Chapter 9
Competition and Niche Overlap Between Gibbons (*Hylobates albibarbis*) and Other Frugivorous Vertebrates in Gunung Palung National Park, West Kalimantan, Indonesia

Andrew J. Marshall, Charles H. Cannon, and Mark Leighton

Introduction

Interspecific competition is considered to be one of the fundamental forces driving a wide range of evolutionary and ecological processes, but its importance in limiting mammalian populations has been hotly debated (Hairston et al. 1960; Fleming 1979; Schoener 1982; Walter and Paterson 1995). Early ecologists held the view that competition between species was of overriding importance in shaping vertebrate communities (e.g., Grant 1972; MacArthur 1972; Cody 1975; Diamond 1978). Others argued that interspecific competition was sporadic, and that its effects may be relatively unimportant compared to other ecological forces, such as climate or predation (e.g., Connell 1975; Wiens 1977; den Boer 1986; Post and Forschhamer 2002), and non-equilibrial and stochastic factors (e.g. Sæther 1997; Hubbell 2001). Despite continued uncertainty over the precise nature of interspecific competition (Schoener 1982; Eccard and Ylönen 2003; Cooper 2004), few ecologists would deny that competition between species can have powerful effects on animal populations. Field experiments have demonstrated that the ecological effects of interspecific competition are widespread (reviewed in Connell 1983; Schoener 1983). Begon, Harper, and Townsend (1996: 800) concluded that competition "appears frequently to be important in vertebrate communities, particularly those of stable, species rich environments." Most primates live in tropical rainforests, among the most stable and species rich environments on earth, suggesting that interspecific competition may be particularly important for these taxa.

Primate field studies have indirectly inferred the importance of interspecific competition, either with primates or other vertebrate species. For example, density compensation—an increase in the density of one species in response to the decline in abundance of a competing species—has been reported in a wide

A.J. Marshall (✉)
Department of Anthropology, University of California, One Shields Avenue, Davis, CA 95616, USA
e-mail: ajmarshall@ucdavis.edu

number of primate communities in South America, Africa, and Asia (Struhsaker and Oates 1975; Struhsaker 1978; Lawes and Eeley 2000; Peres and Dolman 2000; González-Solís et al. 2001). In addition, decreases in dietary overlap during lean periods in primate assemblages at Krau Game Reserve, Malaysia, and Manu National Park, Peru, are thought to be caused by feeding competition between primate species (Waser and Case 1981). Strum and Western (1982) reported that feeding competition with ungulates explained the majority of the variance in indices of the reproductive output of female anubis baboons (*Papio anubis*). Finally, Ganzhorn's (1999) comparative analysis of factors that affected a large number of primate assemblages suggested that competition with non-primate taxa has had profound effects on the evolution of primate communities, particularly in Asian forests.

Such patterns are not universal: the overlap in foraging heights and diets of *Cercopithecus* monkeys increased when they were in polyspecific associations (Gautier-Hion et al. 1983) and the overlap in the consumption of resources between two tamarin species (*Saguinus* spp.) in polyspecific associations increased substantially during periods of lowest fruit availability (Peres 1996). These results are the opposite of what would be expected if interspecific competition were important for these species, and suggest that broad generalizations are unlikely to apply to all primate species or communities.

Here we consider how gibbons in a Bornean rainforest are affected by interspecific competition with other vertebrate frugivores. Many excellent field studies have examined competitive interactions among primate species within communities (e.g. Rodman 1973; Raemaekers 1984; Waser 1987; Guillotin et al. 1994; Ungar 1996; Wrangham et al. 1998; Reed 1999; Stevenson et al. 2000; Simmen et al. 2003), but only a limited number permit the examination of interactions with a wider set of frugivorous vertebrates (e.g., Leighton and Leighton 1983; Estrada and Coates-Estrada 1985; Gautier-Hion et al. 1985; Charles-Dominique 1993; Poulson et al. 2002). Consideration of primates within the context of the broader vertebrate community promises to provide a richer understanding of the ecological and evolutionary forces that shaped primate adaptations.

We present an analysis of long-term data on vertebrate feeding ecology gathered over a 6-year period of intensive sampling at Gunung Palung National Park, West Kalimantan, Indonesia. We use these data to address three general sets of questions: First, how specialized are gibbon diets when compared to other vertebrate frugivores? Second, which species are gibbons' major competitors for food? Third, how similar (or different) are the feeding niches of gibbons and their main competitors, and what are the effects of this competition?

How Specialized Are Gibbon Diets?

While primates are broadly considered to be dietary generalists, numerous studies have demonstrated a high degree of feeding selectivity, indicating that

all primate species specialize on a relatively small subset of available foods (e.g., Oates et al. 1977; Milton 1979; McKey et al. 1981; Davies et al. 1988; Leighton 1993; McConkey et al. 2002). Here we consider how specialized gibbon diets are relative to the diets of other vertebrate frugivores that inhabit the same forests. We also consider whether the degree of specialization of gibbon diets is related to the abundance of food. Specifically, we test the following hypothesis:

H1: Gibbon diets are more diverse during periods of low fruit availability than during periods of high fruit availability.

Classic foraging models predict that diet breadth increases as the total availability of food decreases, because individuals can restrict feeding to the more preferred food items during periods of high food availability (Charnov 1076; MacArthur and Pianka 1966; Emlen 1968; Levins and MacArthur 1969; Schoener 1971). Although many empirical studies have documented this inverse relationship between food availability and diet breadth (e.g., Schoener 1971; Wrangham et al. 1991; McKnight and Hepp 1998; Rödel et al. 2004; Murray et al. 2006), other field studies have failed to detect this relationship (e.g., Wrangham et al. 1998; Di Fiore 2003), or have shown that in some species more items are included in the diet during periods of high food availability (Renton 2001; Simmen et al. 2003). Thus, some species appear to become more generalized during periods of resource scarcity while others become more specialized. However, some ambiguity may result because the relative abundance of foods of different preference rank was not monitored; *specialization* may occur because a low-ranked food is very abundant.

Here we hypothesize that gibbons adopt the former strategy (i.e., we predict an inverse relationship between food availability and diet breadth). Gibbons focus on a very limited set of high-quality, super-abundant resources during periods of highest resource availability (i.e., mast fruit events), but they must add more and more less-preferred items to their diet as food becomes scarce. We tested this prediction by comparing the total number of fruit taxa in gibbon diets during periods of high, medium, and low resource abundance, controlling for sample size. In order to compare the relationship between fruit availability and dietary diversity in gibbons to that of other vertebrates, we present the results of this simple comparison for several other species.

Which Taxa Are the Major Competitors of Gibbons?

Vertebrate frugivores in Bornean forests experience extreme temporal fluctuations in food availability due to the unusual community-wide phenological patterns characteristic of the island (Leighton and Leighton 1983; Curran and Leighton 2000; Marshall and Leighton 2006). While we assume that both intra- and interspecific feeding competition intensify during periods of fruit scarcity, little quantitative information exists that might allow us to identify which vertebrate taxa compete most intensely (or at all) with gibbons. Although for

a variety of reasons there need not be a direct positive correlation between niche overlap and competition (see Discussion), we here follow convention and use dietary overlap as an indicator of potential feeding competition (MacArthur and Levins 1967; Schoener 1982).

