Ranging behavior and habitat use patterns of Hanuman langurs *(Semnopithecus entellus*)

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Abstract of the Thesis

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Availability and distribution of food, demography, or mating strategies may be important factors in determining the daily path length (DPL), and the size and evenness of an animal’s home range use. This study uses multi-year data from two Hanuman langur (*Semnopithecus entellus*) groups in Ramnagar, Nepal, to test the effect of behavioral (activity, diet, drinking), ecological (temperature, rainfall, phenology), and social variables (number of receptive female, intergroup encounters) on DPL (on both a daily and monthly scale), range size, and the evenness of use. Principle component analyses were performed to reduce activity, dietary, and ecological variables before performing stepwise multiple regressions for predictor variables. For both groups, ecological variables accounted for the greatest levels of variance in analysis of DPL, although the relative importance of different ecological variables depended on the timescale. In one group home range size was best predicted by ecology variables which predict smaller home range sizes during periods of high rainfall and mature leaf presence and larger home ranges with high temperatures and when young leaves and flowers were available. The number of receptive females accounted for the greatest levels of variation in the evenness of use within the range, with a more concentrated ranging pattern as the number of receptive females increases. In the second group both variation in range size and its use were best explained by an activity variable which predicts ranges to be larger when groups are inactive and feeding less. These results support the idea that ecological, behavioral, and social factors are all important in determining ranging behavior and should be considered simultaneously. In contrast to previous findings on folivores, fruits turned out to be less important predictors than leaves. Young leaves may have the same effect on DPL as fruits, because of a similar distribution, and this should be considered when making predictions for folivore ranging behavior.

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II. Chapter 2: Determinants of home range size and utilization in Hanuman langurs (*Semnopithecus entellus*)

Chapter 1: Effects of behavioral, social, and ecological factors on daily path length

Introduction

Ranging behavior and group movements reflect the amount of energy a group is expending and it should be expected that individuals will try to minimize their daily path length in relation to the benefits they accrue from travel (Charnov 1976). Such group movements are usually expressed as daily path length, DPL, defined as the distance that a group/ individual travels within a twenty-four hour period and have been measured in several ways (see Isbell et al. 1999). However, there is marked variation in the length that primates will travel -per day. The literature is replete with examples of both inter- and intra-species differences in ranging (Terborgh 1983; Bennett 1986; Barton et al. 1992; Bobadilla and Ferrari 2000; Singleton and van Schaik 2001; DiFiore 2003; Scholz and Kappeler 2004). Even groups within the same population may have varying ranging patterns in the same time period and show remarkable levels of plasticity (Bronkowski and Altmann 1996).

Explaining such variation in ranging behavior can be useful in understanding the connection between behavior and ecology important to both evolutionary ecologists and conservationists. Ecologists use this information while testing foraging and socioecological models. Conservationists can also incorporate knowledge of important influences on ranging to better manage populations. Ranging data is especially important in metapopulation analysis to understand rescue and source/sink effects (Caro 1999). This information is also used to conserve biodiversity in the creation of habitat corridors. Iindividual species ranging patterns affect whether or not it will use these corridors (Beier and Noss 1998). Habitat loss and fragmentation are the leading causes of extinction at the present time and a keen understanding of animals' habitat use and behavior in these fragmented forests would be useful in protecting animals in degraded habitat (Irwin 2008).

Ecological Factors

The decisions that animals make while foraging have long been known to be important in determining animal ranging behavior. Since MacArthur and Pianka (1966) first distinguished the difference between prey and patch their ideas have been used to develop several influential foraging models that examine the interplay between resource distribution, resource quality, and foraging decisions, which in turn affect ranging. Models by Charnov and Orians (1973; prey model) and Charnov (1976; patch model) outline two different scales at which rate maximizing foragers can optimize resource use.

The prey model predicts which food items (prey) will be taken when handling time and energetic content are considered in comparison to other prey. The basic question is whether to continue searching or start eating in the patch that is already found (Stephens and Krebs 1986). Decisions will be made relative to the abundance of other resources in the environment and their quality. The patch model focuses on decisions made within a patch of food that is already found. It deals with the question of how long it is economical to stay within a patch. If a patch contains finite resources then it can and will become depleted with continued feeding. Foragers that are maximizing their feeding rate will choose a different residence time in each patch and leave when the rate of energy intake equals that of the surrounding environment. Ranging behavior can be seen as the summation of these foraging decisions and is important in understanding how resource distribution and resource quality interrelate.

Historically most studies on ranging behavior have found a strong relationship between DPL and food characteristics (Clutton-Brock and Harvey 1977a; Raemaekers 1980; Isbell 1983; Bennett 1986; Garber 1993; Olupot et al 1997; Goldsmith 1999; Di Fiore 2003; Doran et al 2004; Buzzard 2006). Most, but not all, of these studies found animals to have significantly greater DPLs when high quality foods were patchily distributed. This supports the idea that animals expend more energy to feed on particular resources. Traditionally this idea has been applied to frugivores who feed on supposedly patchily distributed foods (i.e., fruits). The encounter rate for these patchy resources is relatively low and animals must travel long distances to obtain these high quality foods.

Application of foraging models has been less successful for folivorous primates. Predictions for folivorous primate ranging behavior are based on the idea that their major food source (leaves) occur in superabundant and slowly depleted patches with relatively uniform levels of nutrition (e.g. Wrangham 1980). This idea of folivore food distribution has been used as the link in predicting many aspects of folivore behavior (Koenig et al. 1998). Foragers using a rate maximizing strategy would not need to pursue any other patches if there was no resource depression (Charnov et al. 1976) within these ubiquitous patches. These abundant patches would also have a high encounter rate and distance between patches would be short. Folivores should exhibit shorter DPL and smaller home ranges because food resources are hyper-abundant throughout their range, rendering extensive ranging unnecessary.

While this has been found to be correct on the general level of home range size and DPL (Milton 1980; McKey and Waterman 1982; Sekulic 1982; Vedder 1984; Guryama 1986; Dunbar 1987; Meyers and Wright 1993; Watts 1991; Decker 1994; Fuentes 1996; Bravo and Sallenave 2003), more recent evidence has called into question the validity of assuming behaviors based on specific dietary categories while not considering varying ecological conditions and behavioral plasticity of species labeled “folivores” (Mitchell et al 1991; Barton et al. 1996; Koenig et al. 1998; Snaith and Chapman 2005). Longer DPLs during periods of higher food availability are seen in primarily folivorous primates which is contrary to expectations if animals are feeding in large, non-depletable patches (e.g. Ganas and Robbins 2005; Koenig 2002; Koenig et al. 1998). It has been argued (Snaith and Chapman 2005) that folivores do in fact deplete their feeding resources which is another pattern traditionally observed in frugivorous primates. The increase in DPL is expected if these folivores are feeding not only in depleteable resources but in patchy resources. Young leaves are higher in nutrients than mature leaves (Waterman and Kool 1994) and are distributed in patchy clumps throughout the environment. If young leaves are a significant enough benefit then groups should utilize this resource when available and DPL should increase. It has even been shown that individuals have incentive to contest for this high quality resource (Koenig et al. 1998) because of the phytochemical heterogeneity between mature and young leaves so they appear to be significant. If folivores are using patchy resources (young leaves) the encounter rate with food is lower and DPL should go up when exploiting such resources. When feeding behavior shifts and animals become more dependent upon abundant, low quality foods their behavior should also shift back to shorter DPLs.

Ambient temperature is another factor thought to affect animal ranging but has not been examined as intensely as diet and food distribution. It is important to remember that thermoregulation occurs at both high and low temperatures. Animals thermoregulate varying temperature both physiologically and behaviorally (Stelzner 1988; Bronkowski and Altmann 1996). Stelzner (1988) showed that even when temperatures were within the range of physiological tolerance animals still showed behavioral thermoregulation. The responses to thermoregulatory stress can range widely. Even closely related species can have rather different responses including staying longer and resting more in areas with high levels of shade (Stelzner 1988: yellow baboons) and using caves to thermoregulate during both hot and cold seasons (Barrett et al. 2004: chacma baboons). Many non-human primates habitually rest during the hottest parts of the day (reviewed in Clutton-Brock 1977) but those species in more temperate climates exhibit other behaviors that are associated with low ambient temperature including sun-bathing (Stelzner 1988), increased feeding (Bernstein, 1972, 1975, 1976), huddling (Ostner 2002), and postural changes (Stelzner and Hausfater 1986; Dasilva 1993; Takemoto 2004). At sites with large daily and seasonal fluctuations in temperature the responses needed could significantly affect ranging and distance traveled per day. It is predicted that travel should increase as temperature increases until a threshold is met when behavioral and physiological tolerances are exceeded. At this point travel will decrease.

Rainfall is another factor to affect group and individual movement patterns (Chivers 1967; Altmann and Altmann 1970; Raemaekers 1980; Goldsmith 1999). It has been shown that anthropoid primates tend to halt movement during periods of heavy rainfall and therefore daily path length on dry days exceeded that of wet days (Raemaekers 1980; Isbell 1983). This would indicate that on a daily scale rainfall would negatively affect DPL (Raemaekers 1980; Goldsmith 1999). However when examined at a longer scale rainfall often has a very different effect. High rainfall levels can correlate with increased food availability and longer DPL can be seen. This would confound the correlation between rainfall and DPL (Goldsmith 1999). Even though overall food encounter rates increase with rainfall, an increase in DPL would be expected only if high rainfall correlates with an increase in patchy resources. Therefore increased rainfall can be predicted to increase ranging behavior in animals exhibiting highly selective feeding behavior on patchily distributed resources but not in animals feeding on lower quality more ubiquitous resources.

One additional idea that has not received as much attention in connection with ranging behavior is the location of specifically used locations such as water holes or other strategically used places. Animals relying on key resources that are spatially dispersed should incur significant travel costs and show longer DPLs when these resources are used frequently (Doran et al. 2004). This can even lead to whole range shifts to accommodate specific locations (Scholz and Kappeler 2004). Animals might be constrained to revisit these sites for either water or nutritional benefits and must adjust their daily travel accordingly (Campos and Fedigan 2008). These sites can include water holes (Altmann and Altmann 1970; Scholz and Kappeler 2004; Campos and Fedigan 2008), swamps (Doran et al. 2004), areas of geophagy (Pages et al. 2005), and sleep sites (Newton 1992;

Dietz et al. 1997; Anderson 1998; Di Bitteti et al. 2000). To truly affect ranging patterns and DPL they should be discrete locations that occur rarely within a group's range.

Behavioral Factors Influencing DPL

Group size has long been thought to play an important role in the ranging behavior of primate groups (Clutton-Brock and Harvey 1977; Waser 1977; Janson and Goldsmith 1995; Chapman and Chapman 2000). The main ecological cost to grouping is reduced foraging efficiency because of intragroup feeding competition (e.g. Janson 1988; Terborgh and Janson 1986; Chapman and Chapman 2000a). Animals must range over an area that will support the group's energetic demands. With increasing group size, more area must be covered to find the adequate amount of food for all members (Terborgh 1983; Chapman 1990). It has been documented that foraging effort can set the upper limit for group size if the energetic costs become too great in frugivores (Janson and Goldsmith 1995) and longer DPL in larger groups of a population has been argued to be synonymous with higher levels of within group scramble competition (Isbell 1991; Gillespie and Chapman 2001). The ecological constraint model (Chapman and Chapman 2000b) makes the assumption that increased feeding competition will express itself as an increase in DPL until travel costs exceed energy gained from the environment. Increased competition from increasing group size should increase foraging effort only if food resources are depleteable (Chapman et al 1995). Folivores were traditionally thought to be immune to feeding competition because of the food resources that they utilize, even in large groups. There is however evidence that suggests scramble competition is present in folivores and is related to group size (Snaith and Chapman 2005). If variation in DPL is, at least partially, determined by increased feeding competition within depleteable patches then increasing group size should increase DPL.

Intergroup encounters have been thought to provoke longer group DPLs (Struhsaker 1975; Waser 1977; Stanford 1991a; Watts 1991). Trivers (1972) argued that males would defend females because male fitness is primarily a function of access to females. Group males are expected to not tolerate extra group males and herd females away from such males. This is expected especially in species with higher rates of infanticide or in those species with highly aggressive male takeovers (e.g. Sugiyama et al. 1965). Watts (1991) showed that ranging in mountain gorillas was significantly longer when there had been an encounter with extragroup male(s), supporting the idea that it is in the best reproductive interest of resident males to keep rivals away from their unweaned offspring and females. Struhsaker (1974) found that there was an increase in the travel distance and in home range use with increasing intergroup encounters in an African colobine. Recent evidence has shown that other factors play a role in determining the reaction of males to intergroup encounters. The location of the intergroup encounter can affect the outcome of an encounter and therefore the shift in DPL. Groups close to their core area will win intergroup encounters more often (Kitchen et al. 2004), even if smaller than the imposing group (Crofoot et al. 2008). Also the familiarity and the threat of an opponent should illicit different responses to by group males (Wich and Sterck 2007). Familiar foes or those of little threat will not cause large shifts in DPL. Participation in and results of an intergroup encounter can be dependent on the presence of dependent offspring in the group as well (Kitchen 2004). Males therefore should be most defensive during the mating season (Kitchen et al. 2004) and when unweaned offspring are present that would be killed if a takeover event occurs (Kitchen 2004). In general it is predicted that if groups have high levels of infanticide/ hostile takeovers then DPL should increase with increasing numbers of intergroup encounters. This should particularly be the case in the presence of receptive females and dependent offspring.

