

Chapter 9

Effect of Habitat Quality on Primate Populations in Kalimantan: Gibbons and Leaf Monkeys as Case Studies

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Introduction

Primate ecologists seek to answer fundamental questions about how and why particular ecological factors influence primate individuals, groups, and populations (Isbell 1991; Sterck et al. 1997; van Schaik 1983; Wrangham 1980). While primatologists have used a variety of approaches to address these questions, the study of a particular taxon across a range of ecological conditions provides a particularly useful framework for investigating key questions about the interactions between primates and their habitats (Davies 1994; Doran et al. 2002; Morrogh-Bernard et al. 2009; Strum and Western 1982; van Schaik et al. 2009). Studies conducted on small spatial scales may be especially useful in this context because they permit investigation of the effects of variation in some ecological conditions while controlling for others (e.g., Caldecott 1980; Chapman and Chapman 1999; Dunbar 1992a; Iwamoto and Dunbar 1983). While such studies may address fundamental ecological questions in ways that other research designs cannot, they remain relatively underutilized. Understandably, given the difficulties of sampling long-lived, generally rare vertebrates, most primate studies have focused on a single or small number of groups. Equally reasonably, most studies are conducted in relatively high quality habitats, where behavioral data can be most efficiently collected. The focus on a small number of groups and disproportionate sampling of high quality habitats may limit our ability to observe variation in a species' ecology, hamper examination of the full range of behavioral plasticity that a primate species exhibits, and bias our understanding of how ecological factors affect primate populations.

In this chapter, I provide an overview of selected results from my study of gibbon and leaf monkey populations inhabiting seven distinct forest types at the Cabang Panti Research Station (CPRS) in Gunung Palung National Park (GPNP), West Kalimantan, Indonesia. These seven forest types comprise the full range of habitats

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that these species occupy at GPNP, thereby providing the unusual opportunity to address two fundamental ecological questions: (1) what determines habitat quality? and (2) what are the consequences of variation in habitat quality for individuals, groups, and populations? Gibbons and leaf monkeys have fundamentally different diets (frugivores vs. grammivores/folivores, respectively), social systems (socially monogamous vs. polygynous), and life histories (“slow” vs. “fast”), and simultaneous investigation of these two taxa can indicate how such characteristics mediate a species’ response to environmental variation. CPRS is an exceptional study site that permits sampling of a large number of primate groups across a broad range of forest types, the quality of which markedly, providing a rare opportunity to examine how ecology and social systems interact under a wide range of environmental conditions.

Here, I provide a brief introduction to the study site, species, and field methods; consider what determines habitat quality for gibbons and leaf monkeys; describe some important effects that habitat quality has on these species; and discuss the theoretical and practical relevance of these results.

Study Site and Subjects

CPRS, located in southwestern Borneo (Fig. 9.1), is composed of seven distinct, contiguous forest types, determined by elevation, soils, and drainage: (1) *peat swamp forest* on nutrient-poor, bleached white soils overlain by variable amounts of organic matter (5–10 m asl); (2) *freshwater swamp forest* on nutrient-rich, seasonally flooded, poorly drained gleyic soils (5–10 m asl); (3) *alluvial forest* on rich sandstone-derived soils recently deposited from upstream sandstone and granite parent material (5–50 m asl); (4) *lowland sandstone forest* on well-drained sandstone-derived soils with a high clay content and sparse patches of shale (20–200 m asl); (5) *lowland granite forest* on well-drained, granite-derived soils (200–400 m asl); (6) *upland granite forest* on well-drained, granite-derived soils (350–800 m asl); and (7) *montane forest* on largely granite-derived soils (750–1100 m asl). These forest types differ substantially in their floristic composition, temporal patterns of food availability, structure, and temperature (Cannon et al. 2007a, b). As a result, these habitats support densities of gibbons and leaf monkeys that differ by more than an order of magnitude (Table 9.1). This substantial variation occurs over a very small spatial scale (~5–10 km), so that variation in predators, disease, biogeography, and climate that confound comparative studies of more distant sites is controlled (Chapman and Chapman 1999; Marshall and Leighton 2006). The site had been the location of a long-term research since the mid 1980’s (e.g., Knott 1998; Curran and Leighton 2000; Cannon et al. 2007b), but was closed between 2002 and 2006 because of tensions with illegal loggers.

Bornean White-bearded Gibbons (*Hylobates albibarbis*, hereafter referred to as “gibbons”) and Red Leaf Monkeys (*Presbytis rubicunda rubida*, here “leaf monkeys”) are an excellent pair of species for comparative study because they differ