The methods used to calculate dietary overlap can strongly affect the results obtained (Poulson et al. 2002). Several pioneering studies of feeding competition among vertebrate frugivores assessed resource overlap by simply calculating the number of items that two species consumed in common (Fleming 1979; Gautier-Hion et al. 1985). However, these simple indices tend to inflate the true extent of dietary overlap as they do not account for the relative abundance of items in the diet. More recent studies of resource competition in primates have used more sophisticated measures that incorporate both the dietary composition and the relative proportion of individual food items (e.g., Stevenson et al. 2000; Poulson et al. 2002). In this chapter we use a measure of dietary overlap that incorporates both factors to identify gibbons' major potential competitors at Gunung Palung. As the absolute and relative densities of vertebrates vary substantially between peat and non-peat forests (e.g., Janzen 1974, Leighton, unpubl. data), and since phenological patterns (Marshall 2004; Wich et al. unpubl. data) and floristic composition (Cannon and Leighton 2004) of peat forests differ substantially from other forest types, we conducted additional analyses to determine whether the ranking or degree of dietary overlap of gibbons' major vertebrate competitors differed between these two forest types.

How Similar Are the Feeding Niches of Gibbons and Their Major Competitors?

Ecological theory states that no two species can occupy exactly the same niche (Hutchinson 1957). Therefore, in order to coexist with other sympatric vertebrate frugivores, gibbons must occupy a unique part of multidimensional niche space. As diet is one of the major components defining gibbon fundamental niches, we test three hypotheses that address the mechanisms gibbons might employ to reduce feeding competition with other vertebrates.

H2A: Gibbon diets diverge more from their competitors during periods of low resource availability than during periods of high food availability.

Models of niche partitioning predict that resource overlap between competitors decreases when resources are limited (Schluter 1981; Schoener 1982). When preferred resources are available, sympatric species may pursue generalist feeding strategies, leading to considerable overlap in resource utilization. In contrast, during periods of food scarcity competition intensifies, causing feeding niches to diverge (Schoener 1982; Schluter 1994). Such a pattern has been reported from several primate communities. Waser (1987) compared the dietary overlap of 23

pairs of primates during seasons of high and low fruit availability and found that diets diverged during lean times in over 90% of the pairs examined. Similarly, Guillotin et al. (1994) reported that the lowest periods of dietary overlap between three frugivorous primate species in French Guiana occurred when fruit production was lowest. Finally, Wrangham, Conklin-Brittain, and Hunt (1998) found that when fruit availability was low, the diets of cercopithecines and chimpanzees in the Kibale forest diverged. Although niche divergence during lean periods is not universal (e.g., Peres 1996), it is the most common response in primate communities, particularly in species that do not engage in poly-specific associations. Therefore, we predicted that the diets of gibbons and their major potential competitors would be more divergent during periods of low food availability than during periods of higher food availability.

H2B: Gibbons feed in smaller patches than their major competitors.

Another mechanism by which gibbons may reduce direct competition with species that consume similar diets is by utilizing small patches that are ignored by other vertebrate frugivores (Raemaekers and Chivers 1980). Some major vertebrate frugivores in Bornean rainforests are known to preferentially feed in large patches (e.g., orangutans: Leighton 1993; orangutans and long-tailed macaques: Wich et al. 2002), presumably because the total number of patches that can be visited in 1 day are tightly constrained by high travel costs (Wheatley 1982; Rodman 1984; Leighton 1993). Gibbon brachiation is an unusually rapid and efficient locomotor adaptation, allowing them to cross larger gaps and follow more direct travel routes between food patches than other primates (Cannon and Leighton 1994, 1996). This suggests that gibbons may be able to overcome the costs of travel that tightly limit the number of patches that can be visited by species with larger body size or less efficient locomotor adaptations, permitting them to visit more, smaller patches in a single day than is possible for other frugivores. Therefore, we hypothesize that gibbon fruit patches are significantly smaller than those of their major competitors. We use fruit tree diameter at breast height (dbh) as a measure of patch size, as it is highly correlated with tree fruit crop size (i.e., pulp weight/patch: $r = 0.72$, Leighton 1993).

H2C: Gibbons occupy different forest types than their major competitors.

Habitat selection can act to substantially reduce or eliminate interspecific competition between species that utilize very similar sets of resources (Schoener 1974; Pianka 1976; Pyke et al. 1977). For example, Rodman (1979; 1991) showed that despite high degrees of dietary overlap, populations of *Macaca nemestrina* and *Macaca fascicularis* coexist by using different habitats in Kutai National Park. Gibbons may reduce feeding competition by occupying different habitats than vertebrates with whom their diets overlap substantially, or by preferentially occupying habitats where the densities of potential competitors are low. Following Rodman (1973) as a preliminary test of this hypothesis, we predict that gibbon population densities are significantly negatively correlated with the densities of their major competitors.

Methods

Study Site and Subjects

We gathered data at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park, West Kalimantan, Indonesia (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 rock type. Detailed descriptions of these forest types and the research site can be found in Cannon and Leighton (2004), Webb and Peart (2000), and Marshall (2004). When the data presented here were collected, little hunting or timber extraction had occurred within the immediate study area since the establishment of the national park in 1937, with the exception of hand extraction of *gaharu* (*Aquilaria malaccensis*) and *belian* (*Eusideroxylon zwageri*) (Webb 1997; Paoli et al. 2001). The vertebrate and plant communities at the site are therefore diverse and presumably at the densities characteristic of the area over recent ecological history. Species lists from the site have been published for birds (Laman et al. 1996) and mammals (Blundell 1996).

The populations of Bornean white-bearded gibbons (*Hylobates albibarbis*) found at CPRS have been the subjects of focused study intermittently since 1984 (Mitani 1987, 1990; Cannon and Leighton 1994, 1996; Marshall 2004; Marshall and Leighton 2006; Marshall in press). Their diet comprised mainly the pulp of ripe non-fig fruits (65% of the diet on average), augmented by figs (23%), flowers (6%), leaves (3%), and seeds (3%). The relative importance of different plant parts in gibbon diets at CPRS varies substantially across seasons: flowers comprise from 0 to 28% of the feeding observations, fruit pulp and seeds from 25 to 95%, figs from 0 to 75%, and leaves from 0 to 25% (Fig. 9.1). During times when preferred foods are unavailable, figs become an increasingly important portion of the diet (i.e., they are a fallback food; Marshall and Leighton 2006; Marshall and Wrangham 2007).

Vertebrate Feeding Observations

We used a long-term data set of 4090 independent vertebrate fruit feeding records collected between March 1985 and March 1992. Feeding observations were gathered while walking standardized vertebrate census routes across all forest types (n = 1909 observations, 47% of the total) and from opportunistic observations made while conducting other fieldwork (n = 2181, 53%). Data collected on fruit tree watches or in other contexts that would bias estimates of vertebrate dietary intake were excluded, as were observations of vertebrates feeding on non-fruit items (e.g., leaves, insects, pith). Thus, all comparisons of dietary overlap between species incorporate only the fruit portion of the diets of each species.

Our data set includes the observations of feeding by a wide range of mammalian and avian taxa. There are roughly twice as many observations of
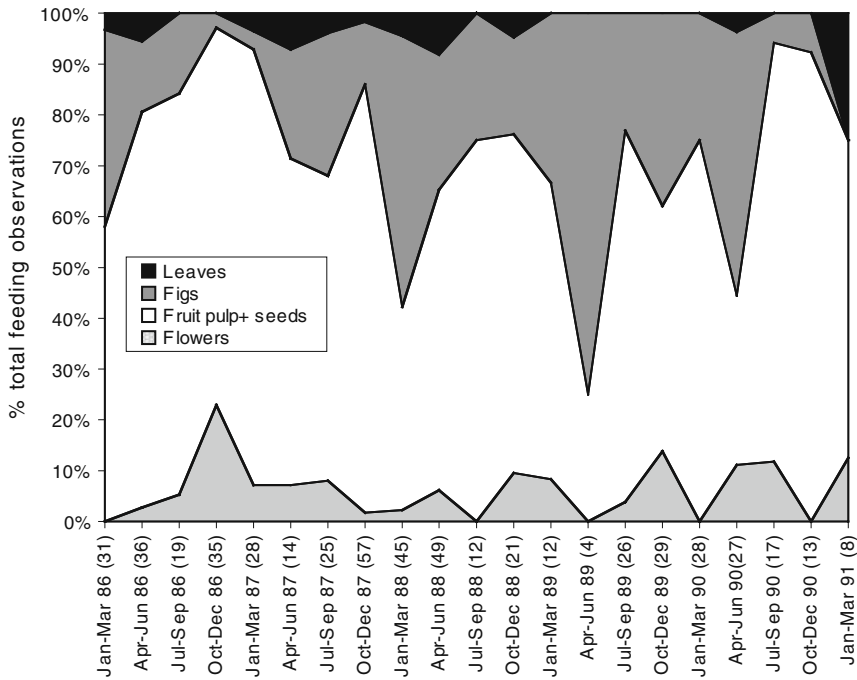
Fig. 9.1 Gibbon dietary composition over time by plant part. Figure is based on 536 independent feeding observations recorded between January 1986 and March 1991. Data are lumped into 3-month periods to reduce the effects of sampling error associated with small sample sizes. Parentheses indicate the number of independent feeding observations during each period. See Marshall (2004) for details of the analysis