The number of receptive females is another variable that has not been traditionally tied to ranging behavior. It may skew the ranging behavior of the group because, with increasing numbers of receptive females, males may become more limiting and there is potential for non dominant males or extra group to copulate (Emlen and Oring 1977). This effect would be more intense in seasonal breeders because more than one female is receptive at a time. Also, females should be inclined to mate with extra group males if those matings will either increase paternity confusion or confer genetic benefits to their offspring, or both. It has already been shown in various species that females may have longer receptive periods to increase the number of sexual partners and increase paternity confusion in populations with multimale groups and seasonal breeding (Borries et al. 2001). Chimpanzees also drastically alter their ranging and association behavior during estrus periods (Wrangham and Smuts 1980). They may be employing other strategies to even further increase their fitness. Paul (2002) has argued that females have a more important role in mate choice than previously thought and if extra group copulations increase viability or lower the risk of infanticide than females may employ this strategy. Koenig (pers. comm.) noted that receptive females have been seen leading group movement towards the periphery of the range and to engage other groups in intergroup encounters in a Hanuman langur population. Females initiate 90% of group movements in capped langurs (Stanford 1992), so it seems reasonable that females in other, closely related, species might lead the groups toward an intergroup encounter, either for reproductive strategizing or between-group contests over food resources. These usually occur outside of the core area and would be expected to result in increased group DPLs (Bermejo 2004). I predict that the presence of receptive females could account for at least some variation in the DPL of these groups. There should also be a positive correlation between the presence of receptive females and the frequency of intergroup encounters. The prediction that receptive females would increase DPL contrasts with predictions for intergroup encounters. If males are keeping groups within the core area to avoid extra group males this could conflict with female strategies.

Activity budgets are another useful tool in understanding the connection between ranging and behavior. Activity budgets give an estimate of the relative importance of behaviors. It is expected that moving/traveling should positively influence DPL because the more travel the further the group should move. This does not necessarily correlate with DPL because it does not take the direction (individual movements even when group is not moving) or rate of travel into account. Other activity variables (inactive, feeding, and grooming) reflect the choices that individuals make in their energy budget, especially if they are balancing feeding optimally and conserving energy in a stressful environment (Dunbar 1992). The decisions incorporated within activity variables could manifest themselves when compared with DPL. This concept has been utilized when comparing behaviors across sites and seasons (Doran 1997; Fashing et al. 2007) with the importance of activity categories primarily dependent on the ecological conditions but the direction of the response (feeding optimally verses conserving energy) varying even between the same species (e.g. chimpanzees; Doran 1997 and Basabose 2005).

Here I explored the causes of variation of DPL in two groups of Hanuman langurs by examining the interaction of diet, temperature, rainfall, group size, intergroup encounters, specifically used locations, receptive females, phenology, and general activity with DPL.

Study Species

Hanuman langurs are a highly adaptable primate species that thrives in extremely diverse habitats. They range across the Indian subcontinent from the Himalayas to the island of Sri Lanka, and are studied at over 30 locations (see Koenig and Borries 2001). With a flexible social system and sacred status they live successfully in a wide variety of habitats, including those that have been heavily disturbed (Borries et al. 2001; Koenig and Borries 2001). While female Hanuman langurs are usually philopatric (but see Newton 1987 and Sterck 1998), males leave their natal group at adolescence and live in all male bands or solitarily until joining a bisexual group (Sugiyama 1965; Rajpurohit 1995) or stay in their natal group until dispersing directly into neighboring groups without a transition phase (Borries 2000; Koenig and Borries 2001). Males exhibit varying residence patterns including full time residency after natal dispersal, influxes during breeding seasons, and frequent transfer near the end of their reproductive lives (Borries 2000). Hanuman langurs are mainly considered folivores but they may heavily supplement their diet with fruit, seeds, flowers, and lianas (Stanford 1991b; Podzuweit 1994; Koenig and Borries 2001).

Hanuman langurs are well suited for examining questions concerning varying ecology because of their flexible social system which seem to reflect ecological condition (Borries et al. 2001; Koenig and Borries 2001) and because of their ability to thrive in varied environmental conditions. Groups size ranges from 11 to 64 members and the number of resident males ranges from 1-14 (Newton 1988; Moore 1984). Female feeding competition ranges from despotic dominance hierarchies (Hrdy and Hrdy 1976; Borries et al. 1991; Sterck 1998) to sites with no discernable dominance relationships amongst females (e.g. Jay 1965; P.N. Newton, unpublished work, cited in Newton and Dunbar 1994). Group compositions can vary spatially and temporally as well. Studies from 29 Hanuman langur study sites found that male composition ranges from 100% single male at certain sites to 100% multimale at others (Oppenheimer 1977; Bishop 1979; Koenig and Borries 2001). This phenomenon is thought to be a result of the differing ability of males to monopolize females between sites (Emlen and Oring 1977). Those sites where it is feasible to monopolize females one-male groups dominate and visa versa. Because of the documented plasticity of Hanuman langur social systems and high environmental adaptability of this species, they are ideal subjects in an attempt to understand environmental and social correlates of ranging behavior. Combining all of these ecological and behavioral variables is important in understanding their relative importance and what factors are shaping primate behavior.

Goals

For this study I explore a select number of proximate ecological and social factors that are expected to influence variation in DPLs for two groups of Hanuman langurs at Ramnagar, Nepal. I will investigate how animal diet, ambient temperature, rainfall, phenology and specifically used locations (ecological factors) along with groups size, intergroup encounters, number of receptive females, and activity patterns (social factors) contribute to ranging behavior at a monthly scale. Another analysis has been completed on the daily scale (for which no feeding, activity data or phenological data is available). There I will account for variation in leaf and fruit phenology, food availability, climate, and other factors that vary within the different seasons, by breaking up the year into two sections, the dry season and the wet season. The predictions for daily variables can be seen in Table 1 and for monthly variables in Table 2.

Materials and Methods

Study site and langur population

All data were collected at a study site located close to the village of Ramnagar located (latitude 27°44’N, longitude 84°27’E; 300 m asl) between July 1991 and April 1996 for P group and between January 1994 and April 1996 for O group. Ramnagar is located near the feet of the Siwalik Hills of southern Nepal (Podzuweit 1994). The study site encompassed roughly 12 km² and there were at least 290 individual Hanuman langurs present at the site in 19 bisexual groups. All were known individually and could be reliably identified. Groups compositions averaged 1-6 (mean= 2.6) adult males and 1-15 (mean= 6.7) adults females (Koenig et al 1997). Group compositions varied over time. Seventy-six and a half percent of groups are multimale multifemale, while the remaining 23.5% of groups are single male multifemale (Koenig et al 1997).

The semi-evergreen monsoon forest around Ramnagar consisted of 125 tree and climber species, with 105 of these identified at the genus level (Wesche 1995). The forest is dominated by Sal trees (*Shorea robusta*, Diperocarpaceae) and contains 4 forest types: Sal-forest (two types), Tropical Deciduous Riverine Forest, and East Nepal Tropical Evergreen Forest (Wesche 1997; forest types in Stainton 1972).

Data were obtained from 2 different groups, groups O and P. Group P contained 15.4 individuals and O group contained 22.5 individuals on average with some variation across the study period (P= 13-20; O= 21-25). All group members were recognized as individuals and were fully habituated to human observation. Group P’s range bordered the village of Ramnagar on the south-west side with a road running along the western edge of the range (see Figure 1). Groups from the east side of the road were rarely seen crossing over into P group’s home range (C. Borries, personal communication). Group O also bordered the village but interacted with several more groups throughout the year. This fact could have an effect on the intergroup encounter rate for the two groups.

The langurs of Ramnagar lived in a seasonal environment, but because of a high degree of home range overlap, there was less variation in resource availability than might be expected between-groups during a given period. Total range overlap between the two groups throughout the entire study period was 48.8% for group P and 44.3% for group O. In the dry season the monkeys rely mainly on mature leaves and in the wet season they have a much wider breadth in diet (Podzuweit 1994; Koenig et al. 1997). Figure 2 shows how dietary breadth varies between seasons.

Climate at Ramnagar

Data on climate were continuously recorded by a thermohygrographic instrument between July 1991 and May 1996. Temperature was analyzed every second hour for each day, and average, maximum, and minimum temperatures were calculated. Precipitation was recorded using a commercial rain gauge.

For the daily analysis the climate was broken up into wet and dry seasons. The wet monsoon season, which is classified as humid or perhumid, lasts from May through October (see e.g., Koenig et al. 1997). For example in 1994 2345 mm rain fell during this season and the average temperature during was 27.47° C, ranging from 42.5°-15.0° C. The dry season starts in November and lasts until April. During this period there is little precipitation (114 mm) and temperatures dropped down to an average of 19.1° C in 1994.

There is also considerably more variation in the temperature during the dry months (42.0°-5.5° C). Figure 3 shows the variation in the climate at Ramnagar with the temperature on the left y axis and the recorded rainfall on the right y axis.

Intergroup Encounters

Intergroup encounters were defined as instances when the focal group came within visual contact of another bisexual group or solitary individual(s) and the group perceived that the animal neared. This did not include those situations in which only vocalizations were heard and the extra party was not visually identified. Encounters were coded for each day as follows in what can be assumed as increasing threat level for a takeover event: 0) no intergroup interactions the entire day, 1) meetings with lone adult or subadult males (single male of all-male band), 2) meetings with another bisexual group, 3) meeting with another bisexual group and an adult male on the same day or meeting two groups in the same day. Data were collected whenever encounters occurred. Because group usually reacted noticeably to the presence of conspecifics, data collection represents all-occurrence sampling (Martin and Bateson 1993).

Drinking behavior

During all seasons the study groups were seen traveling to several open ponds spread across the home ranges of group P and O. During the height of the dry season most of these ponds dry up with the exception of one. This pond is located at the southeastern tip (group P) or the eastern border (group O) of the home ranges. For all days on which a trip to a water hole was observed the day was recorded as containing drinking as a 1-0 variable (presence vs. absence). This value is separate from the drinking variable within the diet because this value comes from only drinking at these semi-permanent or permanent ponds.

Number of Receptive Females

The number of receptive females used in the analysis was based primarily on the number of females that were mating (Beach 1976). A receptive period was defined as sexual behavior on consecutive days not interrupted by more than 2 days following Sommer et al. (1992). Females were considered in a receptive period for a single day if it was accompanied by copulations. In addition, females that solicited matings but were not actually in estrus were included in the analysis. Solicitation usually consisted of the females presenting their anogential region to the male and then shaking their head side to side vigorously (Sommer et al. 1992; Borries et al. 2001). In the analysis this variable is labeled #RAF (number of receptive adult females).

Activity

Activity was recorded by instantaneous focal animal sampling (Martin and Bateson 1993) for one hour or 30 minute periods (30 s or 1 min intervals) including all adult males, all adult females or both (P= 36 months; O= 16 months). Scores were averaged over each month for each group. Categories included feeding, moving, social, and inactive. These scores were then used to create percentages for the 4 categories for each month. All values were arcsin transformed before analysis.

Diet

Diet was recorded by instantaneous focal animal sampling (Martin and Bateson 1993) for one hour or 30 minute periods (30 s or 1 min intervals) including all adult males, all adult females or both (P= 36 months; O= 16 months). Diet categories included young leaves (plus leaf buds), mature (and old) leaves, flowers (including flower buds), fruits (unripe and ripe), insects, geophagy and stone licking, and other (including for example bark, pith etc.). Scores were used to create percentages for each diet category. All scores were arcsin transformed before analysis.

Phenology

Phenological data was collected between July 92 and April 96 at the midpoint of each month. Individual phytophases were sampled from 307-317 known Hanuman langur foods by the crown density method (Koelmeyer 1959) on a 4 fold scale (from 0 = none to 3 = many). For the purposes of this analysis, data was transferred to a 1-0 scale where any data point 1-3 was recoded as 1. From this recoded data a percentage of plants exhibiting a given phytophase were calculated per month. Values were then arcsin transformed before analysis.