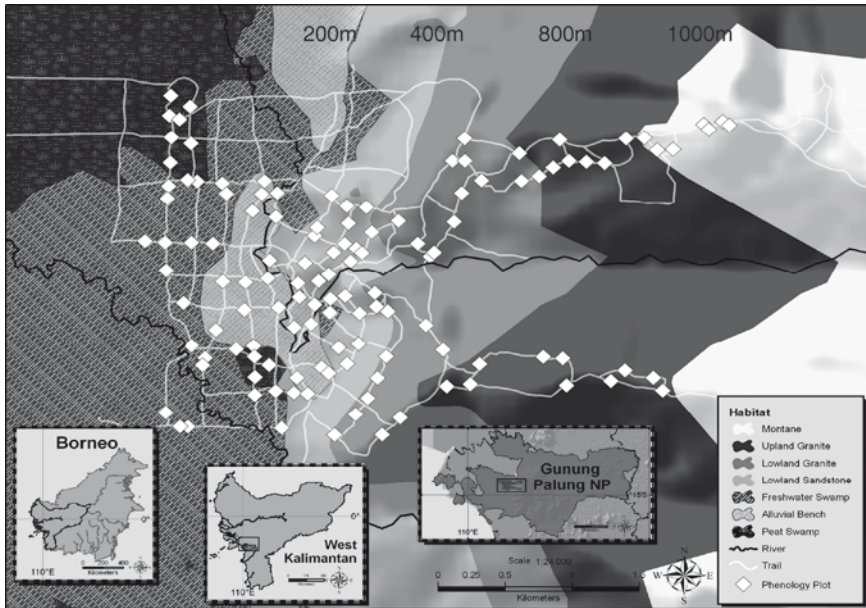


Fig. 9.1 Site map of the Cabang Panti Research Station (CPRS), located in GPNP. Shading depicts the seven forest types: shading top to bottom on legend=habitats right (montane) to left (peat and freshwater swamp) on figure. The 70 botanical plots (10 per forest type) are indicated by white diamonds; 2 vertebrate census routes (not shown) are also located in each forest type. Elevation of major contours is indicated along the top of the figure.

substantially in their diets, social systems, and life histories. Gibbons are frugivores; their diet at CPRS comprises mainly the pulp of ripe fruits (65% of the diet on average, range 0–95%, based on data collected between 1985 and 1992), augmented by ripe figs (23%, range 0–75%), flowers (6%, range 0–28%), leaves (3%, range 1–25%), and seeds (3%, range 0–8%; Marshall and Leighton 2006; Marshall et al. 2009a). On the other hand, leaf monkeys are seed and leaf specialists (seeds: 52%, range 25–95%; leaves: 25%, range 0–42% during the same period as the gibbon data), and also consume unripe fruit pulp (13%, range 2–72%; confined to plant taxa that are dispersed by bats and whose nutritional quality is similar to that of leaves), figs (5%, range 0–25%), and flowers (5%, range 0–20%; Marshall 2004; Marshall et al. 2009b). Gibbons at GPNP fall back on figs (Marshall and Leighton 2006), whereas leaf monkeys fall back on a combination of young and mature leaves (Marshall 2004). Gibbons are socially monogamous (each of the 33 groups observed at GPNP between 2000–2002 contained one adult male and one adult female), whereas leaf monkeys are polygynous (each of the 13 study groups during the same period contained a single adult male and 1–4 females). Primate life history data from CPRS are limited, but suggest that gibbon life histories are roughly half as fast as leaf monkey life histories (e.g., gibbon inter-birth intervals are approximately twice as long as leaf monkeys’: Mitani 1990; Marshall 2009; Marshall et al. 2009b),

Table 9.1 Overview of key variation among forest types at GPNP. For each forest type the following data are listed from left to right: mean altitude (m asl); structural data (stems per ha of trees in two size classes, woody climbers, and figs); fruit productivity (for trees, woody climbers, and figs); and the population density of gibbons and leaf monkeys (based on census routes walked between 2000–2002). Data from Marshall (2004, 2009) and Cannon et al. (2007a, b)

Forest type	Mean altitude	Stem densities (stems/ha)			Fruit productivity per month			Gibbon density \pm SE (indiv/km ²)	Leaf monkey density \pm SE (indiv/km ²)	
		Small trees (15–25 cm dbh)	Big trees (\geq 25 cm dbh)	Woody climbers	Figs	All trees (m ² /ha)	Woody climbers (m ² /ha)			Figs (stems/ha)
Peat swamp	5	238.0	160.4	112.1	6.7	0.97	59.19	0.39	7.28 \pm 1.25	2.52 \pm 1.06
Freshwater swamp	5	241.5	152.6	138.5	11.5	0.99	79.99	0.37	5.90 \pm 1.34	7.79 \pm 2.16
Alluvial bench	34	171.0	148.7	61.7	15.7	1.39	44.78	0.49	7.10 \pm 1.70	10.53 \pm 2.81
Lowland sandstone	120	157.0	162.1	79.5	9.0	1.66	82.74	0.30	10.27 \pm 2.12	5.85 \pm 1.76
Lowland granite	255	194.4	203.8	46.9	7.6	1.21	23.51	0.17	6.23 \pm 1.33	7.26 \pm 1.87
Upland granite	545	244.4	215.2	65.7	8.6	1.24	61.31	0.12	4.17 \pm 1.17	6.89 \pm 1.76
Montane	880	285.7	140.0	30.0	0.0	0.65	10.82	0.00	0.44 \pm 0.25	1.24 \pm 0.64

a result that is in accordance with more general comparisons between primate species showing that ape life histories are generally slower than monkey life histories (Schultz 1968; Smith 1989).

Field Methods

Between August 2000 and August 2002, three local assistants and I carried out direct observations of animals along transects to systematically measure the habitat-specific densities of gibbon and leaf monkey populations and to augment data on gibbon and leaf monkey group composition (see below). We established a pair of replicate census routes in each of the seven forest type at CPRS and walked a total of 409 censuses (1,374 km); with an average of 58 censuses (range 38 to 87) in each forest type (Marshall 2004; 2009). Census routes averaged 3.5 km in length and followed existing trails through the forest. We walked each route at least twice per month (starting at opposite ends) at the same speed and time of day (beginning at 05:30 h), and gathered standard line transect data for all vertebrates encountered (e.g., perpendicular sighting distance, group size, group spread). Whenever gibbon or leaf monkey groups were encountered, we ensured that full group counts and information on group composition were recorded by following the group until these data were collected.