mammal feeding ($n = 2828$ observations, 69% of the total) as there are for birds ($n = 1262$, 31%). The most commonly represented mammalian orders in the data set are Primates ($n = 1711$, 42%) and Rodentia ($n = 784$, 19%), with additional observations of Artiodactyla, Carnivora, and Chiroptera, (5, 1.6, and 1.5%, respectively). The most commonly represented avian orders are Bucerotiformes ($n = 553$, 14%), Passeriformes ($n = 282$, 7 %), and Piciformes ($n = 251$, 6%); with additional observations of Columbiformes, Galliformes, Psittaciformes, and Trogoniformes (1.9, 1.4, 0.6, and 0.2%, respectively). The following families each contribute >2.0 % of total observations: Sciuridae (squirrels: $n = 782$, 19%), Cercopithecidae (macaques and leaf monkeys: $n = 756$, 19%), Bucerotidae (hornbills: $n = 553$, 14%), Pongidae (orangutans: $n = 515$ obs, 13%), Hylobatidae (gibbons: $n = 440$, 11%), Megalaimidae (barbets, $n = 251$, 6%), Suidae (pigs: 181, 4%), and Pynotidae (bulbuls: 99, 2%); the remaining observations are divided among 16 other avian and mammalian genera. Mammalian taxonomy follows Payne and Francis (1985); avian taxonomy follows Inskipp, Lindsey, and Duckworth (1996).

We gathered the observations of vertebrates eating the fruits from trees, lianas, and hemiepiphytes from 115 plant families and 167 genera. In order to boost sample sizes and reveal general patterns, we used genera as the taxonomic unit for our analyses (see Marshall and Leighton 2006, for further discussion). The following families comprised more than 2% of feeding observations: Moraceae ($n = 1414$, 35%), Annonaceae ($n = 214$, 5%), Fagaceae ($n = 199$, 5%), Burseraceae ($n = 159$, 4%), Dipterocarpaceae ($n = 152$, 4%), Euphorbiaceae ($n = 132$, 3%), Myrtaceae ($n = 127$, 3%), Myristicaceae ($n = 126$, 3%), Meliaceae ($n = 125$, 3%), and Apocynaceae ($n = 123$, 3%). The most commonly eaten plant genus was *Ficus* ($n = 1348$ obs, 31%). After figs, the most commonly eaten fruit genera were *Lithocarpus* ($n = 164$, 4%), *Shorea* ($n = 142$, 3%), and *Willughbeia* ($n = 124$, 3%). The following genera each comprised more than 2% of the total feeding observations: *Syzygium* ($n = 107$), *Diospyros* ($n = 93$), *Hydnocarpus* ($n = 91$), *Alangium* ($n = 88$), and *Canarium* ($n = 88$). Thirty six other plant genera were represented by at least 20 independent observations.

Fruit Phenology

We used data from 126 phenological plots that were monitored monthly between January 1986 and September 1991 ($n = 69$ months) to assess temporal variation in fruit availability for gibbons at CPRS. Phenology plots were 0.10 ha in size and were placed using a stratified random design across all seven habitat types (Cannon and Leighton 2004; Cannon et al. 2007a, b). In these plots all trees larger than 14.5 cm dbh, all lianas larger than 3.5 cm dbh, and all hemi epiphitic figs whose roots reached the ground were identified, measured, and tagged. The phenological phase of each tagged stem in these phenology plots was recorded each month (or two out of every 3 months during some periods). Based on the objective, the operational criteria that incorporated the density of trees with ripe fruit available (# stems per ha per month), and the diversity of gibbon food trees in fruit (# of distinct food taxa per month), each month was assigned to one of three classes (in order of decreasing food availability): mast, high fruit periods (HFP), and low fruit periods (LFP). Since the phenological patterns of the peat swamp forest differ significantly from the other habitats, analyses that incorporated food availability were done separately for peat and non-peat forest types (see Marshall 2004; Marshall and Leighton 2006, for details on all analyses). We consider peat swamp forests to be non-masting habitats (Marshall 2004; Cannon et al. 2007a; Wich et al. unpubl. data).

Primate Density Transects

AJM established a pair of replicate 2–4 km-long census routes in each of the seven forest types found at CPRS (total $n = 14$ routes), and systematically recorded all observations of primate species using a standardized protocol between September 2000 and June 2002 ($n = 409$ censuses; 1,374 km). Details of transect methodology are provided in Marshall (2004). As a complete

treatment of the habitat-specific densities of all major frugivorous vertebrates at Gunung Palung is beyond the scope of this chapter, we use the number of independent observations per census as a simple index of the density of the four most common primate species at Gunung Palung in each habitat.

Analyses

We conducted analyses using Mathematica 5.1, SPSS 11.0.4, and JMP 5.0.1. To accommodate different sample sizes for different species, we used a randomization approach to test most of our hypotheses (Manly 1997). We performed all randomizations 1000 times and set significance at $\alpha = 0.05$. As a measure of specialization and feeding selectivity, we calculated use ratios for all fruits in the gibbon diet by dividing the number of times a plant genus was observed to be eaten by the number of times it was included in a random sample of the same size that was drawn from the entire set of vertebrate feeding records. Plant genera observed to be eaten more or less than expected by chance were classified as sought or avoided foods.

In order to compare diets we used an index of dietary identity that incorporated both diet composition and frequency of consumption. The index was calculated by compiling complete lists of all feeding observations for each consumer (i.e., items eaten multiple times were listed multiple times) and examining the overlap between the lists of two consumers in comparison to the food items eaten by each consumer. The index can be used from either consumer's perspective; from the perspective of consumer A:

$$A \cap B_N / A_N$$

or from the perspective of consumer B:

$$A \cap B_N / B_N$$

where $A \cap B_N$ is the number of food items shared by the two consumers and A_N, B_N are the number of food items in each respective consumer's diet. The index can vary from 0 to 1, where 0 indicates no overlap in diets and 1 indicates complete overlap of the competitor's diet with the focal consumer's. We generated a null model for this index by comparing random diets across a range of feeding observations up to the maximum number obtained for any species. These random diets were drawn from all feeding observations, pooled together, without regard to the taxonomic identity of the feeding organism. This null distribution represents the amount of dietary identity expected, given purely stochastic processes. The mean dietary identity of the observed diet for each species to the random diets was then compared to the null model, given the number of observations for each species, to determine significance. The same analysis was performed at the family level to increase the sample size for vertebrates with small samples for individual species.