Daily Path Length

To record ranging behavior a grid system covering 370 hectares with grid cells at 0.4 hectares had been established in the forest (Koenig et al. 1997). Three groups were present within the grid system and data on two of those are represented here. The grid system can be seen in Figure 1 with groups labeled at the center of their home range. The location of each group was recorded via 30 minute scan samples (Martin and Bateson 1993) throughout the day. Every quadrant that contained a group member was counted as occupied at the interval. Later the geometric means of the quadrants was found of each sample point and the distance between each successive point was calculated. This distance was found using the Pythagorean Theorem where the distance between two points is:

$$\text{distance} = \text{square root } [(x1-x2)^2 + (y1-y2)^2]$$

Daily path length was then calculated as the sum of all the 30 min samples for a given day. A visual representation of this can be seen in Figure 4.

In cases where groups were not found after they had left their sleeping place the straight line distance between the sleeping site and the first measure for that day was calculated and added to the daily path length of that day. Only those days for which there was a complete sample for the entire day were included in this analysis. In addition, only those days were included when the group had been followed the previous day (i.e., the sleeping site was known). Group O was followed for 722 days and group P for 1028 days with a range of 5-31 days per month over the study period. On average 23.8 and 22.9 scans were performed per day for groups O and P respectively. All values were log transformed before analysis.

Statistical Analysis

In order to find the best predictors for DPL I performed a multiple stepwise regression analysis (Tabachnick and Fidell 2001). This analysis is used to find predictive variables that account for variation in a dependent variable. Independent variables that are most important to ranging behavior should have high predictive power on DPL. In the analysis DPL was the dependent variable and temperature, rainfall, use of specific locations (drinking), group size, IGE, and number of receptive females as the independent variables for daily measures. This analysis was run for all days for each group and then all days during the dry and wet seasons. This separate analysis was conducted because of the ecological conditions that could not be controlled for on the daily level. Specifically the phenology of the site was vastly different between seasons and this variation was not addressed by any variables available on the daily scale.

On the monthly scale the same analysis was run with averages of all daily scores. However, diet categories (young and mature leaves) or activity data (feeding versus inactive) are highly correlated as are some of the ecological variables (e.g., rainfall and young leaves). Thus, instead of selecting few variables that were uncorrelated, I conducted three Principle Component Analyses (Quinn and Keough 2002) to reduce diet categories, activity categories, and ecological [temperature (mean, max, and min), rainfall, and phenology] variables to uncorrelated factors. Factors with an Eigenvalue above 1 were included in the analysis except when noted. Subsequently I performed a stepwise multiple regression analysis (Tabachnick and Fidell 2001) with DPL as the dependent variable and diet factors, activity factors, ecological factors and averages for daily scores of use of specific locations (drinking), group size, IGE, and number of receptive females as the independent variables.

Statistical analyses were completed using SPSS version 13.0.

Results

Daily Path Length – Daily Values Analysis

All seasons

Over the entire observation period (P: N=949; O: N=719) the daily path length for both groups was less than one kilometer on average with high levels of variation as reflected in the standard deviation (P=883.0±441.0m; O:746.3±333.7m) (Table 3). All descriptive statistics are given in Table 3 and many variables had significant differences between each group. Valid N is the number of days when all variables were available for use in the analysis. DPL was significantly longer in P group (p<.001, two tailed T-test) while O group was significantly larger (p<.001, two tailed T-test), drank more often (p<.001, two tailed T-test), and had more receptive females (p<.001, two tailed T-test). The average scores for intergroup encounters, however, showed no significant difference between groups (p=.489, two tailed T-test). Pearson correlations are given in Table 4 and the highest correlation for both groups is between temperature and DPL (r_P=0.467; r_O=0.489). While many others pairs are significantly correlated, no other correlation between any two variables is above 0.267 in either group so there is little correlation between any of the independent variables within the regression analysis.

The first multiple regression analysis was performed on all the daily values in the sample. Analysis of these variables showed that temperature accounted for the most variation in DPL for each group (P=21.8%; O=23.9%) as seen in Table 5 and Table 6. For P group significant amounts of variation were also accounted for by the number of receptive females (3.1%), rainfall (2.4%), and drinking (1.3%). O group had five factors that were significant including group size (4.7%), drinking (2.9%), number of receptive females (1.2%), and intergroup encounters (0.8%). The total amount of variation accounted for in each group was 28.6% in P and 33.5% in O. Because of the low levels of variance explained within the all days analysis the year was broken up into the wet and dry seasons and those smaller data sets subjected to the same analysis.

Wet Months

Analysis of wet months showed longer DPL on average with lower levels of variation for both groups (P=900.9±391.6m; O=773.4±314.9m; Table 7). Both average temperature and rainfall were higher than the average for the dry season, as was expected. Table 8 shows the Pearson correlations and again mean temperature has the highest correlation for both groups (r_P=0.336; r_O=0.298). Within P group no other variable reached a correlation coefficient over or below r=±0.157 but O had several variables that were close to mean temperature (DPL/Drink= 0.234; Gr Size/Drink= 0.267; Rainfall/Drink= -0.250; Rainfall/Temp= -0.208). All of these correlations were highly significant with p<0.001.

Data from wet months was also subjected to a multiple regression analysis and results are shown in Table 9 and Table 10. Temperature was again the greatest factor for both groups (P=11.3%; O=8.9%). No other factor was found to be significant for both groups or accounted for over 3.6% of the variation. Total variance explained was the lowest of the three daily analyses at 14.1(P) and 13.6% (O).

Dry Months

Dry month analysis showed greater variation in DPL than the wet season. Table 11 of descriptive statistics shows that the mean DPL is shorter but standard variation is higher (P= 866.3±482.4m; O=722.3±348.3m). Rainfall (P=0.65mm; O=0.84mm), temperature (P=19.27°C; O= 19.50°C), and the number of receptive females (P=0.467; O=0.489) was also lower than in the wet months. Pearson correlations (Table 12) showed the same trend of mean temperature and DPL having the highest correlation (r_P =0.686; r_O =0.680, for both p<0.001). Each group had several other dependent variables with correlations over or under r=±0.200 [(P: Gr Size/#RAF=0.220; IGE/Temp.=0.299; Temp/Drink=0.240)(O: IGE/Temp.=0.223)]. All of these correlations were highly significant with p<0.001.

Regression analysis of dry month data again showed that temperature was the single most important factor at the daily scale (Table 13 & 14), temperature accounts for the greater amounts of variation (P=47.1%; O=46.3%) during the dry season than either the wet season or the all days analysis. In both groups the occurrence of drinking was the second greatest influence on DPL (P=5.3%; O=2.6%). Group O also has two other variables that yielded significant results in the regression. Group size (4.3%) and intergroup encounters (0.5%) were only significant in O group. None of these other variables accounted for over 5.3% of the variation and temperature was the overwhelming factor in the analysis. Total variance explained during the dry season was also the highest of all the daily analyses. In group P 49.6% and in group O 56.3% of the variation in DPL was accounted for.

Principal Component Analysis of Activity, Diet, and Ecology

Activity

All 4 activity variables were analyzed (see Table 15) and in both groups, P and O, there were two components with Eigen values over or close to 1. In group P the second component was slightly under 1 but included. Total variance accounted for in P and O was 82.97% and 85.15% respectively. Table 16 shows the component matrix and both groups have similar but not identical trends in component 1. The highest loadings were for inactivity (P=-0.977; O=0.940) and feeding (P=0.914; O=-0.945) for both groups followed by moderate scores for grooming (P=0.699; O=0.566). Inactivity and feeding have very similar values but have opposite signs for the two groups. Component 1 mainly represents the feeding and inactivity variation but also has a grooming affect. Component 2 has a high positive loading for moving (P=0.974; O=0.872) in groups P and O with all other variables being less important. Component 2 appears to represent most of the variation in moving but little else.

Plotting these components gives a better idea of how these variables interact. Figure 5 shows that there are discrepancies between the two groups in activity patterns. Group P shows high levels of moving and moderate to high levels of feeding during most of the dry months (Dec-Feb) but more grooming, feeding and inactivity during most of the wet months. In group O most of the dry months are also characterized by moving and feeding (and grooming) but the wet summer months by inactivity.

Diet

Combining the diet variables in a PCA was less successful than the activity and accounted for 77.35% and 62.38% of the variation in groups P and O respectively (Table

17). Group P had 4 components that fell above an Eigen value of 1 and Group O had 2. Inspecting the loadings of the components the first two are very similar. Table 18 contains the loadings for the diet PCA and shows that both groups have a high negative value for mature leaves (P=-0.882; O=-0.826) and high positive values for young leaves (P=0.671; O=0.755) and fruits (P=0.592; O=0.657). There is less consensus on the other values except for the fact that the variable "Other" is highly negative (P=-0.698; O=-0.806). Component 1 represents differences in feeding patterns on mature leaves, other items, young leaves, and to a lesser extent fruits. In component 2 fruit has relatively large negative loadings (P=-0.690; O= -0.492) while flower (P=0.488; O=0.747) and geophagy (P=0.772; O=0.657) are both positive. Drinking has a large positive loading in group O (0.722) but a smaller and negative one in group P. Component 2 appears to be accounting for the influences of 3 variables: fruit, flower, and geophagy. The final two components for group P have reduced significance and account for the least amount of variation. Component 3 has its highest positive loading for insects (0.768) and highest negative for drinking (-0.670). Component 4 does not have loadings as high as in other components but has similar levels for flowers, insects and drinking.

When components 1 and 2 are plotted against each other (Figure 6) the dry winter months (Jan and Feb) are grouped to the far left of the component 1 axis (x axis), late spring group at the right of component 1 and along the range of component 2. March appears to be heavily influenced by geophagy and lies between the winter and late spring. For the rest of the year (Jun-Dec) there is less clarity but in both groups these months cluster towards mature leaves in component 2 and somewhere between mature and young leaves on component 1.

Ecology

A PCA of the ecological variables [temperature (mean, max, and min), rainfall, and phenology] resulted in high levels of variation accounted for within those variables. Of the three PCAs this contained the highest cumulative percentage with 85.38% (P) and 87.81% (O) (Table 19). This analysis also had the highest Eigenvalues (near or above 5.0 for the first component; see Table 19). The component matrix (Table 20) was the most similar between the two groups, as would be expected, because the variables contained identical data for those days when both groups were followed. The three measures of temperature (P and O=0.929-0.980) and young leaf availability (P=0.950; O=0.955) had highest positive loadings. Other midrange positive factors included the availability of fruit (P=0.660; O=0.609), flower (P=0.615; O=0.584), and rainfall ((P=0.573; O=0.567). The lone negative loading was for the presence of mature leaves (P=-0.409; O=-0.498). This axis is mainly comprised a continuum between mature leaves on one side and young leaves and temperature on the other with several other phenology variables and rainfall in the middle. Component 2 is quite different in that mature leaves has the highest positive loading (P=0.822; O=0.826) followed by rainfall (P=0.720; O=0.745). The main negative loadings come from flowers (P=-0.612; O=-0.674) and fruits (P=-0.347; O=-0.471). Component 2 is comprised of periods with high levels of mature leaves and rainfall along with low flowering and fruiting.

The interaction of these two components is seen in Figure 7. As can be seen in Figure 6 for both groups the dry winter months (Nov and Feb) are clustered negatively on the x axis which corresponds to high levels of mature leaves and lower temperatures.

March and April grouped together with high levels of new leaves and flowers and the warmer months (May-Oct) had both mature and young leaves along with a heavy influence of temperature. This general pattern was seen in the diet components but with less clarity.

Daily Path Length – Monthly Values Analysis

After performing PCAs on the previously 3 sets of data, a multiple regression analysis was performed on those variables plus group size, IGE, drinking, and the number of receptive females. Descriptive statistics were very similar to the all days analysis and is not included here. Pearson correlations given in Table 21 and Table 22 show that several variables have correlation coefficients that are greater than or below r=±0.300 in both groups and are underlined. DPL is significantly correlated with two variables (Diet 1 and Ecology 1) in both groups. It should be noted that Diet 1 and Ecology 1 (P=0.734; O=0.850) and Diet 2 and Ecology 2 (P=-0.572; O=-0.579) are both highly and significantly correlated in both groups. The number of receptive females was also significantly correlated with intergroup encounters and Ecology 2 in both groups as well.

Final multiple regression analysis revealed similar results between groups P and O and results are shown in Table 23 and Table 24. Ecology component 1 (mature leaves to young leaves-temperature) accounted for the greatest amount of variation in DPL (P=65.7%; O=59.7%) for both groups, i.e., with higher temperature and more young leaves available DPL is longer while with low temperatures and many mature leaves DPL is shorter. The second factor in the analysis, however, was different. In group P the second ecological component (flower-fruit to rainfall-mature leaves) is also significant and accounts for 15.4% of the variation, i.e., with more rain and many mature leaves available DPL is shorter with many flowers and fruits available it is longer. In group O the second factor affecting DPL is group size (12.6%), i.e., DPL increased with the number of group members. This analysis which included measures of diet, activity, and ecology accounted for variation in DPL better than on the daily scale. Total variance explained was 81.2% for group P and 72.3% for group O.