We followed standard methods for the analysis of line transect data using Distance 5.2 (Thomas et al. 2006), calculating detection functions separately in each forest type and controlling for size bias in sampling (Buckland et al. 2001). For analyses in which territory- or home range-specific indices of habitat quality were required, I calculated an index of the population density that could be supported in a particular group's territory or home range (i.e., the carrying capacity of the territory or home range). For groups whose entire range was contained within one forest type, this number was the habitat-specific density for the forest type that the group occupied (determined from line transects). For groups whose territory spanned multiple forest types, I summed the habitat-specific density of all forest types occupied, scaled by the proportion of the territory in each. For example, if 80% of a gibbon group's territory was in peat swamp and 20% in freshwater swamp, then this index would be equal to $0.8 * \text{habitat-specific gibbon density for peat swamp} + 0.2 * \text{habitat-specific gibbon density for freshwater swamp}$ (i.e., $0.8 * 7.28 \text{ individuals/km}^2 + 0.2 * 5.90 \text{ individuals/km}^2 = 7.00 \text{ individuals/km}^2$).

Although data gathered during censuses generally provided complete and accurate data on group size and demographic structure, in 2002, I closely observed and followed all gibbon and leaf monkey groups detected on the census routes to estimate the extent of each territory and to ensure that my field assistants and I had accurately counted the total number of individuals in each group. In order to increase the sample size of groups, I thoroughly searched the study site to

identify additional groups that might have been missed on the census routes. This resulted in reliable demographic data on 33 groups of gibbons and 13 groups of leaf monkeys. I observed each of the 46 groups for a minimum of 3 consecutive hours in each of 3 separate months, although in most cases, sample sizes were far greater: each gibbon group was observed a mean of 11.5 times (range 3–73) and for an average of 11.0 months (range 3–23 months); each leaf monkey group was observed a mean of 25.2 times (range 3–96) and for an average of 17.1 months (range 6–25 months).

In order to assess the size of gibbon territories and leaf monkey home ranges, I plotted all group sightings for each species on a map superimposed with a 50 m × 50 m grid. I counted the number of squares inside the smallest polygon that included all group observations, and multiplied this number by 0.25 ha to estimate the home range size of each group (in ha). In cases where sample sizes were sufficiently large (i.e., $n \geq 10$ observations over at least 6 months), these home range estimates were accurate because groups tended to deflect at territorial boundaries during the course of longer group follows. Observed inter-group encounters at territorial boundaries provided useful additional information while estimating a group's home range. Nevertheless, in many cases, sample sizes were inadequate to accurately determine the full home range size. In addition, as estimated home range size increased in a curvilinear fashion with the number of observations of a group, comparing home range sizes among groups with different numbers of observations would be inappropriate. Therefore, I used the home range residuals (HRR, the residuals from the polynomial regression of home range size on observation number) as an unbiased estimate of home range size.

To compile a list of food taxa utilized by gibbons and leaf monkeys, I used a large sample of independent feeding observations from M. Leighton's long-term census data gathered between April 1985 and December 1991, additional opportunistic feeding observations from the same period, and my own data from August 2000 – August 2002 ($n_{\text{GIBBONS}} = 536$; $n_{\text{MONKEYS}} = 895$). When coupled with phenological data from the same period, I was able to identify preferred foods for gibbons and leaf monkeys, and foods that were eaten during periods when such foods were scarce (i.e., fallback foods, see section "What Determines Habitat Quality for Primates?"). Details are provided in Marshall (2004) and Marshall and Leighton (2006).

We measured the habitat-specific availability of food resources by randomly placing ten 0.5 ha plots in each forest type ($n_{\text{total plots}} = 70$). In these plots, we conducted a full census of all fig roots and liana stems with diameters at breast height (dbh, 137 cm above the ground) greater than 4.5 cm, and all trees with boles greater than 14.5 cm dbh. The dbh and botanical identification (using scientific nomenclature) of each stem was recorded ($N = 9,282$ total stems). Details on sampling methodology and botanical nomenclature are provided in Marshall and Leighton (2006). On the basis of stem density data from these plots, we computed the habitat-specific density of each plant taxon. From these data, the density of particular preferred or fallback foods, or the total preferred or total fallback foods, in a habitat could easily be calculated.

Habitat-Specific Population Densities

Population density differs substantially among forest types. Point estimates of gibbon densities range from 0.44 individuals/km² in montane forest to 10.27 individuals/km² in lowland sandstone habitats; estimates of leaf monkey density range from 1.24 individuals/km² in montane forests to 10.53 individuals/km² in alluvial bench forest (Table 9.1). During the observation period, population density was stable within each habitat; no changes in population size were detected on surveys conducted bi-monthly between September 2000 and July 2002. In order to ascertain whether population densities were stable over longer periods, I examined the data collected using an identical protocol between May 1985 and January 1992. Populations were stable over this longer period, and there were no significant differences in habitat-specific encounter rates of either species between 1985–1992 and 2000–2002 (Leighton and Marshall, unpublished data). These results indicate that habitat-specific population densities of both species did not fluctuate over time, an interpretation that fits expectations for species exhibiting risk-averse life-history strategies and low intrinsic rates of population increase (Charnov and Berrigan 1993; Marshall 2004).

What Determines Habitat Quality for Primates?