We used the same procedure to compare the observed dietary identity between gibbons and each of the major vertebrate species with the expected dietary identity, given random feeding behavior. First, we drew 1000 random diets out of the pooled feeding observations, given the number of observations for the non-gibbon species in each comparison. The dietary identity of the observed gibbon diet to each random diet then represented the null distribution of identities. The dietary identity of the observed gibbon diet with the observed diet of the non-gibbon species was then compared to the null distribution and its significance determined. We conducted this comparison for the full data set, and also conducted separate analyses that assessed dietary overlap in different seasons and habitats.

For our analysis of diet breadth we sub-sampled seasons with more feeding observations so that sample sizes were equal across seasons. This eliminated biases that would have been introduced by the fact that observed diet diversity is related to sample size in a positive but non-linear way.

We compared the distribution of feeding tree sizes among vertebrate species with a one-way ANOVA, and used post-hoc Tukey-Kramer honestly significant difference (HSD) tests to identify pairs of species that differed significantly. Finally, we used Spearman's rho to assess the strength and direction of correlations between the habitat-specific densities of the four most common primate species at CPRS.

Results

How Specialized Are Gibbon Diets?

Our analysis of gibbon use ratios identified 21 fruit genera that were sought by gibbons and 14 that were avoided at CPRS (Table 9.1). The most strongly sought fruits were *Artabotrys*, *Aglaia* (including only species with primate dispersed fruits), *Garcinia*, and *Diospyros*; the most strongly avoided were *Lithocarpus*, *Dysoxylum*, *Strychnos*, and *Shorea*. Interestingly, few plant families contained both sought and avoided taxa; genera in the common families Fagaceae, Lauraceae, Myristicaceae, and Burseraceae were avoided by gibbons.

Gibbon dietary identity is significantly below the null model (Fig. 9.2), confirming that, as indicated by the use ratio analysis, gibbons do not forage randomly for fruits. However, our data suggest that gibbons are relatively unspecialized compared to most other vertebrates in our sample. With the exception of Prevost's Squirrel, the frugivorous portion of gibbon diets are less specialized than those of all vertebrates for which we have more than 100 feeding observations (two hornbill species, pigs, giant squirrels, macaques, leaf monkeys, and orangutans; Fig. 9.2). Of the other species in our sample, tufted ground squirrels, dog-faced bats, and long-tailed parakeets appear to be particularly specialized in their frugivory. The analysis of dietary specialization by

Table 9.1 Family, genus, growth form (T = Tree, L = liana, H = hemiepiphyte), and use ratio of plant genera observed to be consumed by gibbons at Gunung Palung between 1985 and 1992

Family	*Genus*	Form	Use ratio[a]
Annon	*Artabotrys*	L	+3.86*
Melia	*Aglaia*[b]	T	+3.75*
Clusi	*Garcinia*	T	+3.50*
Ebena	*Diospyros*	T	+3.43*
Rubia	*Unknown*	T	+2.50*
Tilia	*Microcos*	T	+2.33*
Sapot	*Chrysophyllum*	T	+2.00*
Annon	*Friesodielsia*	L	+2.00*
Rubia	*Psychotria*	T	+2.00*
Eupho	*Baccauria*	T	+1.83*
Flaco	*Hydnocarpus*	T	+1.80*
Fabac	*Dialium*	T	+1.67*
Sapot	*Palaquium*	T	+1.67*
Polyg	*Xanthophyllum*	T	+1.67*
Sapin	*Nephelium*	T	+1.67
Elaeo	*Elaeocarpus*	T	+1.60*
Melas	*Pternandra*	T	+1.50
Morac	*Artocarpus*	T	+1.44*
Chyrs	*Parinari*	T	+1.33*
Anaca	*Gluta*	T	+1.33
Myrta	*Syzygium*	T	+1.20
Apocy	*Willughbeia*	L	+1.14
Rubia	*Anthocephalus*	T	+1.00*
Eupho	*Antidesma*	T	+1.01*
Areca	*Calamus*	L	+1.02*
Sapin	*Unknown*	T	+1.04*
Fagac	*Lithocarpus*	T	−9.00*
Melia	*Dysoxylum*	T	−5.00*
Logan	*Strychnos*	L	−4.00*
Dipte	*Shorea*	T	−3.5*
Burse	*Canarium*	T	−3.00*
Laura	*Cryptocarya*	T	−3.01*
Burse	*Dacryodes*	T	−3.02*
Irvin	*Irvingia*	T	−3.03*
Myris	*Myristica*	T	−3.04*
Laura	*Nothapheobe*	T	−3.05*
Fagac	*Quercus*	T	−3.06*
Annon	*Polyalthia*	T	−2.67*
Burse	*Santiria*	T	−2.50*
Laura	*Litsea*	T	−2.00*
Tetra	*Tetramerista*	T	−1.66

Table 9.1 (continued)

Family	Genus	Form	Use ratio[a]
Myris	*Horsfieldia*	T	−1.50
Annon	*Mezzettia*	T	−1.50
Morac	*Ficus*	H	−1.09

