including 95% confidence intervals) for averaged models. As these estimates were calculated based on log-transformed data, expected use is proportional to a value of the predictor raised to the coefficient estimate. Coefficient estimates less than zero result in a lower expected count while those greater than zero result in a higher expected count. Coefficient plots such as these depict the direction and relative reliability of each estimate, not the relative effect size. Predictors are displayed in descending order of relative importance assigned by AICc comparison.

well as their role as a heavily used keystone resource for many tropical frugivores (Janzen 1979). Because of this, and due to heavy use of *Ficus* by gibbons at CPRS (Marshall & Leighton 2006, Marshall *et al.* 2009a) we examined whether *Ficus* alone was responsible for the finding that low fruiting *synchrony* strongly predicted gibbon feeding observations. Notably, we found that *Ficus* did not drive this result. The general importance of asynchronous fruiting, beyond solely the genus *Ficus,* therefore suggests that for some foragers, *Ficus* may simply be an important example within a larger set of asynchronous food resources. In particular, three of the next four most heavily used genera had comparable *synchrony* values (*Artabotrys* (Annonaceae), CV = 66; *Syzygium* (Myrtaceae), CV = 75; *Diospyros* (Ebenaceae) CV = 81; see Fig. 3C). A diet biased toward genera exhibiting low fruiting *synchrony* likely buffers animals from food scarcity. Furthermore, because a single genus, such as *Ficus*, is unlikely to be sufficiently common to solely support large, diverse assemblages of tropical frugivores, vertebrate populations likely also rely on other taxa with low synchrony for persistence (Leighton & Leighton 1983, Terborgh 1983, Peres 2000). These results suggest that asynchronously fruiting plant genera may be particularly important for habitat restoration of tropical forests and the conservation of frugivore populations that inhabit them. This is likely to be especially important in hyper-variable environments exhibiting prolonged periods of fruit scarcity, such as those found at CPRS.

TAXONOMY, PHENOLOGY AND ASYCHRONY.—Plant genera can offer frugivores constant fruit availability as a result of individual stems either fruiting often (*i.e.*, high *fruit frequency*) or out of phase with each other (*i.e.*, low *synchrony*). Our results demonstrate that gibbons prefer to feed on plant genera that provide consistent fruit availability due to fruiting asynchrony rather than those that are consistently available due to high individual fruiting frequency. Because our analyses were conducted at the genus level, low *synchrony* between stems could have arisen either from asynchrony among all congeners, or asynchrony between synchronously fruiting species. Future work focused specifically on intra- and inter-specific fruiting asynchrony within these genera would be valuable for examining alternative explanations for fruiting asynchrony among congeneric plants, which has been hypothesized to reduce competition for dispersers between closely related species (Snow 1965, Wheelwright 1985, van Schaik *et al.* 1993). Because genera that fruit asynchronously are fed on more often, this phenological strategy might increase the likelihood of seed dispersal. This is probably due at least in part to the fact that they are available during periods of fruit scarcity (Marshall *et al.* 2009a).

Although both high fruiting frequency and low synchrony would tend to promote availability during times of general scarcity, it is unclear why genera with low fruiting synchrony would be more important to gibbons than those with high fruiting frequency. Perhaps nutritional or metabolic constraints on plant reproduction (or life history tradeoffs) preclude individuals from continuously producing high quality fruit. However, the fruits of some highly used genera, such as those of *Ficus*, are considered to be of relatively low nutritional quality (Leighton 1993), so alternative reproductive constraints, such as those placed on large crop sizes, may be operating as well. Regardless, genera whose stems produce attractive crops (whether due to high nutritional quality or large quantities of fruit) may represent optimal food sources for some frugivores if they are consistently available due to partitioning of fruiting events between individuals. Work comparing the morphological and chemical differences between fruits produced under asynchronous and continuous phenologies, as well as crop sizes associated with these reproductive habits, is needed.

CONCLUSION

Feeding behavior of a tropical frugivore is influenced by general ecological and phenological characteristics of plant resources. While there was no evidence that gibbons avoided mast fruiting genera, which are characterized by high values of forest *productivity*, their diets were biased toward genera with particularly low inter-individual fruiting synchrony. By incorporating a range of ecological characteristics and a large number of genera, we determined that asynchronous fruiting, which is well-recognized from *Ficus* studies, may be important across a broader range of plant taxa. Considering the amount of variation in the ecological characteristics of plants and the diversity of frugivores, the patterns we report for gibbons likely do not apply to all frugivores. One possible reason comes from gibbons' preference for traveling, and to a lesser extent feeding, in upper canopy trees (Cannon & Leighton 1994, Marshall *et al.* 2009b), which as a whole fruit much less frequently than understory trees (Sakai 2002). This could potentially make asynchronous fruit sources particularly more important for these canopy feeders, than for frugivorous taxa that feed predominantly on frequently fruiting understory trees and shrubs (*e.g.*, many birds) or those that can migrate in response to spatial and temporal variation in food availability (*e.g.*, orangutans, hornbills, pigs; Leighton & Leighton 1983, Curran & Leighton 2000, Marshall *et al.* 2014). Additional research on the ecological and phenological characteristics influencing fruit consumption by other frugivores would help determine how broadly our results apply, as well as deepen our understanding of frugivore ecology and contribute to conservation and restoration efforts.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *List of models used in AICc model comparison and averaging.*

TABLE S2. *Correlation coefficients of continuous predictor variables.*

TABLE S3. *List of 154 genera considered in this analysis, along with their associated values for each predictor variable.*

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