Discussion

Ecological Variables

Ecological variables were the best predictors of DPL in every analysis performed. Temperature dominated the daily scale analysis during both the wet and dry season. But results for the dry season showed substantially greater predictive power. This is probably due to the fact that, during the dry season, temperature fluctuation was much greater than during the wet. Dry season temperature ranged from 5.5 – 42°C and during the wet season the largest variation was from 15.0 – 42.5°C. This wide range in temperature during the dry season and the corresponding increase in explanatory power suggest that low temperatures have great influence on movement patterns. It remains unclear whether the upper threshold of temperature stress was reached during warmer periods and associated thermoregulatory behavior was displayed. It has been shown that ambient temperature has an effect on a wide range of behaviors (Bernstein, 1972, 1975, 1976; Stelzner and Hausfater 1986; Stelzner 1988; Dasilva 1993; Ostner 2002; Takemoto 2004) and correlation coefficients (Table 4, 8, 12) show DPL and temperature being positively correlated, supporting my prediction. Temperature for the monthly analysis was one of the largest contributors to the ecological component 1 that accounted for the most variation for both groups. It was highly loaded for all 3 measures of temperature (Table 20) and positively correlated with DPL in the regression. These results support the prediction that variation in temperature can be considered an important factor in determining DPL in this population of Hanuman langurs. More generally, temperature should have a great influence on species that occupy more seasonal ecosystems that experience a larger range of temperature variation.

Rainfall was a significant factor in several analyses (Table 5 and 9) but never accounted for over 3.9% of variation in DPL and was negatively correlated with DPL in 5 of 6 daily measures. On the daily scale it may be negatively correlated as expected but without high levels of predictive power. One limitation of this analysis, however, is that it does not account for the time of day that the rain occurred. If heavy rainfall occurs during the late evening or night it could not be reflected in the DPL of that day. In the monthly analysis rainfall is the smallest positive factor in the first ecological component but has a higher loading in ecology 2. Rainfall is important in each component but does not have the highest loading in either. In analysis of both monthly and daily measures of rainfall it appears, however, that rainfall is only moderately influential on Hanuman langurs at Ramnagar.

Another ecological factor was the use of specific locations within the environment which included areas of geophagy and water hole locations. In the daily analysis the use of specific and discrete locations (waterholes) had a significant effect during the dry season when few places have open water. This is consistent with past research which has shown a reliance on permanent access to water across primate taxa (Altmann and Altmann 1970; Scholz and Kappeler 2004; Campos and Fedigan 2008) when living in a seasonal environment. Geophagy was part of the diet variables and not considered in the daily analysis. The monthly analysis does not show an effect of either drinking or geophagy but that does not mean that during specific periods animals rely on these resources and it has an effect on DPL. Taking monthly averages could have reduced the variance in DPL and masked the effect of days when animals relied on these resources.

Further analysis of days when geophagy occurred could reveal a connection between geophagy and ranging behavior.

The phenology of the forest was the last ecological variable to be considered here. Available only on the monthly scale, phenology had a highly significant effect on langur DPL (Tables 23 and 24). Variation in phenology, even when measured in strict presence absence, had (with temperature) the greatest loadings in the two ecological components which were the best predictors of DPL in the monthly analysis. The availability of certain phytophases (young leaves and mature leaves) have the greatest loadings and are the main components of phenology driving DPL. Ecology 1 is positively correlated with DPL and has high positive loadings for young leaves and negative loadings for mature leaves. Conversely, ecology 2 is negatively correlated with DPL and has strong positive loadings for mature leaves. The availability of a high quality food, young leaves, is increasing DPL which is expected if the animals are foraging optimally. The presence of mature leaves corresponded with a decrease in group movement, which is predicted. This, however, does not mean that the presence of mature leaves necessarily decreases DPL because mature leaves are present in high percentages throughout the year even when other high quality foods are abundant. During these periods it would be expected that langurs would switch to a higher quality food.

Behavioral Variables

Group size should be an influential force in determining day range if higher numbers of individuals decreases foraging efficiency. Correspondingly, an increase in DPL with increasing group size would suggest greater levels of scramble competition. While this has been shown repeatedly in frugivorous primates (e.g., Janson & Goldsmith 1995), results for folivorous primates are equivocal (e.g., Snaith & Chapman 2007). In this study group size did not predict high levels of variation in DPL for both groups but was significant in group O in several analyses. In the monthly analysis it was the second best predictor and accounted for 12.6% of the variation. Group O was the larger of the two groups (Table 3) and therefore would be expected to experience the greatest stress due to feeding competition. Conversely, group P had fewer individuals but a wider range in group membership (P=13-20; O= 21-25). It would be expected that groups with more variable group size would also present higher levels of variation in DPL. Also the only regression in which group size did not have a significant effect is during the wet season (Table 10) which also has greater food abundance. Perhaps larger groups do experience reduced foraging efficiency with increasing group size but only during periods of low food availability and beyond a certain number of group members. This would suggest that there may be a threshold level where group size begins to act on ranging behavior in this population but only manifests itself during periods of lower food availability. This idea is consistent with theoretical predictions on the effects of scramble competition with group size (see e.g., Sterck et al. 1997).

Intergroup encounters can be an important factor in determining DPL (Strusaker 1975; Stanford 1991a; Watts 1991). In species exhibiting hostile male takeovers, especially those with high levels of infanticide, both males and females should avoid other groups and extra group males. Males are defending their access to females and (along with females) preventing infanticide of dependent offspring. While evidence for an effect of intergroup encounters was seen in an African colobine (Strusaker 1974) there is little support for this hypothesis in the Hanuman langurs at Ramnagar. Intergroup encounters were only significant in one group (O) and accounted for 1.2% of variation during the wet season which is also the mating season. With high levels of home range overlap (P= 48.77%; O= 44.30%: between these 2 groups) surrounding groups are likely quite familiar with each other. With such high levels of overlap there is probably little core area that is not shared with one of the 11 surrounding groups. Therefore intergroup encounters are highly likely and appreciable shifts in DPL to accompany these would incur significant costs. If males base their reaction to an encounter based on the familiarity and threat of an opponent then this may negate the need for groups to lengthen DPL substantially because of intergroup encounters. If they are meeting familiar groups there may be no need to change ranging patterns because other bisexual group males are not a threat to take over the group. The lack of stable all male bands at Ramnagar (Borries 2000) may contribute to encounters accounting for less variation than expected because risk of takeover is lower with males that are members of another group than younger males which have left their natal group but not entered a bisexual group (Robbins and Sawyer 2007; Wich and Sterck 2004). Group males may make decisions dependent on the composition of groups in an encounter. Groups with many young males may be avoided. One factor not included in this analysis is the group or individual that "wins" the encounter. When encounters do result in a change in ranging, only one group may be affected. Data to test this is not available and may have rendered more significant results.

Receptive females did not account for much variation in DPL in any analysis. The greatest value was in the all days regression of P group (Table 5) and no value was greater than 3.1%. It was expected that this would be most obvious during the wet season when most mating occurs but the number of receptive females was only significant in P group at low levels (Table 9) during the wet season. In all analyses, the number of receptive adult females was negatively correlated with DPL which contradicts the prediction. There are high levels of range overlap in this population, however, and the availability of extra group males may not lead to significant increases in travel. Overall it is unclear whether female mate choice has any affect on DPL, further research on group association patterns and female mate choice of extra group males seems to be necessary.

No dietary variable was significant in either group but Diet 1 was strongly correlated with DPL (Table 21 and Table 22: P=.669; O=.763). There are also strong correlations between the dietary variables and the ecological variables. The phenology of a given period seems to be driving the feeding behavior recorded. The feeding behavior exhibited is contingent on the availability of certain food types and all major diet variables (ML, YL, Fruit, Flower) were positively correlated with the average phonological score (Table 25). This does not, however, show dietary preference, because it does not show that individuals were choosing food types out of proportion to their availability. Thus, while measuring diet is important for understanding many areas of primate behavioral ecology, in this analysis DPL was better predicted by the availability of food resources, not only the feeding behavior observed.

Applicability of model on daily scale

Analysis of DPL on the daily scale did not explain high levels of variance and results were inconsistent between the two groups. The one exception was temperature the single greatest significant factor for both groups. With no control for food preference or availability the combination of all days in the year leads to results with little clarity and many variables that account for little variance. It appears that an analysis of these variables is ineffective in exploring questions of DPL on this scale without some measure of diet and food availability. Such measures seem to be necessary due to the strong seasonality of Ramnagar with distinct wet and dry seasons and corresponding changes in other ecological factors. Seasonality has been shown to influence primate activity and feeding behavior and cannot be overlooked in affecting DPL.

When data was broken up into seasons it yielded different results. During the wet season, which also coincides with high levels of resource availability, analysis of daily DPL actually accounted for less variation than when using all days (P=14.1%; O=13.6%). Results during the wet season appear to be confounded by the breadth of resources available to the langurs in this seasonal environment. Figure 7 shows the monthly diet of group P in 1993 and shows that during the wet season (May-October) langur feeding habits shift to a wider range of foods. If animals are foraging optimally they will focus foraging effort on high quality foods when they are available if the benefits outweigh the costs of increased travel. Groups P and O both traveled further during this period on average than during the dry season. If food availability and diet are the greatest influences on travel decisions during these periods then DPL would be affected by variables not measured on this scale and analysis lacks the capacity to predict important factors.

Dry season results show the highest levels of total R^2 values for the daily analysis at around 50% of the variation. There are several possible reasons why this trend is seen. The availability of water has historically been shown to be critically important to group movement (Altmann and Altmann 1970; Scholz and Kappeler 2004). Although water hole visits were significant, temperature was again the best predictor. With greater variation during the dry season (5.5 - 42°C) than the wet (15.0°C to 42.5°C) it may be that lower temperatures are truly influencing group travel more than high and temperatures. Or temperatures never reached a point where behavioral thermoregulation was not sufficient enough to deal with thermoregulatory stress. This period of the year is also characterized by lower food availability and animals are reliant on mature leaves for much of their diet (up to 80.85%). During these periods when feeding on mature leaves the influence of feeding behavior on DPL is relaxed. Travel decisions are then made based on ecological variables, more specifically, temperature. This model can be effective at the daily scale but special care must be exerted to ensure that all ecological variables are accounted for.

Applicability of model on Monthly Scale

Monthly analysis which included data on diet and phenology produced much greater predictive power. But even when diet, activity, and phenology are added to the analysis the results show that the ecology of the area is having the greatest effect on primate ranging. In both the daily and monthly analyses ecological variables account for the most variation. However when temperature is combined with rainfall and phenology it gives two overall scores for the ecology of the area. Ecology 1, which has the highest loadings for temperature and young leaves and the lowest loading for mature leaves, accounts for 65.7% and 59.7% of the variation in DPL in groups P and O respectively. So the combination of leafy food availability and temperature was the variable most significant in predicting DPL. The second factor in group P was the Ecology 2 which had high loadings for rainfall and mature leaves and the lowest loadings for flowers and fruit. It is apparent that the ecology of the environment had the greatest influence on the amount of travel that a group undertakes. These ecological components however could be ineffective when phenological phytophases are more evenly distributed throughout the year. In those analyses dietary variables might well account for greater levels of variation when food preference has a greater influence on ranging. This total model, however, is effective at predicting DPL on a monthly scale and could theoretically be used across Hanuman langur research sites and across taxa.

Comparison to other Hanuman langur sites

Results presented here are consistent with ranging behavior reported from other Hanuman langur populations. Two populations with published DPL values and analysis are those at Kanha Tiger Reserve (Newton 1992) and Langtang National Park (Sayers and Norconk 2008). At the most marginal location (Langtang) langurs prefer resources that at lower altitudes are not utilized at all (tubers) and preferred foods at Langtang were fallback foods at Kanha and Ramnagar (mature leaves). Deciduous mature leaves in this high elevation are patchily distributed and feeding upon deciduous mature leaves is correlated with longer DPL. This coincides with longer DPL when young leaves are present and temperatures are high (i.e. ecology 1) at Ramnagar. Feed on mature leaves at Kanha Tiger Reserve also negatively affected DPL and increased when groups are using preferred food. Fallback foods (regardless of type of food) at each site are associated with shorted DPL when animals are utilizing an energy saving strategy. At all sites langurs can be classified as generalist feeders which have positive correlations between phenological availability and resource use. If dietary variables are strongly correlated with phenology and these dietary factors are significantly affecting DPL then it stands to reason that other ecological factors would also help explain variation in DPL at Kanha Tiger Reserve and Langtang National Park as well.

Conclusion

Many factors have been explored when trying to understand the variation that is seen in DPL across primate taxa. Undoubtedly factors explored here will have drastically different effects depending on the species in question. But it is clear that the ecology of an area has far reaching effects that are not fully understood. These ecological conditions are influencing foraging and travel decisions and should be included in further investigations of ranging and habitat use.