[a] Only plant taxa with use ratios with an absolute value greater than 1.0 are listed. Positive numbers indicate foods sought by gibbons; negative numbers indicate plant genera that were avoided. See text for details.
[b] Only trees of the genus *Aglaia* that produce primate-dispersed fruits (i.e., those with seeds surrounded by a watery, sugary pulp) are included.
[*] $p < 0.05$.
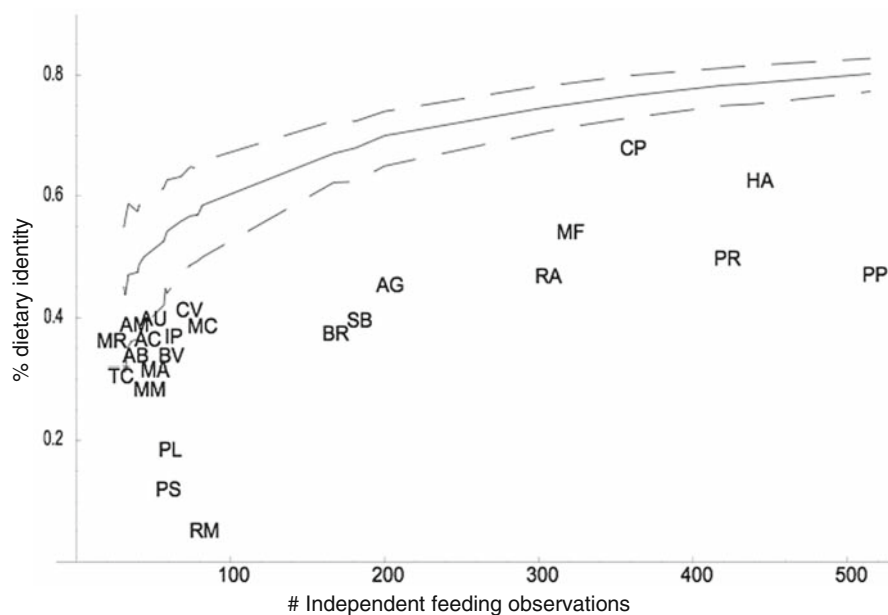
Fig. 9.2 Dietary specialization of vertebrate frugivores by species. The *x*-axis represents the number of independent feeding observations, the *y*-axis represents the percent dietary identity (a measure that integrates diet composition and frequency of specific items in the diet). The solid line shows the expected dietary identity between two randomly selected diets of a given sample size, the dashed line gives the $\alpha = 0.05$ significance limits based on 1000 iterations (see Methods). The further a species is below the line, the less their diet resembles a randomly sampled diet of the same sample size. Therefore, species further from the line can be considered to be more specialized than those close to the line. Abbreviations indicate: bushy-crested hornbill (*Anorhinus galeritus*, AG), Binturong (*Arctictis binturong*, AB), black hornbill (*Anthracoceros malayanus*, AM), bearded pig (*Sus barbatus*, SB), Prevost's squirrel (*Callosciurus prevostii*, CP), dog-faced bat (*Pteropus* spp., PS), fairy bluebird (*Irena puella*, IP), long-tailed macaques (*Macaca fascicularis*, MF), green broadbill (*Calyptomena viridis*, CV), Bornean white-bearded gibbon (*Hylobates albibarbis*, HA), helmeted hornbill (*Buceros vigil*, BV), red leaf monkey (*Presbytis rubicunda rubida*, PR), little barbet (*Megalaima australis*, MA), gold-whiskered barbet (*Megalaima chrysopogon*, MC), gaudy barbet (*Megalaima mystacophanes*, MM), red-crowned barbet (*Megalaima rafflesii*, MR), Western Bornean orangutan (*Pongo pygmaeus wurmbii*, PP), long-tailed parakeet (*Psittacula longicauda*, PL), giant squirrel (*Ratufa affinis*, RA), rhinoceros hornbill (*Buceros rhinoceros*, BR), Little green pigeon (*Treron capellei*, TC), tufted ground squirrel (*Rheithrosciurus macrotis*, TG), wreathed hornbill (*Aceros undulatus*, AU), and wrinkled hornbill (*Aceros corrugatus*, AC)
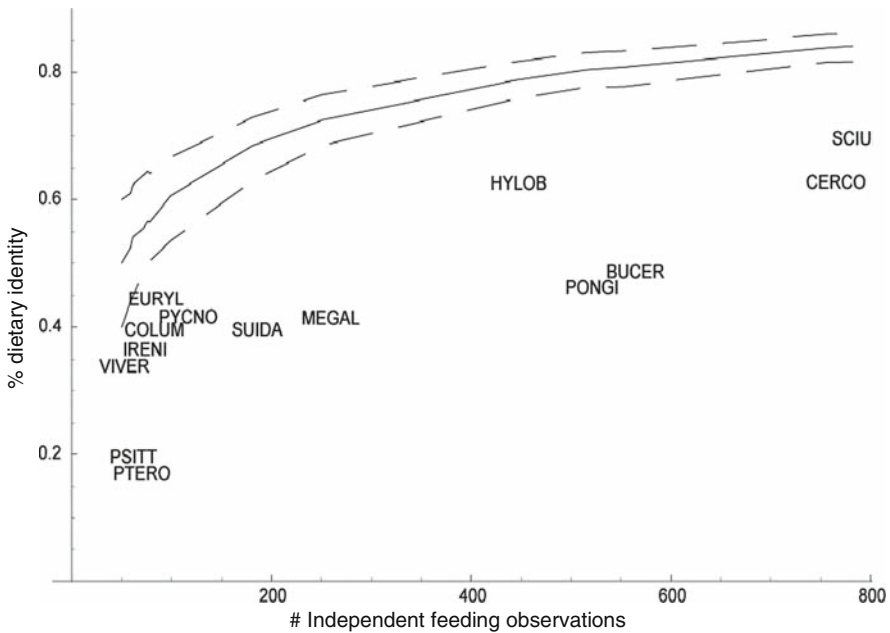
Fig. 9.3 Dietary specialization of vertebrate frugivores by family. Axes and lines are the same as in Fig. 9.2. Abbreviations indicate Bucerotidae (BUCER), Cercopithecideae (CERCO), Columbidae (COLUM), Eurylaimidae (EURYL), Hylobatidae (HYLOB), Irenidae (IRENI), Megalaimidae (MEGAL), Pongidae (PONGI), Psittacidae (PSITT), Pteropodidae (PTERO), Pynotidae (PYCNO), Sciuridae (SCIUR), Suidae (SUIDA), and Viveridae (VIVER)

family shows a similar pattern: the hylobatids are less specialized than hornbills (Bucerotidae), monkeys (Cercopithecidae), and barbets (Megalaimidae), and about as specialized as squirrels (Sciuridae; Fig. 9.3).

Gibbon diets are slightly less diverse during HFP than LFP in peat forests, and during masts gibbon diets include 25% fewer items than during other seasons (Fig. 9.4). This provides modest support for H1, although the pattern is not strong. Patterns in other taxa vary considerably, both within a taxon in different forest types (e.g., orangutans increase dietary diversity in peat swamp forests during lean periods, but show the opposite trend in non-peat forests; Fig. 9.4) and between taxa (e.g., barbets show a pattern that is consistently opposite to that exhibited by squirrels; Fig. 9.4).

Which Taxa Are the Major Competitors of Gibbons?

The species with the highest degree of dietary overlap with gibbons was Prevost's squirrel, (*Callosciurus prevostii:* 51% overlap), followed by the three most common diurnal primates at CPRS: orangutans (*Pongo pygmaeus wurmbii*: 49%), long-tailed macaques (*Macaca fascicularis*: 48%), and red leaf monkeys
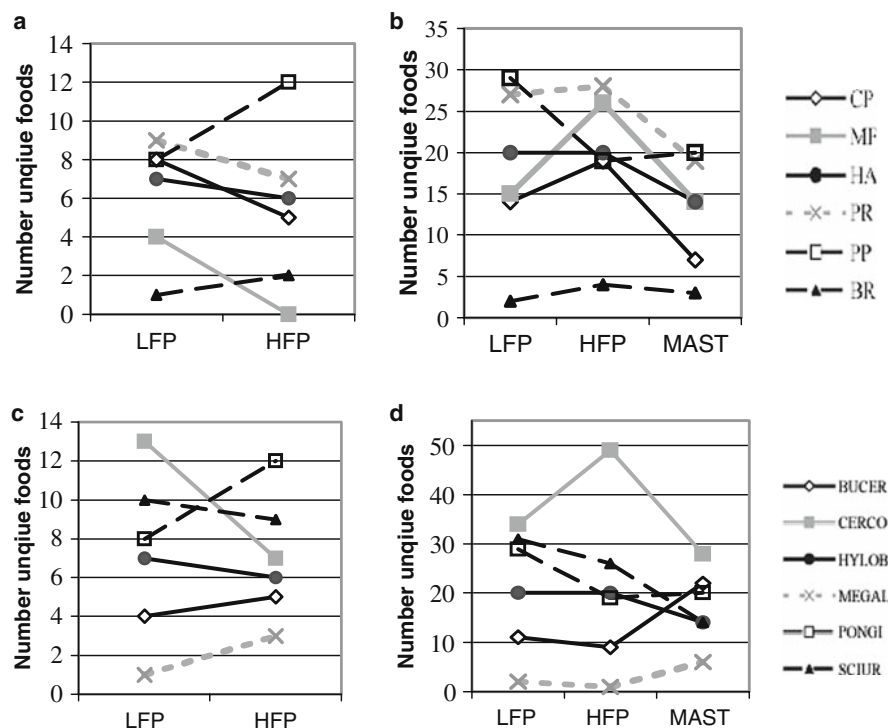
Fig. 9.4 The number of unique food items included in the diets of gibbons and their major vertebrate competitors. Graphs show the number of distinct plant taxa fed on by vertebrate species during (**a**) peat forests and (**b**) non-peat forests, and those fed on by vertebrate families in (**c**) peat forests and (**d**) non-peat forests during high fruit period (HFP), low fruit periods (LFP), and masts. The analysis controls for differences in sample sizes between periods. See legends to Figs. 9.2 and 9.3 for abbreviations

(*Presbytis rubicunda rubida*: 41%, Table 9.2). Given various types of sampling error, overlap with at least the first three species should be considered co-equal and not significantly different. Other taxa with substantial dietary overlap (>5%) with gibbons included bearded pigs (*Sus barbatus*), binturong (*Arctictis binturong*), and several species of hornbill (Bucerotiformes), barbets (Megalaimidae), bulbuls (Pynotidae), and squirrels (Sciuridae).