The most widely used index of habitat quality is the population density that a habitat can support at carrying capacity; high quality habitats support high population densities and low quality habitats support low population densities (Begon et al. 1996; Krebs 2001). Thus, habitat quality (i.e., habitat-specific population density) should be a function of the net energy available to support primate biomass, or the balance between habitat-specific energy availability and habitat-specific costs (Caldecott 1980; Iwamoto and Dunbar 1983). Most previous work exploring the ecological determinants of primate population density has focused on variation in habitat-specific benefits—essentially, different levels of energy input (i.e., food availability; e.g., Davies 1994; Chapman and Chapman 1999). Until recently, measures of food availability have been relatively simplistic, largely failing to consider potentially important variation in what types of food are available. There is both growing empirical evidence and widening conceptual realization that distinct classes of foods can have quite different effects on primate populations on ecological and evolutionary time scales (Laden and Wrangham 2005; Lambert 2007; Lambert et al. 2004; Marshall et al. 2009b; Rosenberger 1992; Vogel et al. 2008; Wrangham et al. 1998).

Particular attention has been paid to the relative importance of preferred and fallback foods. Preferred foods are positively selected (i.e., disproportionately used relative to their abundance; cf. Leighton 1993; Manly et al. 2002). Fallback foods are used in inverse proportion to the availability of preferred foods (Altmann 1988; Wrangham et al. 1998). These two classes of foods differ in their quality (preferred foods are relatively high quality, fallback foods are relatively low quality) and distribution in space and time (fallback foods are generally more abundant and available than preferred foods; Lambert 2007; Marshall and Wrangham 2007).

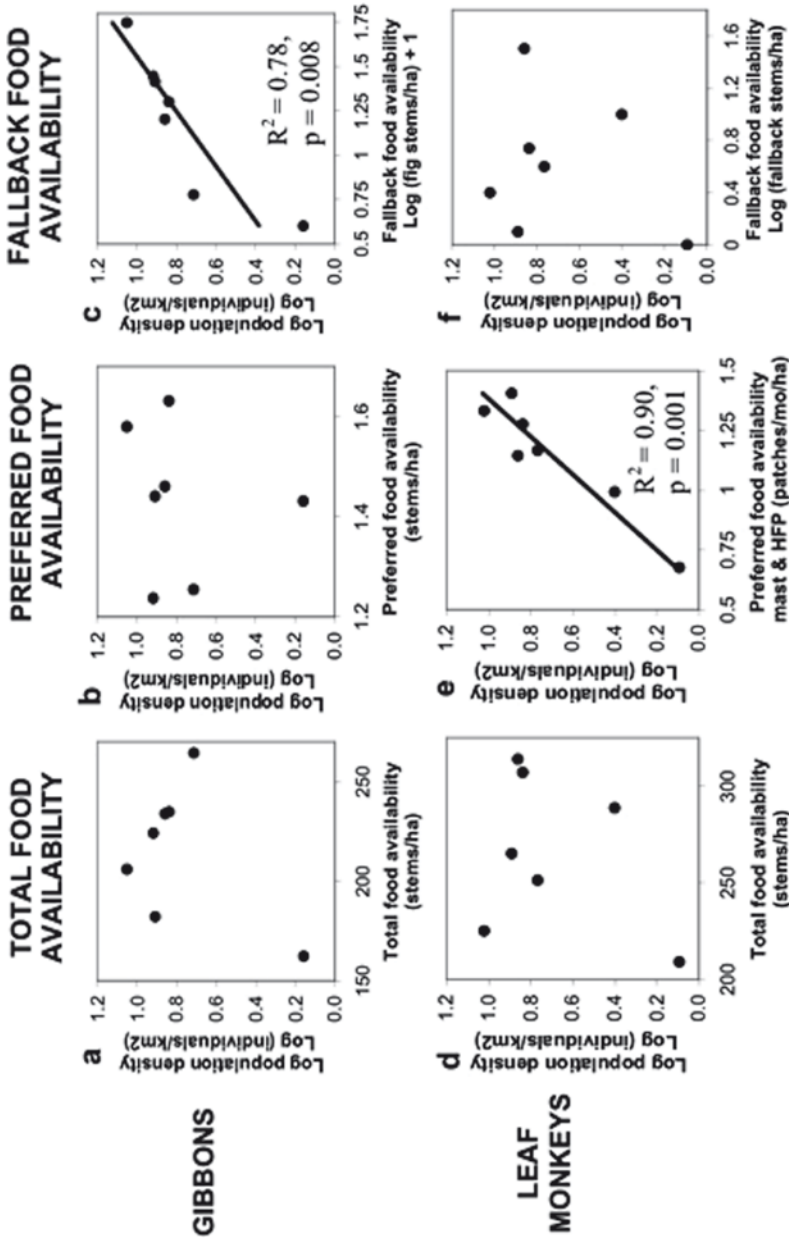


Fig. 9.2. Different classes of food have different effects on gibbons and leaf monkeys. Gibbon population density appears to be limited by the availability of fallback foods (c), but not total food availability (a) or preferred food availability (b). Leaf monkeys are limited by preferred foods (e), but not total foods (d) or fallback foods (f). Modified from Marshall et al. (2009b). For all figures (a–f), $n = 7$ forest types. Statistics and regression lines are provided for significant relationships only

There is some debate about whether preferred or fallback foods determine carrying capacity for primate populations. Some primatologists have suggested that because preferred foods are of high nutritional quality and provide energy necessary for reproduction, habitats with patches of preferred foods that are relatively large or abundant might be expected to maintain higher overall primate densities (e.g., Altmann et al. 1985; Balcomb et al. 2000). An alternative hypothesis suggests that fallback foods limit population density because they provide sustenance during periods of low food availability when competition for food is most intense (e.g., Cant 1980; Foster 1982; Marshall and Leighton 2006; Marshall et al. 2009c). Still other studies have suggested that alternative indices of food availability, such as total or maximum food availability or protein to fiber ratios in leaves, determine habitat quality (Chapman and Chapman 1999; Davies et al. 1988; Hanya et al. 2004; Mather 1992; McKey 1978; Wasserman and Chapman 2003).