For some time authors have noted the misguided assumptions about folivore socioecology based on their feeding preferences (Mitchell et al 1991; Newton 1992; Barton et al. 1996; Koenig et al. 1998; Snaith and Chapman 2005). Langurs at Ramnagar do show plasticity in their ranging behavior depending on the presence of high quality foods. It is shown here that the presence of young leaves is important in determining DPL and langurs are increasing their DPL when foraging on this resource. Young leaves can therefore be included as a patchy resource in socioecological models and predictions for folivorous primates should be adjusted accordingly.

Tables

Table 1: Predictions for factors affecting DPL on a daily basis

Variable	increase in DPL
Temperature	+
Rainfall	-
Specific Locations	+
Group Size	+
IGE	+
Receptive Females	+

Table 2: Predictions for factors affecting DPL on a monthly basis

Variable	increase in monthly DPL	Variable	increase in monthly DPL	Variable	↑ monthly DPL
Temperature	+	Mature Leaves	-	Inactive	+
Rainfall	+	Young Leaves	+	Feeding	-
Specific Locations	+	Fruits	+	Moving	+
Group Size	+	Flowers	+	Grooming	-
IGE	+	Insects	+		
Receptive Females	+	Geophagy	+		

Table 3: Descriptive Statistics of Group P and O on all days

P Group	N	Mean	Std. Deviation	O Group	N	Mean	Std. Deviation
DPL	1028	883.033	440.965	DPL	722	746.269	333.748
logDPL	1028	2.893	0.217	logDPL	722	2.830	0.196
Gr Size	1028	15.42	2.193	Gr Size	722	22.54	1.260
IGE	1020	0.30	0.460	IGE	722	0.32	0.466
Rainfall	1028	5.831	15.016	Rainfall	722	6.59	17.592
T mean	1028	23.24	5.92	T mean	720	23.30	5.93
T max	1027	30.70	6.185	T max	720	30.78	6.243
T min	1028	18.35	6.035	T min	720	18.41	5.965
Drink	950	0.43	0.495	Drink	722	0.52	0.500
#RAF	1028	0.39	0.755	#RAF	722	0.68	0.997
Valid N	949			Valid N	719		

Table 4: Pearson Correlations for all days regression analysis

Group P	logDPL	Gr Size	IGE	Rainfall	T mean	Drink	#RAF
logDPL	1.000	-0.051	0.136***	-0.052	0.467***	0.221***	-0.067*
Gr Size	-0.051	1.000	0.126***	-0.069*	-0.136***	-0.150***	0.074*
IGE	0.136***	0.126***	1.000	0.022	0.267***	0.058(*)	0.122***
Rainfall	-0.052	-0.069*	0.022	1.000	0.235***	-0.023	0.118***
T mean	0.467***	-0.136***	0.267***	0.235***	1.000	0.193***	0.223***
Drink	0.221***	-0.150***	0.058(*)	-0.023	0.193***	1.000	0.002
#RAF	-0.067*	0.074*	0.122***	0.118***	0.223***	0.002	1.000

Group O	logDPL	Gr Size	IGE	Rainfall	T mean	Drink	#RAF
logDPL	1.000	0.171***	0.211***	-0.004	0.489***	0.247***	-0.004
Gr size	0.171***	1.000	0.027	-0.123***	-0.092*	0.066(*)	-0.116**
IGE	0.211***	0.027	1.000	0.030	0.235***	0.081*	0.124***
Rainfall	-0.004	-0.123***	0.030	1.000	0.181***	-0.116**	0.167***
T mean	0.489***	-0.092*	0.235***	0.181***	1.000	0.125***	0.213***
Drink	0.247***	0.066(*)	0.081*	-0.116**	0.125***	1.000	0.118**
#RAF	-0.004	-0.116**	0.124***	0.167***	0.213***	0.118**	1.000

(*) $p<0.10$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Table 5: Model summary of Group P all days regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.467(a)	0.218	0.217	0.186557	0.218	263.259	1	946	<0.001
2	0.498(b)	0.248	0.247	0.182960	0.031	38.565	1	945	<0.001
3	0.522(c)	0.272	0.270	0.180119	0.024	31.045	1	944	<0.001
4	0.535(d)	0.286	0.283	0.178539	0.013	17.785	1	943	<0.001

a Predictors: T mean
b Predictors: T mean, #RAF
c Predictors: T mean, #RAF, Rainfall
d Predictors: T mean, #RAF, Rainfall, Drink

Table 6: Model summary of Group O all days regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.489(a)	0.239	0.238	0.170896	0.239	225.317	1	718	<0.001
2	0.535(b)	0.286	0.284	0.165624	0.047	47.439	1	717	<0.001
3	0.562(c)	0.315	0.313	0.162290	0.029	30.754	1	716	<0.001
4	0.572(d)	0.327	0.323	0.161010	0.012	12.430	1	715	<0.001
5	0.579(e)	0.335	0.330	0.160177	0.008	8.457	1	714	0.004

a Predictors: T mean

b Predictors: T mean, GrSize

c Predictors: T mean, GrSize, Drink

d Predictors: T mean, GrSize, Drink, #RAF

e Predictors: T mean, GrSize, Drink, #RAF, IGE

Table 7: Descriptive statistics for Groups P and O during wet season

P Group	N	Mean	Std. Deviation	O Group	N	Mean	Std. Deviation
DPL	497	900.878	391.570	DPL	339	773.355	314.869
logDPL	497	2.912	0.199	logDPL	339	2.854	0.173
Gr Size	497	15.25	2.148	Gr Size	339	22.31	0.968
IGE	489	0.39	0.489	IGE	339	0.41	0.493
Rainfall	497	11.363	19.809	Rainfall	339	13.08	23.617
T mean	497	27.47	2.38	T mean	337	27.63	2.53
T max	497	34.47	3.180	T max	337	34.73	3.261
T min	497	23.28	2.178	T min	337	23.37	2.191
Drink	475	0.47	0.500	Drink	339	0.59	0.493
#RAF	495	0.67	0.915	#RAF	339	1.17	1.142
Valid N	473			Valid N	336		

Table 8: Pearson Correlations for regression of wet season

Group P	logDPL	Gr Size	IGE	Rainfall	T mean	Drink	#RAF
logDPL	1.000	0.018	0.025	-0.156***	0.336***	0.094*	-0.125**
Gr Size	0.018	1.000	0.157***	-0.063	-0.030	-0.170***	0.065
IGE	0.025	0.157***	1.000	-0.058	0.109	0.059	0.093*
Rainfall	-0.156***	-0.063	-0.058	1.000	-0.101	-0.077(*)	-0.008
T mean	0.336***	-0.030	0.109*	-0.101	1.000	0.099*	-0.044
Drink	0.094*	-0.170***	0.059	-0.077	0.099	1.000	-0.038
#RAF	-0.125**	0.065	0.093*	-0.008	-0.044	-0.038	1.000

Group O	logDPL	Gr Size	IGE	Rainfall	T mean	Drink	#RAF
logDPL	1.000	0.108*	0.122*	-0.061	0.298***	0.234***	-0.028
Gr size	0.108*	1.000	-0.051	-0.137*	-0.023	0.267***	-0.114*
IGE	0.122*	-0.051	1.000	-0.048	0.018	0.046	0.091(*)
Rainfall	-0.061	-0.137*	-0.048	1.000	-0.208***	-0.250***	0.015
T mean	0.298***	-0.023	0.018	-0.208***	1.000	0.157**	-0.237***
Drink	0.234***	0.267***	0.046	-0.250***	0.157**	1.000	0.034
#RAF	-0.028	-0.114*	0.091(*)	0.015	-0.237***	0.034	1.000

(*) $p<0.10$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Table 9: Model summary of Group P wet season regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.336(a)	0.113	0.111	0.179275	0.113	59.906	1	471	<0.001
2	0.358(b)	0.128	0.124	0.177924	0.015	8.177	1	470	0.004
3	0.375(c)	0.141	0.135	0.176832	0.013	6.827	1	469	0.009

a Predictors: T mean

b Predictors: T mean, Rainfall

c Predictors: T mean, Rainfall, #RAF

Table 10: Model summary of Group O wet season regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.298(a)	0.089	0.086	0.165817	0.089	32.553	1	335	<0.001
2	0.353(b)	0.125	0.119	0.162756	0.036	13.720	1	334	<0.001
3	0.369(c)	0.136	0.129	0.161896	0.012	4.560	1	333	0.033

a Predictors: T mean

b Predictors: T mean, Drink

c Predictors: T mean, Drink, IGE

Table 11: Descriptive statistics for Groups P and O during dry season

P Group	N	Mean	Std. Deviation	O Group	N	Mean	Std. Deviation
DPL	531	866.330	482.415	DPL	383	722.294	348.263
logDPL	531	2.876	0.231	logDPL	383	2.809	0.211
Gr Size	531	15.58	2.226	Gr Size	383	22.74	1.443
IGE	531	0.22	0.415	IGE	383	0.23	0.425
Rainfall	531	0.65	3.764	Rainfall	383	0.84	4.487
T mean	531	19.27	5.49	T mean	383	19.50	5.439
T max	530	27.17	6.233	T max	383	27.31	6.178
T min	531	13.72	4.676	T min	383	14.04	4.680
Drink	475	0.38	0.486	Drink	383	0.46	0.499
#RAF	531	0.14	0.434	#RAF	383	0.25	0.574
Valid N	474			Valid N	383		

Table 12: Pearson Correlations for regression of dry season

Group P	logDPL	Gr Size	IGE	Rainfall	T mean	Drink	#RAF
logDPL	1.000	-0.092*	0.219***	0.052	0.686***	0.320***	-0.107*
Gr Size	-0.092*	1.000	0.122**	-0.039	-0.172***	-0.120**	0.220***
IGE	0.219***	0.122**	1.000	0.016	0.299***	0.026	0.013
Rainfall	0.052	-0.039	0.016	1.000	0.090(*)	-0.038	-0.050
T mean	0.686***	-0.172***	0.299***	0.090(*)	1.000	0.240***	-0.073
Drink	0.320***	-0.120**	0.026	-0.038	0.240***	1.000	-0.029
#RAF	-0.107*	0.220***	0.013	-0.050	-0.073	-0.029	1.000

Group O	logDPL	Gr Size	IGE	Rainfall	T mean	Drink	#RAF
logDPL	1.000	0.238***	0.259***	-0.068	0.680***	0.240***	-0.131*
Gr size	0.238***	1.000	0.143**	0.014	0.050	-0.011	0.025
IGE	0.259***	0.143**	1.000	-0.038	0.223***	0.070	-0.060
Rainfall	-0.068	0.014	-0.038	1.000	-0.012	-0.044	-0.044
T mean	0.680***	0.050	0.223***	-0.012	1.000	0.013	-0.168***
Drink	0.240***	-0.011	0.070	-0.044	0.013	1.000	0.136**
#RAF	-0.131*	0.025	-0.060	-0.044	-0.168***	0.136**	1.000

(*) $p<0.10$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Table 13: Model Summary of Group P dry season regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.686(a)	0.471	0.470	0.166208	0.471	420.559	1	473	<0.001
2	0.705(b)	0.496	0.494	0.162300	0.026	24.051	1	472	<0.001

a Predictors: T mean

b Predictors: T mean, Drink

Table 14: Model Summary of Group O dry season regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.680(a)	0.463	0.461	0.155218	0.463	328.138	1	381	<0.001
2	0.718(b)	0.516	0.513	0.147511	0.053	41.852	1	380	<0.001
3	0.748(c)	0.559	0.555	0.141004	0.043	36.878	1	379	<0.001
4	0.751(d)	0.563	0.559	0.140462	0.005	3.934	1	378	0.048

a Predictors: T mean
b Predictors: T mean, Drink
c Predictors: T mean, Drink, GrSize
d Predictors: T mean, Drink, GrSize, IGE

Table 15: Total Variance Explained by PCA of Activity variables

Group P				Group O			
	Initial Eigenvalues				Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %	Component	Total	% of Variance	Cumulative %
1	2.321	58.022	58.022	1	2.175	54.369	54.369
2	0.998	24.948	82.971	2	1.231	30.782	85.151

Table 16: Component Matrix for PCA of Activity Variables

	Component			Component	
Group P	1	2	Group O	1	2
arcsin moving	0.209	0.974	arcsin moving	0.143	0.872
arcsin grooming	0.699	-0.181	arcsin grooming	0.566	0.591
arcsin feeding	0.914	-0.126	arcsin feeding	-0.975	0.187
arcsin inactive	-0.977	-0.038	arcsin inactive	0.940	-0.294

Table 17: Total Variance Explained by PCA of Diet variables

Group P				Group O			
	Initial Eigen values				Initial Eigen values		
Component	Total	% of Variance	Cumulative %	Component	Total	% of Variance	Cumulative %
1	2.274	28.425	28.425	1	2.902	36.274	36.274
2	1.734	21.674	50.099	2	2.088	26.105	62.379
3	1.122	14.020	64.119				
4	1.058	13.228	77.346				