We also examined whether forest type affected the intensity of feeding competition (as indexed by dietary overlap) between gibbons and other taxa. We limited this analysis to taxa for which the percent dietary overlap with gibbons exceeded 30% (Table 9.2), and examined the patterns on both the species and the family level. Although absolute measures suggest that the fruit component of the diets of most species overlapped with gibbon diets substantially less in peat forests than non-peat forests, these results are due to

Table 9.2 The ten vertebrate frugivores with the highest degree of dietary overlap with gibbons at Gunung Palung

Order	Family[a]	Latin name	Common name	Dietary overlap[b] (%)
RODEN	SCIUR	*Callosciurus prevostii*	Prevost's squirrel	50.5
PRIMA	PONGI	*Pongo pygmaeus wurmbii*	Orangutan	48.6
PRIMA	CERCO	*Macaca fascicularis*	Long-tailed macaque	48.2
PRIMA	CERCO	*Presbytis rubicunda rubida*	Red leaf monkey	41.4
BUCER	BUCER	*Buceros rhinoceros*	Rhinoceros hornbill	30.7
RODEN	SCIUR	*Ratufa affinus*	Giant squirrel	27.5
BUCER	BUCER	*Anorhinus galeritus*	Bushy-crested hornbill	17.3
PICIF	MEGAL	*Megalaima chrysopogon*	Gold-whiskered barbet	16.8
ARTIO	SUIDA	*Sus barbatus*	Bearded big	15.5
BUCER	BUCER	*Buceros vigil*	Helmeted hornbill	13.4

[a] Family abbreviations are the same as used in Fig. 9.3.
[b] Analysis combines all fruit-feeding records from all habitat types.

differences in sample sizes between peat and non-peat forests – actually all species showed the same patterns of overlap in peat and non-peat forests (Fig. 9.5). The family analysis revealed some differences between the two habitat types. Cercopithecine monkey diets showed significantly lower dietary
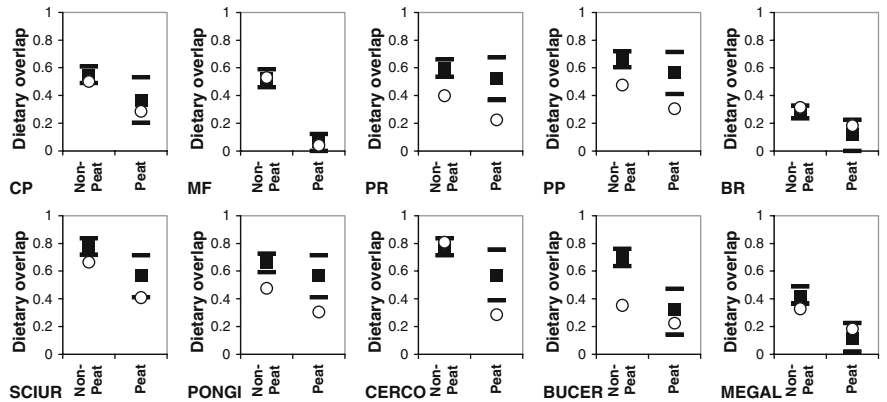

Fig. 9.5 Overall diet overlap between gibbons and other important vertebrate frugivores in peat and non-peat forests. The *y*-axis lists the proportion of overlap with gibbon diets (a measure incorporating both dietary composition and the frequency of items in the diet). Black boxes and lines indicate, respectively, the mean and upper and lower 95% limits of expected overlap with gibbons based on 1000 randomly drawn diets. Open circles indicate observed dietary overlap with gibbons. The top row of graphs shows data for vertebrate species (abbreviations follow Fig. 9.2); the bottom row shows data for vertebrate families (abbreviations follow Fig. 9.3)

overlap with gibbons in peat forests (Fig. 9.5). Hornbill diets overlapped gibbon diets significantly less in non-peat forests, a trend that was also apparent in squirrels and barbets (Fig. 9.5).

How Similar Are the Niches of Gibbons and Their Major Competitors?

Our hypothesis that gibbon diets diverge more from their competitors during periods of low resource availability than during periods of higher food availability (H2A) received mixed support. For most species the results were very similar between peat and non-peat forests; on the family level, most patterns were broadly similar between forest types, but we note some differences. As predicted, the diets of both orangutans and leaf monkeys diverged significantly from gibbon diets during periods of food scarcity and showed greater overlap during periods of resource abundance in both peat and non-peat forests (Figs. 9.6 and 9.7). But, contrary to our prediction, in both peat and non-peat forests food availability had no effect on the degree to which the diets of Prevost's squirrels, long-tailed macaques, and rhinoceros hornbills overlapped with gibbon diets (Figs. 9.6 and 9.7).

Our analysis of the effects of food availability on dietary overlap among vertebrate families showed that the Sciuridae tended to exhibit high dietary overlap with gibbons during periods of high food availability and reduced levels of overlap when resources were relatively scarce in both forest types. A similar pattern was observable for Bucerotidae in non-peat forests and Cercopithecidae
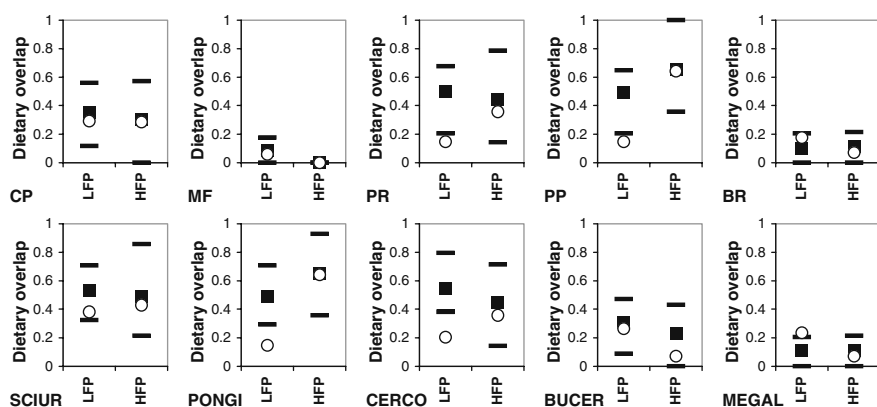

Fig. 9.6 Diet overlap between gibbons and other important vertebrate frugivores during low fruit periods (LFP) and high fruit periods (HFP) in peat forests. Explanation and abbreviations as in Fig. 9.5
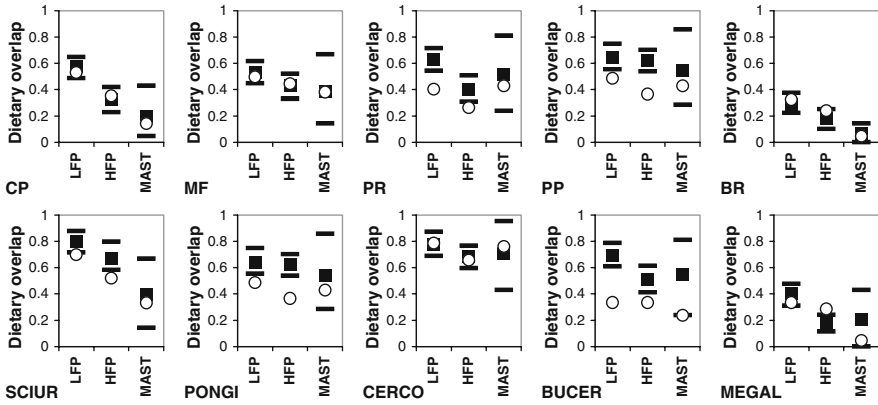
Fig. 9.7 Diet overlap between gibbons and other important vertebrate frugivores during low fruit periods (LFP), high fruit periods (HFP), and masts in non-peat forests. Explanation and abbreviations as in Figs. 9.5 and 9.6

in peat forest, but not for hornbills in peat forests or cercopithecine monkeys in the non-peat forests. These patterns demonstrate that ecological interactions between vertebrate taxa can vary in different habitat types. Finally, the overlap between barbets (Megalaimidae) and gibbons was unrelated to food availability (Figs. 9.6 and 9.7).