Research on gibbons and leaf monkeys at CPRS suggests that consideration of foods in distinct classes (i.e., preferred vs. fallback) is warranted (Marshall et al. 2009b). Data from CPRS show that simple measures of total food abundance were not correlated with population density of either species across the seven habitats at the site (Fig. 9.2a, d). Furthermore, leaf monkey density was highly correlated with the availability of preferred foods during periods of high food abundance, whereas gibbon density was not (Fig. 9.2 b, e). In contrast, habitat-specific gibbon density was closely related to the availability of figs, their primary fallback food, while the availability of fallback foods did not explain any variation in leaf monkey density across the seven forest types (Fig. 9.2 c, f). These results are important because they suggest that only specific types of resources determine habitat quality (rather than general measures of food availability, as is often assumed) and that different species may be limited by distinct types of food resources, perhaps due to key differences in physiology, social system, or life history (Marshall et al. 2009b).

Effects of Variation in Habitat Quality

Primatologists assume that ecological factors (e.g., climate, food availability, disease, predation) drive macro-evolutionary processes (e.g., speciation, radiation, and extinction), and examination of the effects of variation in these factors over time and space has been the central goal of primate ecology for decades (e.g., Bourlière 1979; Chapman et al. 2002; Isbell 1991; Janson and Chapman 1999; Sterck et al. 1997; van Schaik 1983; Wrangham 1980). The unusual range of variation found among the seven forest types at CPRS provides an ideal setting in which to examine the consequences of variation in habitat quality on primate individuals, groups, and populations. Here, I provide examples of the effects of habitat quality on gibbons and leaf monkeys at each of these levels.

Basic ecological theory predicts that habitat quality will have important influences on individual fitness, but that these effects will be mediated by social system. In polygynous systems where females are relatively sedentary (e.g., leaf monkeys), the quality of the territory that can be defended by a male will dictate the number of females that he is able to attract. The logic behind this “polygyny threshold model” (Orians 1969; Verner and Willson 1966) is that in a heterogeneous landscape, a female may gain access to more resources by joining an existing pair in a high quality habitat than by establishing a new pair with a male in a habitat of lower quality. Females should therefore assort themselves in accordance with the “ideal free distribution” (Fretwell and Lucas 1969), and female fitness is equalized across the landscape. In reality, most primate females may not be optimally distributed among groups because a variety of factors might limit their ability to move freely between groups (e.g., dispersal costs, benefits of remaining near kin, the need to secure protection against predation). Nevertheless, the basic prediction is that variation in female fitness among polygynous groups will be small.

In monogamous territorial species (e.g., gibbons), social constraints prohibit females from freely assorting themselves (*sensu* Fretwell and Lucas 1969). Mated pairs typically defend territories to the exclusion of all other individuals. Therefore, fitness is not equalized across the landscape, and female reproductive success should be correlated with habitat quality, unless territory size is inversely correlated with habitat quality (see below). Male reproductive success should be correlated with habitat quality regardless of social system since in both systems, high quality males will outcompete low quality males for access to the best territories (e.g., Owen-Smith 1977). In polygynous systems, these higher quality territories allow a given male to attract more females, whereas in monogamous species, they provide the mated pair with additional resources for use in reproduction and may allow a male to attract a higher quality mate.

I used the average number of offspring (the sum of all infants, juveniles, and subadults) per adult female in each group as a proxy of reproductive success. This serves as a crude approximation of reproductive success as it does not include any effects of differential female life spans or differences in maturation age among groups, but is the best index presently available for populations at GPNP. As predicted, habitat quality had a strong influence on this measure of reproductive success in gibbons and leaf monkeys, but the effects of habitat quality differed between the two taxa. Since they live in monogamous pairs, the reproductive success of both male and female gibbons was positively correlated with habitat quality (Fig. 9.3a). In contrast, among polygynous leaf monkeys, males’ reproductive success was higher in high quality habitats, while females’ reproductive success is unaffected by habitat quality (Fig. 9.3b). This result confirms that social systems can fundamentally alter the way in which ecology affects individuals.

In high quality habitats (i.e., those supporting high population densities), primates might be expected either to live in larger groups or occupy smaller territories, or both. At CPRS, group size is positively correlated with population density in both gibbons (Fig. 9.4a, $r^2=0.58$, $n=33$, $p<0.0001$) and leaf monkeys (Fig. 9.4b, $r^2=0.77$, $n=13$, $p<0.0001$). Because of limited sampling, particularly of groups in