Table 18: Component Matrix for PCA of Diet variables

	Component					Component	
Group P	1	2	3	4	Group O	1	2
arcsin ML	-0.882	-0.222	-0.008	0.041	arcsin ML	-0.826	-0.290
arcsin YL	0.671	0.316	0.089	-0.432	arcsin YL	0.755	0.349
arcsin fruits	0.592	-0.690	0.099	-0.034	arcsin fruit	0.657	-0.492
arcsin flowers	0.231	0.488	0.128	0.550	arcsin flower	-0.355	0.747
arcsin insects	-0.045	0.051	0.768	0.452	arcsin insects	0.656	0.266
arcsin geophagy	0.342	0.772	-0.194	0.038	arcsin geophagy	0.055	0.657
arcsin drinking	0.191	-0.205	-0.670	0.577	arcsin drinking	0.093	0.722
arcsin other	-0.698	0.479	-0.105	-0.167	arcsin other	-0.806	0.240

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Table 19: Total Variance Explained by PCA of Ecological variables

Group P				Group O			
	Initial Eigenvalues				Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %	Component	Total	% of Variance	Cumulative %
1	5.010	62.631	62.631	1	4.941	61.767	61.767
2	1.820	22.753	85.384	2	2.083	26.039	87.806

Table 20: Component Matrix for PCA of Ecological variables

	Component			Component	
Group P	1	2	Group O	1	2
Rainfall	0.573	0.720	Rainfall	0.567	0.745
T mean	0.980	0.087	T mean	0.971	0.139
T max	0.973	-0.022	T max	0.971	0.040
T min	0.944	0.289	T min	0.929	0.333
arcsin %YL	0.950	0.202	arcsin %YL	0.955	0.195
arcsin %flower	0.615	-0.612	arcsin %flower	0.584	-0.674
arcsin %fruit	0.660	-0.347	arcsin %fruit	0.609	-0.471
arcsin %ML	-0.409	0.822	arcsin %ML	-0.498	0.826

Table 21: Pearson Correlations of Group P monthly regression

Group P	logDPL	Gr Size	IGE	Drink	#RAF	Diet 1	Diet 2	Act. 1	Act. 2	Ecol 1	Ecol 2
logDPL	1.000	-0.216	0.450*	0.483**	-0.147	0.669***	0.268	-0.068	-0.466*	0.811***	-0.393*
Gr Size	-0.216	1.000	0.259	-0.513*	0.204	0.027	0.296	0.229	0.130	-0.258	-0.121
IGE	0.450*	0.259	1.000	-0.025	0.522**	0.460*	0.113	-0.024	-0.532**	0.576**	0.163
Drink	0.483*	-0.513**	-0.025	1.000	-0.488*	0.261	0.080	-0.005	-0.020	0.322	-0.376*
#RAF	-0.147	0.204	0.522**	-0.488	1.000	0.149	-0.312	-0.029	-0.323	0.233	0.511**
Diet 1	0.669***	0.027	0.460*	0.261	0.149	1.000	-0.126	-0.087	-0.685***	0.734***	-0.133
Diet 2	0.268	0.296	0.113	0.080	-0.312	-0.126	1.000	-0.037	0.356(*)	-0.058	-0.572**
Activity 1	-0.068	0.229	-0.024	-0.005	-0.029	-0.087	-0.037	1.000	0.205	-0.263	0.037
Activity 2	-0.466*	0.130	-0.532**	-0.020	-0.323	-0.685***	0.356(*)	0.205	1.000	-0.781***	-0.433*
Ecol 1	0.811***	-0.258	0.576**	0.322	0.233	0.734***	-0.058	-0.263	-0.781***	1.000	0.000
Ecol 2	-0.393*	-0.121	0.163	-0.376*	0.511**	-0.133	-0.572**	0.037	-0.433*	0.000	1.000

(*) p<0.10, * p<0.05 , ** p<0.01, *** p<0.001

Table 22: Pearson Correlations of Group O monthly regression

Group O	logDPL	Gr Size	IGE	Drink	#RAF	Diet 1	Diet 2	Act. 1	Act. 2	Ecol 1	Ecol 2
logDPL	1.000	0.209	0.412	0.226	0.125	0.763***	0.347	0.687**	-0.130	0.772***	-0.258
Gr Size	0.209	1.000	0.265	0.183	-0.200	-0.159	0.054	-0.057	-0.196	-0.182	-0.077
IGE	0.412	0.265	1.000	0.274	0.569*	0.171	0.195	0.698**	-0.208	0.507*	0.470(*)
Drink	0.226	0.183	0.274	1.000	0.207	0.214	0.073	0.191	-0.029	0.183	-0.083
#RAF	0.125	-0.200	0.569*	0.207	1.000	0.328	-0.490	0.574*	0.101	0.386	0.812***
Diet 1	0.763***	-0.159	0.171	0.214	0.328	1.000	0.000	0.670**	-0.254	0.850***	-0.122
Diet 2	0.347	0.054	0.195	0.073	-0.490(*)	0.000	1.000	0.169	-0.226	0.313	-0.579*
Activity 1	0.687**	-0.057	0.698**	0.191	0.574*	0.670**	0.169	1.000	0.000	0.828***	0.327
Activity 2	-0.130	-0.196	-0.208	-0.029	0.101	-0.254	-0.226	0.000	1.000	-0.322	0.173
Ecol 1	0.772***	-0.182	0.507*	0.183	0.386	0.850*	0.313	0.828***	-0.322	1.000	0.000
Ecol 2	-0.258	-0.077	0.470(*)	-0.083	0.812***	-0.122	-0.579*	0.327	0.173	0.000	1.000

(*) p<0.10, * p<0.05 , ** p<0.01, *** p<0.001

Table 23: Model Summary of Group P monthly regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.811(a)	0.657	0.644	0.083664	0.657	47.970	1	25	<0.001
2	0.901(b)	0.812	0.796	0.063296	0.154	19.679	1	24	<0.001

a Predictors: Ecology 1

b Predictors: Ecology 1, Ecology 2

Table 24: Model Summary of Group O monthly regression analysis

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.772(a)	0.597	0.568	0.092640	0.597	20.697	1	14	<0.001
2	0.850(b)	0.723	0.680	0.079672	0.126	5.928	1	13	0.030

a Predictors: Ecology 1

b Predictors: Ecology 1, GrSize

Table 25: Correlations between Phenology and feeding scores

	Phenology Scores			
Feeding Scores	arcsin %ma_le	arcsin %yo_le	arcsin %fruit	arcsin %flower
arcsin ML	0.699	-0.570	-0.685	-0.476
arcsin YL	-0.134	0.347	0.259	0.162
arcsin fruits	0.167	0.370	0.365	-0.254
arcsin flowers	-0.249	0.194	-0.091	0.459

Figures

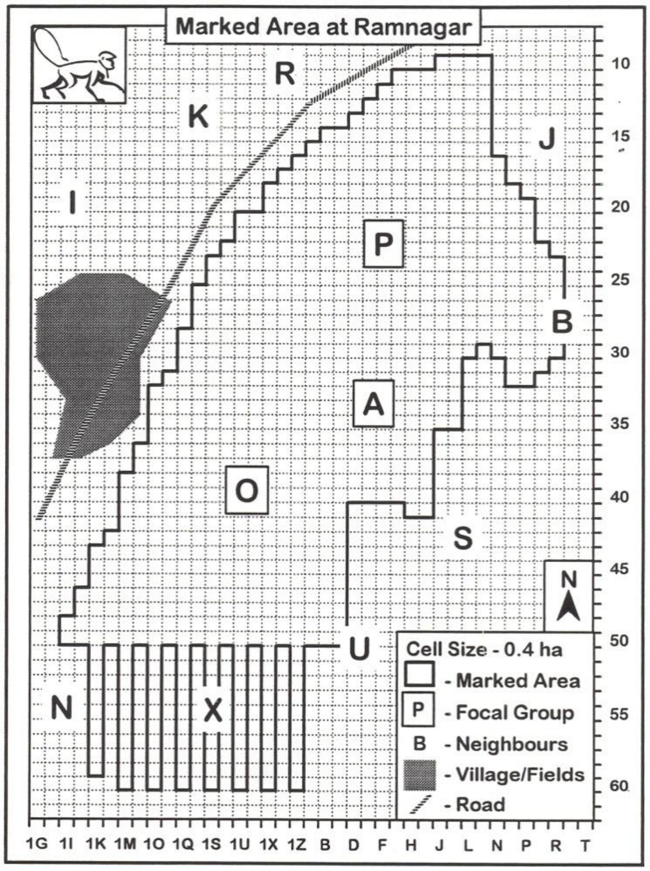

Figure 1: Marked area at Ramnagar. Letters indicate group near the center of their home range. Figure courtesy of A. Koenig.

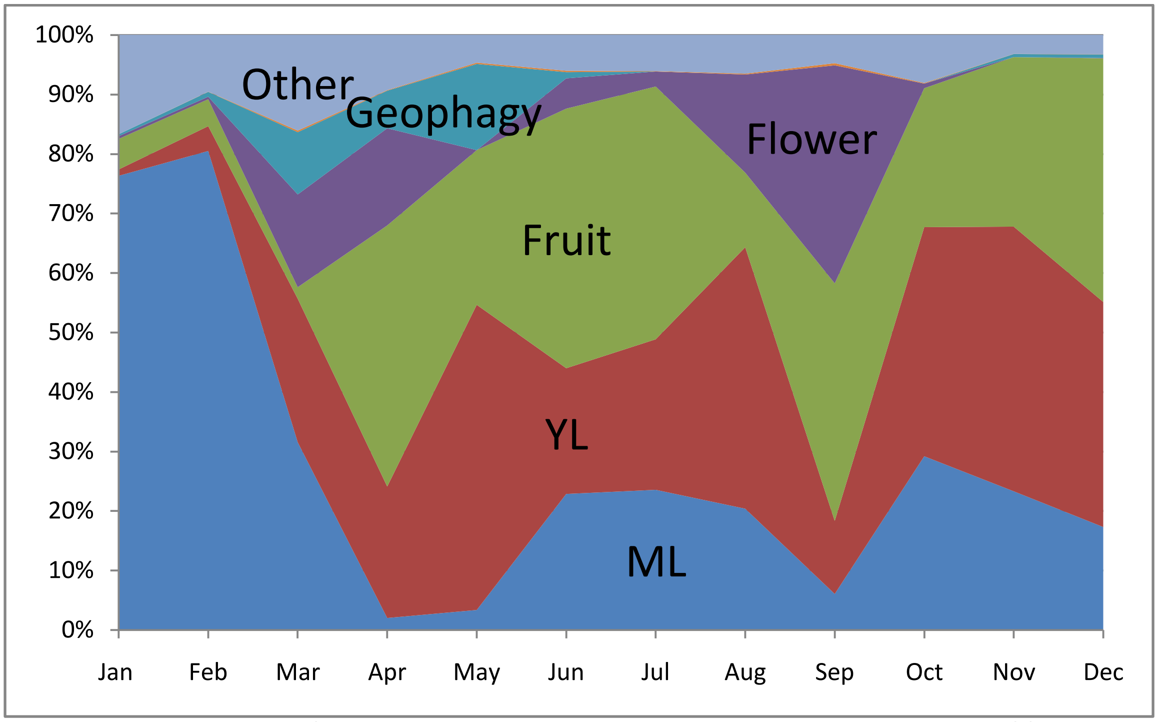

Figure 2: Feeding budgets of P group in 1993. January and February have the highest levels of feeding on mature leaves while April and May have the least.