We tested the hypothesis that gibbons fed in smaller patches than their competitors (H2B) by conducting a one-way ANOVA that compared the average size (dbh) of gibbon feeding trees with those fed on by their five most important competitors: Prevost's Squirrels, orangutans, long-tailed macaques, red leaf monkeys, and rhinoceros hornbills. These species differed significantly in the mean size of feeding trees (F ratio $= 21.3$, df $= 5$, $p < 0.0001$). Post-hoc tests revealed that gibbons fed in smaller trees than red leaf monkeys and orangutans (Tukey-Kramer HSD $q > 2.82$, $p < 0.05$), but that the size of feeding trees did not differ between gibbons and Prevost's squirrels, long-tailed macaques, or hornbills (Fig. 9.8).

Finally, we tested the prediction that gibbons utilize different habitats than their major competitors (H2C) by examining the correlations between indices of gibbon density and the densities of orangutans, leaf monkeys, and macaques. Significant negative correlations would suggest that gibbons preferentially inhabit forest types in which other primates are scarce. Gibbon densities were uncorrelated with the densities of any of these three species. All Spearman's rho values were positive (>0.35), allowing us to reject the hypothesis that gibbons reduce competition with other species by dispersing themselves across space differently. These results are consistent with those from a larger set of censuses conducted by ML and colleagues between May 1985 and January 1992 ($n = 4,588$; 12,889 km, unpublished data).
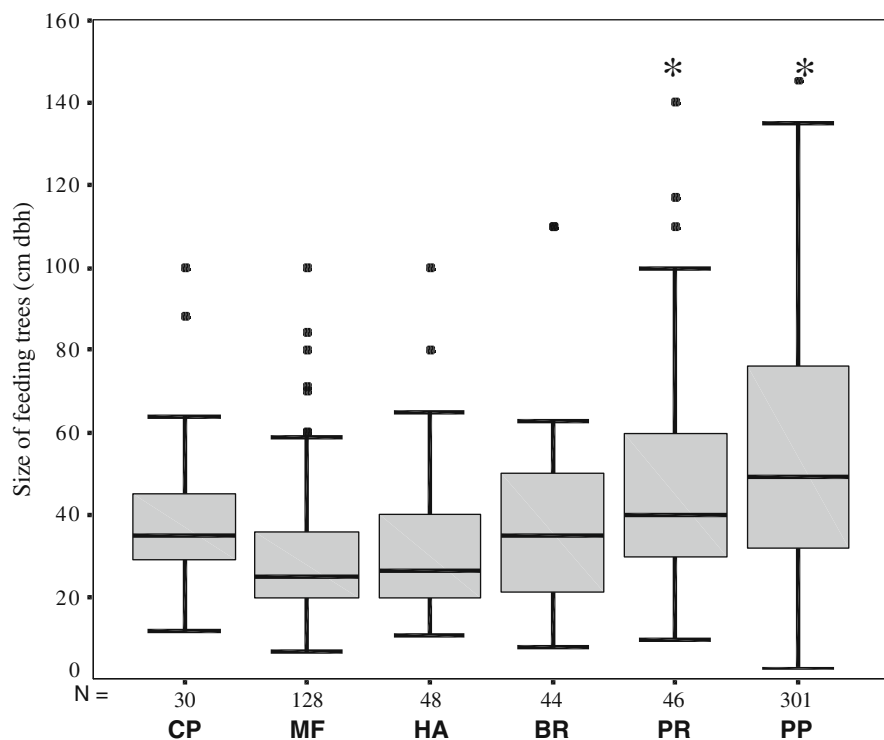
Fig. 9.8 Diameter of feeding trees of gibbons and their major competitors. The boxplots depict the diameter of feeding trees for each vertebrate taxon, showing the median (*black horizontal lines*), interquartile range (*gray boxes*), extent of points within 1.5 of the quartile range (*upper and lower range lines*), and outliers (*points*). Red leaf monkeys (PR) and orangutans (PP) fed in significantly larger trees than did all other taxa (* Tukey-Kramer HSD $q>$ 2.82, $p < 0.05$); the size of trees fed in by gibbons (HA) did not differ significantly from Prevost's squirrel (CP), long-tailed macaques (MF), or rhinoceros hornbills (BR). Sample sizes for each taxon are given above initials

Discussion

In this chapter we have considered the composition of gibbon diets at CPRS in relation to sympatric frugivorous vertebrates found at the site using a broad, long-term data set. This data set provides an unusual opportunity to study gibbon ecology in the context of the broader vertebrate community, and promises to provide a fuller understanding of the ecological and evolutionary forces that shaped primate adaptations. Our data were collected during vertebrate censuses and other instances where observations were random and independent. Therefore, we avoided pseudoreplication and many of the biases that can plague studies of vertebrate, particularly primate, feeding ecology.

Despite these strengths, several limitations of the data set and our analyses warrant discussion. First, as our data were collected during daylight hours, the

importance of nocturnal competitors (e.g., bats, civets) cannot be quantitatively assessed. Second, we based all our randomizations on iterative samples from the database of independent feeding observations. This method carries the assumption that our observations of feeding reflect general patterns of food availability and consumption in the forest (i.e., they are unbiased samples of the full set of feeding occurrences that occurred in the forest at the time they were collected). Although we cannot explicitly test this assertion, the fact that we confined our analysis to independent, random samples allows us to feel confident that this assumption was not violated. Third, all of our analyses were based on only the frugivorous portion of the diets of the vertebrates we studied. Since non-fruit items comprise a proportion of the diets of most of the vertebrate taxa included in this analysis, this may have inflated estimates of overlap in some cases. Finally, as only items that were observed to be eaten at least once were considered in the analysis (because we used the database of vertebrate feeding records), we underestimated degrees of specialization, selectivity, and avoidance relative to the full set of potential foods in the forest.

While we acknowledge these limitations, our results provide new information about gibbon feeding ecology at CPRS and the importance of competition with other vertebrate frugivores. Below we discuss each of the three sets of questions that we have addressed in this chapter.

How Specialized Are Gibbon Diets?

Our analysis of the use ratios of gibbon foods are a fairly course-grained method of detecting dietary selectivity, as they do not incorporate spatial (e.g., habitat-specific plant stem density) or temporal variation in food availability. Nevertheless, the results generally confirm the results from more detailed analyses of gibbon food preference at CPRS (Marshall 2004) and other sites (McConkey et al. 2002; McConkey et al. 2003; McConkey this volume). They confirm that gibbons prefer pulpy, sugar-rich fruits with generally low levels of tannins and toxins, and avoid toxic plant species and those with extremely hard seeds (McConkey et al. 2002).

Despite this evidence for strong selectivity, in our comparison of the frugivorous portion of diets, gibbons appear to eat a relatively unspecialized diet when compared with most other vertebrate frugivores at CPRS. Few studies provide quantitative estimates of the degree of dietary specialization in gibbons relative to all sympatric frugivorous vertebrates, but MacKinnon and MacKinnon (1980) compared the degree of specialization among sympatric primates at Krau Game Reserve, Peninsular Malaysia. In contrast to our results, their intensive study concluded that hylobatids were the most specialized primates in the community (MacKinnon and MacKinnon 1980). It is possible that this discrepancy is a result of differences in analysis or sampling strategy, but MacKinnon and MacKinnon (1980) provide insufficient details to enable us

to address this possibility. The most likely reason for the differences is, however, the fact that the MacKinnons' study was limited to 6 or 7 months. As our analyses demonstrate, the relative degree of specialization between species varies between seasons (e.g., compare red leaf monkeys and orangutans in Fig. 9.4). Therefore, conclusions based on comparisons over such short durations may be misleading, particularly in forests in which plant productivity is so temporally variable. Our longer-term data set includes only independent observations drawn over the full range of variation in resource availability, and therefore is likely to provide a more accurate picture of the comparative feeding ecology of these species.