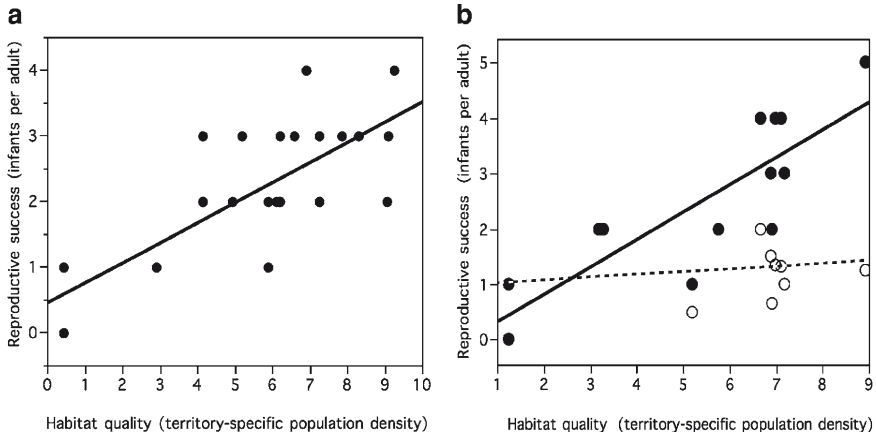


Fig. 9.3 An index of reproductive success (number of infants per adult) plotted vs. habitat quality (for groups whose entire territory was contained within one forest type this is equal to the habitat-specific density for that forest type; for groups whose territory spanned multiple forest types, this is the sum the habitat-specific density of all forest types occupied, scaled by the proportion of the territory in each, see text). Reproductive success of male and female gibbons is positively correlated with habitat quality (**a**; $r^2=0.58$, $p<0.0001$, $n=33$). Reproductive success for male (**b**; dots, solid line, $r^2=0.70$, $p=0.0004$, $n=13$) but not female leaf monkeys (**b**; circles, dashed line, $r^2=0.04$, $p=0.53$, $n=13$) is positively correlated with habitat quality

low quality habitats, the home range size of only a subset of groups was assessed. In this sample, a proxy of home range residuals (HRR) was unrelated to habitat quality for gibbons (Fig. 9.4c: $r^2=0.005$, $n=12$, $p=0.81$) or leaf monkeys (Fig. 9.4d: $r^2=0.004$, $n=10$, $p=0.86$). These results suggest that a given area of high quality habitat can support larger group sizes than the same area of low quality habitat, implying that feeding competition need not be positively correlated with group size. I return to this topic in the discussion below.

Animal taxa generally occupy a number of distinct habitats (Pulliam 1988), and understanding the effects of habitat quality on population growth rates has been a topic of considerable interest for animal ecologists for decades (Begon et al. 1996; Krebs 2001). The quality of a habitat influences the birth, death, immigration, and emigration rates of a population living there. In populations distributed across heterogeneous landscapes, a proportion of individuals can be found in habitats in which births exceed deaths and emigration exceeds immigration (i.e., they are demographic sources with the natural rate of population increase, $r > 0$; Pulliam 1996). In contrast, sink habitats, in which deaths exceed births and immigration exceeds emigration, have net negative population growth rates ($r < 0$; Pulliam 1988). In the absence of immigration from sources, populations in sink habitats will inevitably decline to extinction (Holt 1997). Although there are theoretical (e.g., Holt 1985; Watkinson and Sutherland 1995) and practical (e.g., Dias 1996; Doncaster et al. 1997) difficulties that complicate attempts to empirically demonstrate source-sink population dynamics in wild populations, there are mounting data

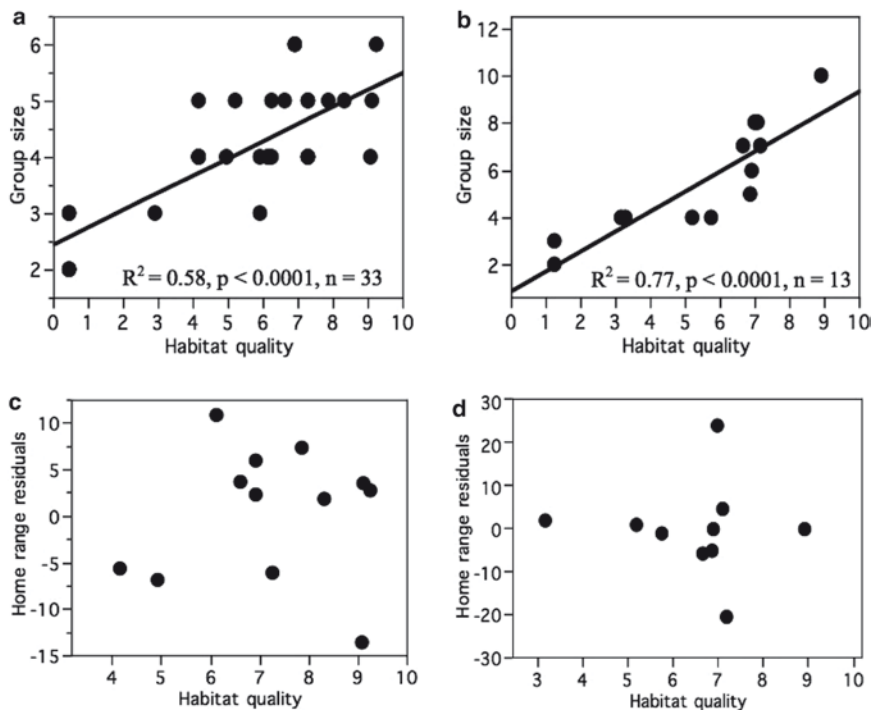


Fig. 9.4 Group size plotted against habitat quality (defined as in Fig. 9.3) for gibbons (a) and leaf monkeys (b). Habitat quality was unrelated to an index of home range size (HRR) for gibbons (c: $r^2=0.005, n=12, p=0.81$) or leaf monkeys (d: $r^2=0.004, n=10, p=0.86$). Statistics and regression lines on plots are provided for significant relationships only

(e.g., Kreuzer and Huntly 2003; others reviewed in Pulliam 1996 and Diffendorfer 1998) to suggest that these dynamics characterize at least some animal species. Since a wide range of mammalian taxa (including primates) exhibit substantially depressed population densities with increased altitude, determining whether montane forests might be demographic sinks at CPRS is particularly relevant.