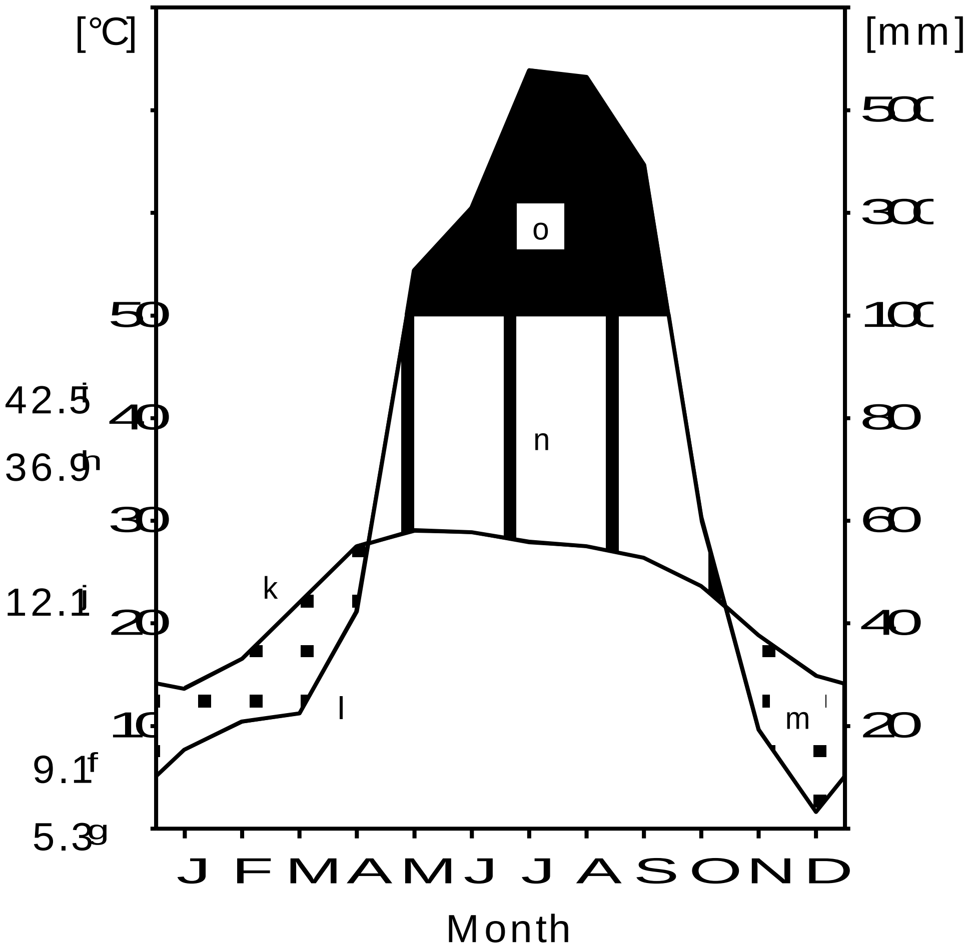

Figure 3: Yearly fluctuations in rainfall and temperatures at Ramnagar. Notice the highly seasonal monsoon season between May and October when the environment is classified as perhumid. April and November are classified as humid and the remaining 4 months are arid. Key: **k**-mean monthly temperature, **l**-mean monthly precipitation, **m**- arid period, **n**-humind period, **o**- perhumid period. (Figure taken from Koenig et al. 1997; keys according to Walter 1990).

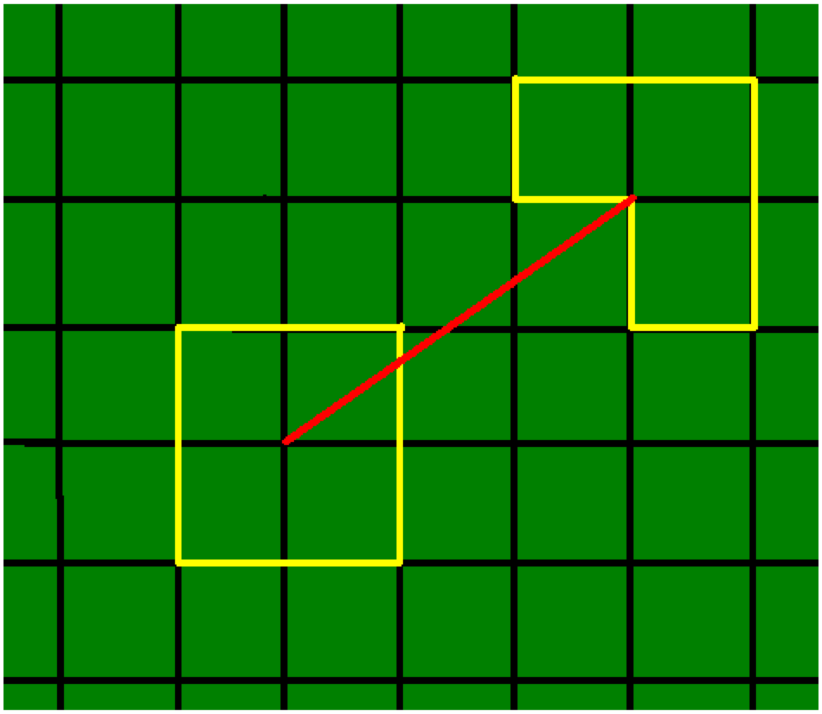

Figure 4: Representation of the creation of DPL between 30 min scan samples.

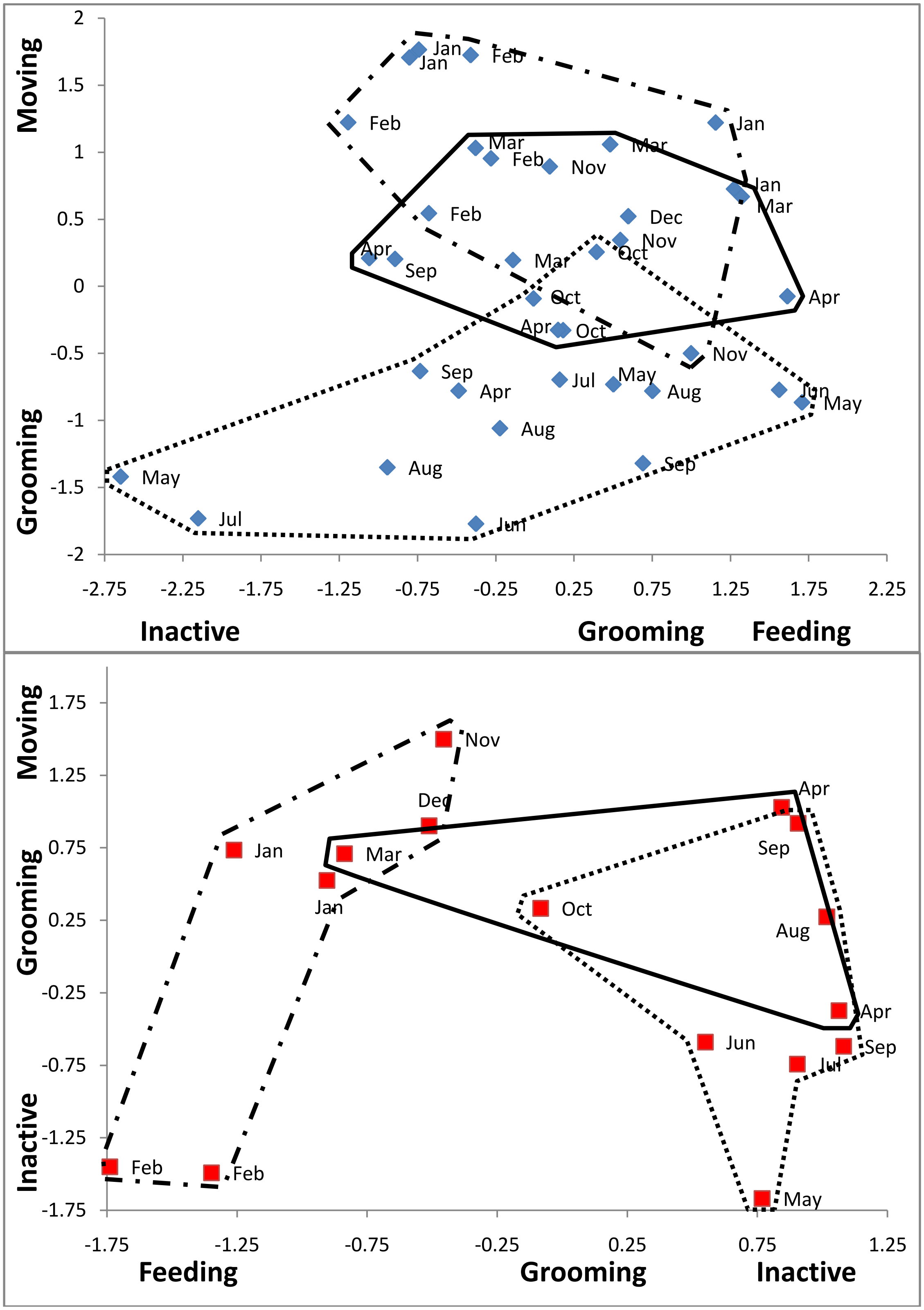

Figure 5: Scatter plot of activity variables in groups P (above) and O (below). Importance of given activities (according to their loading scores) are shown beside each axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

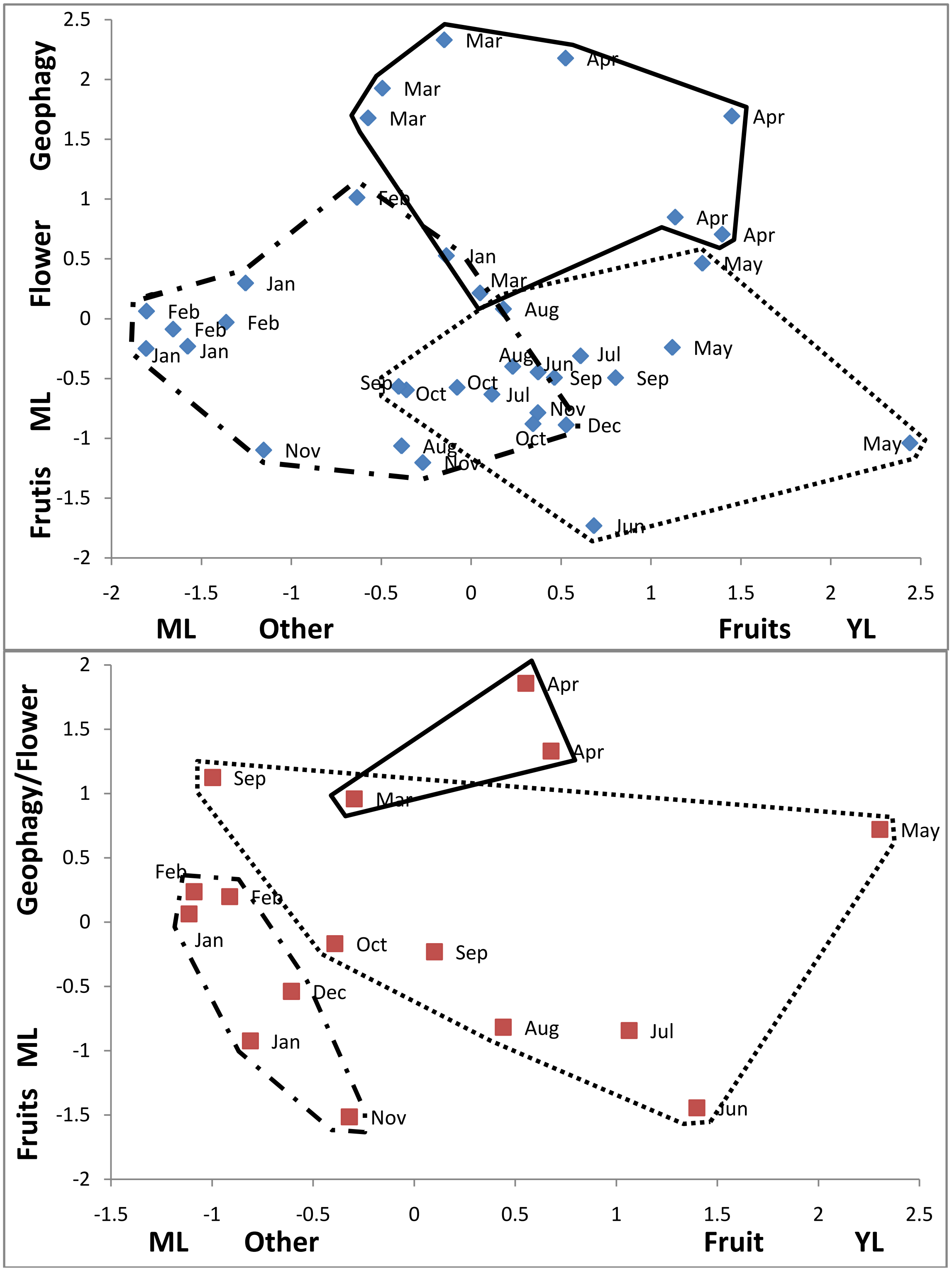

Figure 6: Scatter plot of dietary variables in groups P (above) and O (below). Importance of dietary component (according to their loading scores) is shown beside each axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