Assuming that our results accurately assess the degree of specialization of gibbons compared to other vertebrate frugivores, why are gibbons so relatively unspecialized? One possibility is that gibbons lack a highly specialized gut morphology that would enable (or constrain) them to become highly specialized on a limited set of food items (cf. colobines). Another (and probably complementary) possibility is that gibbons' fast locomotion releases them from the requirement of focusing solely on large fruit patches, and enables them to visit a wider variety of fruit trees and lianas per day than could smaller (e.g., squirrels), larger (e.g., orangutans), or slower (e.g., macaques) species (see below). When compared to their major avian competitors, the most likely reason that gibbons eat a wider range of fruits is that their manual dexterity enables them to open indehiscent fruits that are largely unavailable to the birds. Thus gibbons are released from the factors forcing most sympatric vertebrates to specialize, and are therefore able to reap the benefits of eating a more generalized diet – the greatest of which are likely to be a greater total amount of food available and less temporal variation in food availability.

A third possibility depends on our definition and analysis of specialization and the relative abundance of fruits of different types. Gibbons are generalists in that they consume fruits from many genera, but these genera represent convergence among many families toward a primate-fruit type of similar chemistry and morphology (Leighton and Leighton 1983; McConkey this volume). If this type is rich in genera and relatively common in the forest compared to other types, gibbons may be quite specialized on this type, but generalized in our comparative analysis. We expect to address this possibility in future analyses.

Finally, our analysis suggests that gibbons become more generalized feeders during periods of resource scarcity. This conformed to our prediction (H1) and was the most common pattern in the other primates at CPRS. However, we consider the test presented here to be preliminary. A full examination of this question will require explicit incorporation of a more fine-grained measure of fruit availability, such as the number of food patches per hectare, as well as inclusion of non-fruit items in the diets of all species.

Which Taxa Are the Major Competitors of Gibbons?

In this chapter we use dietary overlap as a simple proxy for feeding competition. We recognize that dietary overlap does not necessarily indicate competition: species utilizing highly overlapping diets may not compete if they occupy different habitats or if factors other than resources (e.g., predation) limit carrying capacity (Colwell and Futuyma 1971; Pianka 1974, 1976; Yamagiwa and Basabose 2003). In this community, however, we would argue that dietary overlap is a good proxy for feeding competition because our study subjects are generally large-bodied, food-limited, canopy-foraging, mainly frugivorous, diurnal species that occupy the same forest habitats. This competition need not be symmetrical; that is, dietary overlap may not have equivalent effects on the fitness of competing species (Connell 1983). For example, pigs that feed on fruits at the base of trees experience reduced food availability due to competition with arboreal frugivores, but arboreal species are not similarly affected by pigs.

Our analysis indicated that the most important competitor for gibbons at CPRS was not another primate species but a squirrel instead. This unexpected result reminds us that competition with non-primate species can have major ecological impacts on primate species. While some primatologists have realized this for some time (Strum and Western 1982; Estrada and Coates-Estrada 1985; Ganzhorn 1999), the role of non-primate competitors, as members of the same ecological community, is rarely considered. Also, two of gibbons' major competitors, Prevost's squirrels and red leaf monkeys, tend to eat immature fruits and seeds before they ripen sufficiently for gibbons to eat them. This pattern results in asymmetrical competition, whereby Prevost's squirrels and red leaf monkeys reduce food availability for gibbons but experience few negative effects from the gibbons' feeding behavior.

How Similar Are the Niches of Gibbons and Their Major Competitors?

We predicted that gibbon diets would diverge more from their competitors during periods of low resource availability than during periods of higher food availability (H2A). This hypothesis was supported for two important primate competitors: red leaf monkeys and orangutans. During fruit-poor times red leaf monkeys utilize toxic seeds and tannic leaves that gibbons are unable to digest (Marshall 2004), and orangutans utilize low-quality pith, cambium, and leaves that would be insufficient to support gibbons during lean times (Leighton 1993; Knott 1999). These species specialize on foods that are unavailable to gibbons and therefore reduce feeding competition with gibbons during fruit poor times. However, there was no relationship between food availability and gibbon dietary overlap with squirrels, macaques, or hornbills. Gibbons, as relative generalists, cannot fall back on a food type that other species ignore. Instead, they rely

heavily on figs as their fallback food (Marshall and Leighton 2006), a pattern characteristic of many Southeast Asian rainforest vertebrates, including macaques and hornbills (Leighton and Leighton 1983; O'Brien et al. 1998). Thus, some species shift their diets away from gibbons during periods of low fruit availability (e.g., orangutans, leaf monkeys), but gibbons appear largely unable to shift their own diets to rely on a fallback food not utilized by other species.

In support of hypothesis H2B, our results indicated that gibbons may reduce competition with two of their major competitors, orangutans and leaf monkeys, by exploiting smaller trees than these species. There are at least two interpretations of this result. First, orangutans and leaf monkeys may displace gibbons from larger feeding sites, relegating gibbons to smaller, less favorable sites. This may occasionally occur with orangutans, although interactions between orangutans and gibbons at feeding trees are very rare and are not always won by orangutans. This explanation seems even less plausible for leaf monkeys, who are generally deferential to gibbons on the rare cases that they interact with them (pers. obs.). Moreover, direct competition over common food resources between gibbons and leaf monkeys is rare, because leaf monkeys eat these items at earlier maturity stages than gibbons. We favor a second interpretation: that gibbons' more efficient locomotor adaptations allow them to profitably visit and feed on a far larger number of food patches in a day than can either orangutans or leaf monkeys (Raemaekers and Chivers 1980). This hypothesis is supported by the observation that gibbon day ranges (mean 1200 m, Leighton 1987) are 1.5 times longer than leaf monkey day ranges (mean 850 m, Bennett and Davies 1994), and 2.5 times larger than orangutan day ranges (<500 m, Rodman 1984). Gibbons did not utilize smaller trees than hornbills, macaques, or squirrels, but may compensate for this by visiting more patches per day than these species (Cannon and Leighton 1996).

Gibbons and their major competitors inhabit all of the forest types found at CPRS, and there was no relationship between gibbon population density and the density of any of their important primate competitors. We therefore rejected our final hypothesis (H2C), which postulated that habitat selection helps to ameliorate competition between gibbons and other primates. Data were unavailable to test this hypothesis for the non-primate competitors, but our observations suggest that high-quality lowland forests have high densities of most non-primate vertebrates as well, and that spatial partitioning of forest types is not an important mechanism that gibbons use to reduce feeding competition.

In this chapter we have used a unique, long-term data set to examine gibbon diets in relation to sympatric frugivorous vertebrates. This analysis provided us with a view of gibbon feeding ecology within the broader community of vertebrate frugivores that is rarely possible. It has demonstrated that gibbons, while clearly highly selective foragers, are nonetheless relative generalists compared with most vertebrates that occupy the same forests. It has allowed us to identify gibbons' major vertebrate competitors, and has indicated the importance of non-primate frugivores as competitors with gibbons. Finally, it has allowed us to test hypotheses about some of the mechanisms that might reduce feeding

competition between gibbons and their competitors. We expect that more refined analyses of these data that incorporate explicit consideration of temporal and spatial variation in patterns of food availability and consumption by vertebrates will expand our understanding of gibbon ecology and their role in the larger community of frugivorous vertebrates.

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