Population density of both gibbons and leaf monkeys was negatively correlated with altitude (Fig. 9.5 a, b). At CPRS, the number of gibbon groups ($n=33$) was sufficiently large to produce a simple demographic model, which indicated that montane forests are likely to be demographic sinks for this species, and suggests that montane forests could not support gibbon populations in the absence of continued input of individuals from higher quality lowland forests (Fig. 9.5a; Marshall 2009). The more limited sample of leaf monkey groups ($n=13$) has precluded population modeling, but population density is clearly negatively related to altitude (Fig. 9.5b). This relationship is strongly significant when peat swamp forests (located in the lowlands but still of poor quality for leaf monkeys due to their very limited productivity) are removed from the analysis, and merely a statistical trend

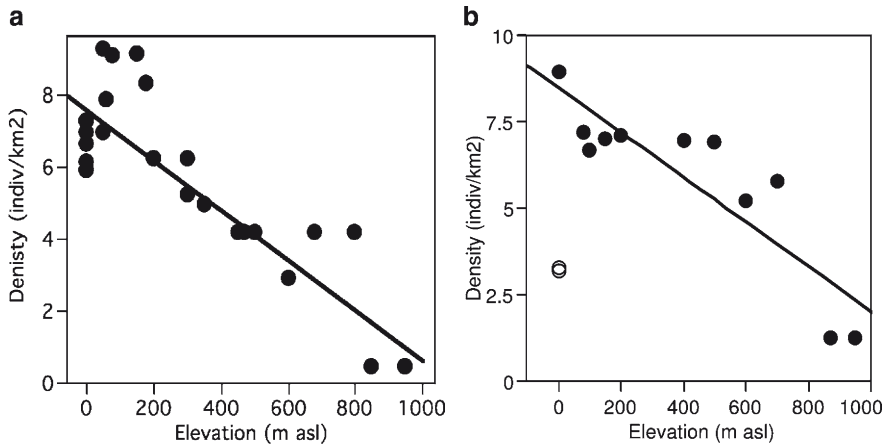


Fig. 9.5 Territory-specific population density (individuals/km², defined as the territory specific habitat-quality, as in Fig.9.3) of gibbons (a) and leaf monkeys (b) plotted against altitude (meters asl). Statistics: (a) $r^2=0.82$, $p<0.0001$, $n=33$, from Marshall 2009; (b) including two peat swamp groups (open circles): $r^2=0.29$, $p<0.06$, $n=13$; excluding peat swamp groups: $r^2=0.77$, $p<0.0004$, $n=11$. A simple demographic model using these cross-sectional data suggested that montane forests are sink habitat for gibbons (Marshall 2009); data are insufficient to estimate habitat-specific population growth rates for leaf monkeys

when the two peat swamp leaf monkey groups are retained. However, the implication of this result is similar to that found for gibbons: if lowland forests (most of which are of high quality for leaf monkeys) were destroyed, montane leaf monkey population densities might not be viable. These results have important conservation implications, which will be discussed at the end of the Discussion section.

Discussion

This chapter presents an overview of results that have emerged from studies of gibbons and leaf monkeys living in a range of distinct habitats. These results indicate that habitat quality (i.e., population density at carrying capacity) can vary substantially across forest types on relatively small spatial scales. These results also suggest that different classes of food resource (e.g., preferred and fallback foods) can have distinct effects on primate populations, that these effects may differ between primate taxa, and, therefore, that simple measures of food availability are inadequate to capture the ecological variation of most relevance to primates. Furthermore, habitat quality can have important implications for primate populations on the individual, group, and population level. For example, habitat quality can influence individual reproductive success, group size, and a population's probability of persistence. This suggests that observations and ecological inferences from one

habitat should be extrapolated to other habitats with caution, and that a full understanding of a primate species' behavior, group and demographic structure, and population dynamics requires study of the species across the full range of habitats that it occupies.

As discussed earlier, most primate field studies are conducted in relatively high quality habitats, for understandable reasons. Therefore, the biological and demographic characteristics, such as reproduction (e.g., weaning age, inter-birth interval), density and demographic composition, and disease burden, observed in these habitats probably represent "best case scenarios" for these groups and are not representative of the natural range of variation in these species. Moreover, these biases likely affect our understanding of social and behavioral traits of certain primate taxa as well. It is hypothesized that long-term differences in habitat quality have led to a divergence of ecological adaptations in closely related species (e.g., Bornean vs. Sumatran orangutans: Delgado and van Schaik 2000; van Schaik et al. 2009; chimpanzees vs. bonobos: Wrangham 1986), and it is likewise reasonable to view some of the variation between different populations of a given primate species (e.g., chimpanzees: Doran et al. 2002; savanna baboons: Kamilar 2006) as a result of variation in habitat quality. Aspects of social behavior that are often considered to be hallmarks of a primate species' biology (e.g., intensity of food competition, presence of female bonding, degree of polygyny, hunting behavior) turn out to be quite variable within that species under different ecological conditions (e.g., rates of inter-group conflict and violent competition in gorillas living at high vs. low density: Yamagiwa 1999; female bonds in captive vs. wild chimpanzees: Baker and Smuts 1994; degree of polygyny in leaf monkeys: this study; hunting frequency and success rates of Kanayawara vs. Ngogo chimpanzees: Mitani and Watts 1999). This suggests that an increased awareness of the influence of habitat quality may improve our understanding of how ecological parameters have influenced the course of primate evolution.

This discussion of the determinants of habitat-specific carrying capacity focused on differences in indices of food availability among forest types, and did not consider the potentially important role of variation in habitat-specific costs. The role of ecological costs in limiting primate population density has generally received less attention from primate ecologists than has the role of food availability (but see, e.g., Caldecott 1980; Chapman et al. 2002; Davies et al. 1988; Dunbar 1992a, b; Ganzhorn 1992; McKey 1978; Milton 1979). This is notable given the extensive attention that has been paid to the costs of primate grouping (e.g., due to feeding competition, infanticide, and disease; Isbell 1991; Janson and Goldsmith 1995; Nunn 2003; van Schaik 1983; van Schaik and Janson 2000; Wrangham 1980). In principle, habitat-specific costs might differ among forest types at CPRS for several reasons, including thermoregulatory costs associated with elevation (Caldecott 1980; Hill et al. 2000; Iwamoto and Dunbar 1983); locomotor costs associated with differences in canopy structure (Cannon and Leighton 1994; 1996; Kappeler 1984); or costs of interspecific competition from other frugivorous vertebrates (Gautier-Hion 1978; Marshall et al. 2009a; Poulson et al. 2002). Ongoing work at CPRS is incorporating explicit consideration of habitat-specific costs, and will clarify how habitat-specific costs and benefits interact to determine primate carrying capacity.

Much theoretical and empirical work in primatology seeks to elucidate the factors underlying gregariousness in primates, and to understand the forces that influence group size (e.g., Wrangham 1980; van Schaik 1983). Factors such as within-group scramble competition and infanticide are thought to limit group size (Janson and Goldsmith 1995; van Schaik and Janson 2000), while predation risk and between-group contest competition are thought to increase the benefits of grouping (Wrangham 1980; van Schaik 1983). Owing to the presumed importance of within group scramble feeding competition, female fitness is predicted to be lower in larger groups (e.g., Borries et al. 2008; van Noordwijk and van Schaik 1999). This prediction is based on the tacit assumption that some variable other than food availability limits group size, and that females in larger groups experience more intense feeding competition. An alternative hypothesis is that fitness is equalized across groups of different size within a population because females distribute themselves according to an ideal free distribution (Fretwell and Lucas 1969). This perspective does not imply that feeding competition is unimportant, it simply suggests that the influence of feeding competition primarily occurs at the level of determining group size (e.g., affecting female decisions about which groups to join). Results from CPRS support the hypothesis that female leaf monkey reproductive success is independent of habitat quality (Fig 9.3b) and group size ($n=13$, $R^2=0.03$, $p=0.52$, Boyko, Boyko, and Marshall, unpublished analysis), implying that increased competition in larger groups is offset by the absolutely greater amounts of food available in higher quality habitats. Some other studies of primarily folivorous primates have also shown no effect of group size on reproductive success (e.g., gorillas: Stokes et al. 2003; Robbins et al. 2007; Thomas' langurs: Steenbeek and van Schaik 2001) although such results are not universal (e.g., Borries et al. 2008; Snaith and Chapman 2008).

Future Directions

The sampling methods employed at CPRS provide an unusually extensive sample of primate groups across a wide range of ecological conditions. This approach has provided a unique perspective on landscape-level processes, but has done little to improve understanding of how habitat quality influences the behavior of gibbons and leaf monkeys. Examination of the influence of habitat quality on behavior may improve our understanding of the range of behavioral flexibility exhibited in these species. For instance, residence times in food patches are predicted to vary as a function of the distribution and abundance of resources in the environment (Charnov 1976; Grether et al. 1992; Schoener 1971), and should vary systematically among forest types at CPRS. Assessment of whether and how preferred and fallback foods for gibbons and leaf monkeys are depleted would elucidate how food type influences foraging behavior, and would contribute to the recent reexamination of the long-held assumptions about the lack of feeding competition in folivorous primates (Koenig 2000; Snaith and Chapman 2005; 2007). Behavioral data collected

across the mosaic of habitat types may also identify the proximate mechanisms that underlie some of the individual, group, and population effects reported here. For example, long-term monitoring of individual life histories (e.g., age at dispersal, offspring mortality, inter-birth intervals) would permit determination of which components of fitness are influenced by habitat quality. Finally, differences in rates of immigration and emigration among habitats would provide behavioral indications of source-sink population dynamics.

Understanding how habitat quality influences populations may improve our ability to protect and manage populations of threatened primate species in a number of ways. For example, if particular classes of foods are disproportionately important in limiting primate populations, special attention may be taken to spare these food resources during selective logging operations (Felton et al. 2003; Johns 1986; Leighton and Leighton 1983), and enrichment planting of these taxa may be used to raise the primate carrying capacity of degraded areas (Marshall et al. 2009b). Identifying and protecting habitats that are disproportionately used during periods of overall fruit scarcity also may be crucial for maintaining populations in heterogeneous landscapes (Cannon et al. 2007b; Curran and Leighton 2000; Furuichi et al. 2001; Johnson et al. 2005). In addition, understanding how species respond to natural variation in habitat quality may provide insight into their responses to future habitat alteration, through either human-induced habitat degradation or climate change (Marshall et al. 2006; Meijaard et al. 2008).

Explicit consideration of habitat-specific carrying capacity and an understanding of source-sink population dynamics suggest that higher elevation forests contribute relatively little to maintaining viable populations of some primate species (e.g., gibbons at CPRS, Marshall 2009; Bornean orangutans, Husson et al. 2009). Similarly, conservation plans that include population estimates based on remaining habitat area without regard to habitat quality will likely substantially overestimate the size of primate populations remaining in forest fragments, and lead to unrealistically optimistic estimates of their long term stability and viability (Chapman and Lambert 2000; Cowlshaw and Dunbar 2000; Marshall et al. 2009d). For example, the population densities of primates and other vertebrates may be extremely low in the large tracts of forest in Central Kalimantan (McConkey and Chivers 2004). Therefore, although these areas are attractive targets for conservation due to their high diversity and relatively limited disturbance, they may not support viable populations of threatened vertebrates unless the areas protected are very large (McConkey and Chivers 2004).

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