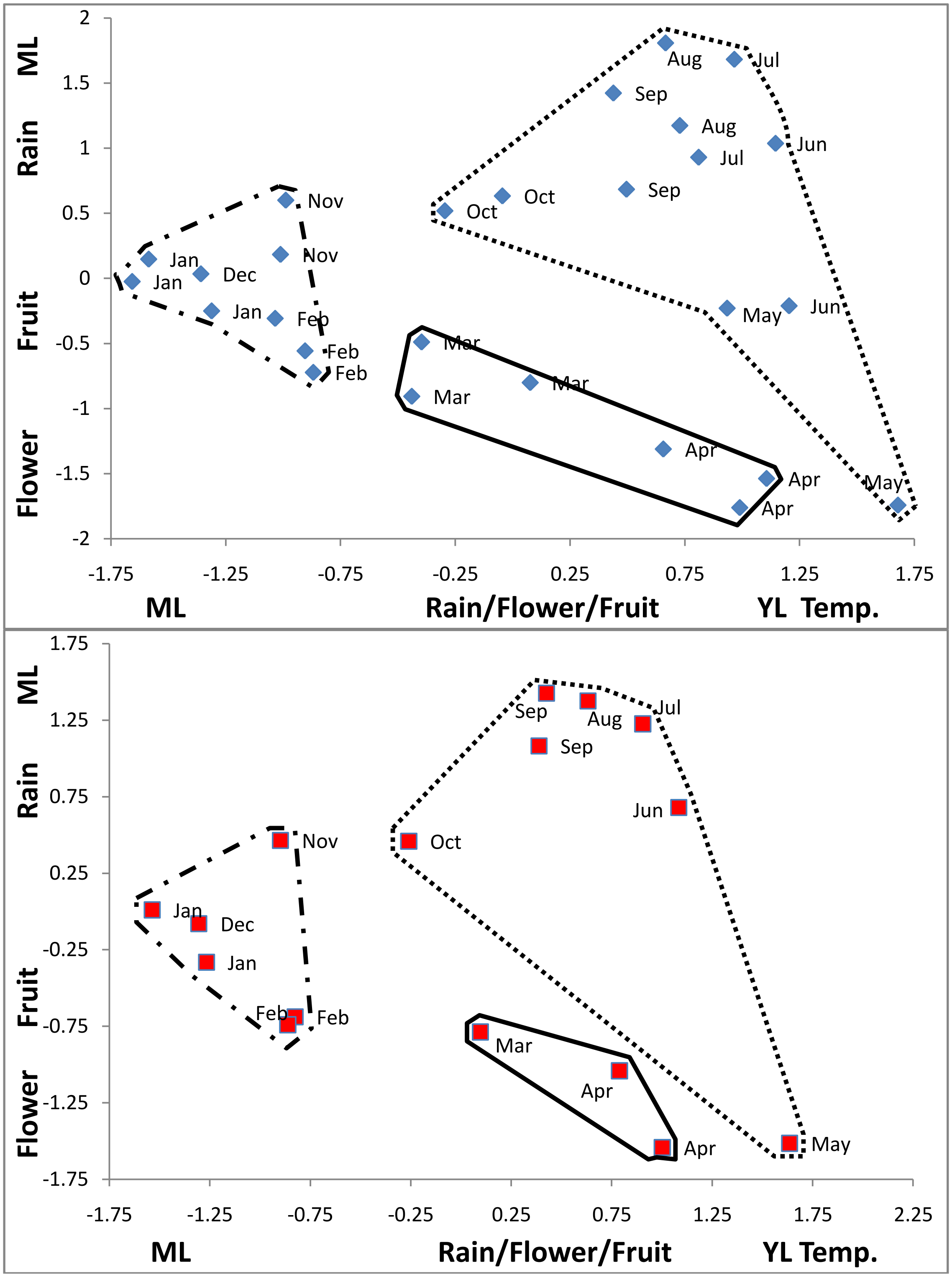

Figure 7: Scatter plot of ecological variables in groups P (above) and O (below). The importance of component (according to their loading scores) is shown beside each axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

Chapter 2: Determinants of home range size and utilization in Hanuman langurs (*Semnopithecus entellus*)

Introduction

The space animals are using in search of food and mates and in raising young (home range) depends allometrically on their body size (McNab 1963; Nunn and Barton 2000) and varies with a wide range of additional factors. A group's home range must include all the resources that they need for survival (Burt 1943). How groups navigate and utilize this area is important in understanding spatial needs for a given species and the importance of specific areas within a home range (Singleton and van Schaik 2001). The decisions that animals make while traveling can reveal the important factors that affect why and how groups utilize their home range (Janson 1996; Garber 2000). This information can be used to manage and/or protect populations and to test scientific models of foraging and socioecology. Ecological and social factors have been shown to correlate with how groups utilize their range but few studies have combined them when examining these questions.

Many factors that have been shown/ demonstrated to influence the home range of primate groups. First and foremost, a strong relationship between group home range size/use and high quality food abundance has been found (Clutton-Brock and Harvey 1977; Raemaekers 1980; Isbell 1983; Bennett 1986; Garber 1993; Olupot et al 1997; Goldsmith 1999; Kaplin 2001; Di Fiore 2003; Doran-Sheehy et al. 2004), though not always (Fashing 2001; Robbins McNeilage 2003; Buzzard 2006; Porter et al. 2007). Other variables have also been proposed to affect group and individual movement patterns, including rainfall (Chivers 1967; Altmann and Altmann 1970; Raemaekers 1980; McKey and Waterman 1982; Bronikowski and Altmann 1996; Goldsmith 1999), group size (Janson and Goldsmith 1995; Goldsmith 1999), body size (Milton and Day 1976), intergroup encounters (Struhsaker 1975; Waser 1977; Isbell 1983; Stanford 1991a; Watts 1991), location of water holes or other specifically used locations (Altmann and Altmann 1970; Doran-Sheehy et al. 2004; Scholz and Kappeler 2004), ambient temperature (Clutton-Brock 1975; Stelzner 1988; Barrett et al. 2004), predation risk (Cowlishaw 1997; Boinski et al. 2000), parasite avoidance (Freeland 1980), presence of heterospecifics (Porter et al. 2007), the size/age of juveniles on maternal ranging (Pontzer and Wrangham 2006), the fighting ability of group males (Lehmann and Boesch 2002), and the presence and number of receptive females (Small 1988; Paul 2002). With so many factors possibly influencing a group's range size and use patterns, it seems important to understand which variable(s) is (are) most important when determining the ranging patterns in a given species.

One of the most influential factors seems to be the interplay of diet and resource availability. The Marginal Value Theorem (Charnov 1976) states that animals will forage in a patch until the average intake rate for that patch falls below the average intake rate for the entire habitat. Patches characterized in this way are considered depletable

(Charnov et al. 1976) and animals using such patches must travel further to use multiple patches (Stephens and Krebs 1987). Not only is more travel required but, if depleted areas are avoided, home ranges would also be used more evenly. Groups should have different residency times in each patch depending on the quality of that patch, the quality of the surrounding environment and group size. This assumption is contingent on the fact that patches are, in fact, depletable. The interplay of patch size, patch quality, and spatial heterogeneity should account for variation in home range size and use patterns.

Attempts have been made to model these effects in primate populations and make predictions for both interspecific and intraspecific variation in home range size and use. The spatial distribution of primate foods and primate food preference strongly influence patterns of movement (Oates 1987). It is expected that frugivorous species will exhibit larger home ranges and longer daily travel because their patches are depleteable, and spatially scattered throughout the environment. This characteristic of feeding sites leads to a low encounter rate and several feeding sites may have to be visited to meet the members' energetic needs and home ranges increase accordingly. Folivores, alternatively, are assumed to feed on larger and more ubiquitous resources which do not deplete as quickly as fruit patches do. With higher encounter rates and larger patches folivores are expected to have smaller home ranges because of the restricted travel needed to fulfill their dietary demands (Clutton-Brock and Harvey 1976; Milton and May 1976).

Support for these predictions has been mixed. In general, studies on frugivorous species have supported these predictions by showing increased home range size and diversity (less concentrated ranging in small part of home range) during periods of high fruit consumption (Raemaekers 1980; Bennett 1986; Strier 1987; Garber 1993; Olupot et al 1997; Goldsmith 1999; Di Fiore 2003; Doran-Sheehy et al. 2004; Wallace 2006). Feeding on these high quality, spatially dispersed foods is correlated with an increase in home range size and home range use is comparatively even rather than concentrated in certain areas. Foraging models have been less successful when applied to folivorous primates. While folivores generally have smaller home ranges than frugivores of similar body mass (Milton and May 1976; Hladik 1977; for exception see Kaplin 2001) this does not mean that folivores do not vary ranging patterns based on food availability and food quality (Newton 1992). Many researchers have challenged the assumption that folivorous primates feed in superabundant food patches (Dasilva 1994; Oates 1994; Chapman et al. 2002) and propose that even folivorous resources tend to be scattered both temporally and spatially (Oates 1994; Koenig et al. 1998) and can be considered patchy (Astrom et al. 1990). Young leaves are both more digestible and have higher protein content than mature leaves (Waterman and Kool 1994) and they are a spatially and temporally patchy resource (Koenig et al. 1997). Folivores therefore appear to be feeding more selectively when they are feeding on young leaves. This creates a situation where groups are expected to act in a manner traditionally proposed for frugivores and movements should be at least partially explained by the availability of high quality foods. The presence of contest competition within several folivorous primates (Koenig 2000; Korstjens et al. 2002) supports the idea that folivores are feeding selectively and consequently effects on ranging might be expected.

There is general agreement that, on average, young leaves "offer a better nutrient package at lower processing cost than do the mature leaves of the same species" (Waterman and Kool 1994, pg 262). There is, however, little research showing if and how this discrepancy in nutrients affects ranging behavior (Fimbel et al. 2001). If indeed young leaves are a higher quality food and more spatially and temporally variable than mature leaves, their use should lead to similar consequences (large home range) than use of other preferred foods such as fruits. It is important to consider these phytochemical differences when studying how diet affects other aspects of primate behavior as well.

Seasonal habitats require animals to be flexible in their foraging decisions. How animals compensate for both high and low food availability should depend on both their behavioral and physiological abilities. There are two distinct strategies in dealing with variation in resource abundance: maximize benefits or minimize costs (Oates 1987). During periods of low resource abundance maximizing benefits leads to compensation via increased foraging time. This not only increases total energy intake but also energy expenditure (Terborgh 1983; Boinski 1987; Overdorff 1996; Basabose 2005; Grueter et al. 2008). A species which is minimizing costs will decrease energy expenditure by feeding on lower quality foods which are readily accessible and do not require additional ranging (Richard 1978; Zhang 1995; Doran 1997; Kirkpatrick et al. 1998). Groups that are energy economists would show smaller home ranges, a disproportional use of their range, and decreased diet breadth when food availability is low. These strategies should not be assumed to be species wide and groups in varying ecological conditions can adopt either strategy (e.g. *Pan troglodytes* : Basabose 2005 and Doran 1997; *Rhinopithecus bieti*: Kirkpatrick et al. 1998 and Grueter et al. 2008).

How an animal partitions it’s time between basic activities can give an indication of the relative importance of these activities compared to social and ecological factors. The percentage of time in any given activity is thought to be plastic and increasing foraging demands would decrease time spent in resting or in social activities (Altmann 1980; Bronkowski and Altmann 1996), even in very social primates where maintaining bonds is important and there can be significant differences between groups in activity patterns (Isbell and Young 1993). Shifts in activity should reflect the decisions made to either maximize energy gained or minimize energy used (see above). Not only are groups changing their feeding patterns but also their activity schedules and variation in these categories could explain some of the shifts seen in home range size and use. Groups conserving energy would be expected to have low levels of movement while groups not concerned with conservation would have a more diverse ranging pattern and larger range. It is expected that there will be an inverse relationship between time spent feeding and inactivity (Boinski 1987; Newton 1992; Koenig et al. 1997). When animals are feeding on patchy, high quality resources feeding time is shorter because they can meet their energetic demands quickly and then remain inactive to digest. Travel will increases and groups use their home ranges more evenly to reach these patches but there is a high net energy gain during these periods.

Another factor that has been linked to changes in habitat use is changes in ambient temperature. Animals must thermoregulate if temperatures fall outside a given range of tolerances. There is evidence, however, that animals behaviorally thermoregulate even when temperatures are within the range of physiological tolerances and this can be an important way to mitigate heat stress (Seltzner 1988; Campos and Fedigan 2008). Ambient temperature can have significant effects on several different aspects of primate behavior including sun bathing (Stelzner 1988), increased feeding (Bernstein 1972, 1975, 1976), huddling (Ostner 2002), postural changes (Stelzner and

Hausfater 1986; Dasilva 1993; Takemoto 2004), changes in activity catagories (Stelzner 1988), and habitual use of caves (Barrett et al. 2004). It is expected that when temperatures are consistently below or above tolerances that home ranges would be smaller and used very intensely. As temperature increases groups should move further and more evenly through their home range until upper tolerances are exceeded. At this point travel would decrease because of increasing heat stress (Campos and Fedigan 2008).

Rainfall is another factor that could account for variation in home range size and use. A negative correlation between daily path length and rainfall has been reported (Raemaekers 1980; McKey and Waterman 1982; Goldsmith 1999) but little evidence is available for home range size or use. Bronikowski and Altmann (1996) attributed weather patterns to shifts in activity variables but not to changes in monthly home range size or use. Home range shifts were noted as a possible behavioral response to environmental variability. Home range size would be expected to be smaller and home range use should be used unevenly if rainfall is having a negative effect on travel. There is, however, a dichotomy between how rainfall affects animals depending on the temporal scale being examined. Periods of high rainfall can be highly correlated with increased resource availability which can confound the effect of rainfall when animals are actively seeking dispersed and clumped food sources. An effect of rainfall might therefore be weaker in species in which food availability is closely tied to rainfall.

The dependence of animals on specific locations within a group's home range can have significant effects on the size and the evenness of its use. These specific locations include several different types such as water holes (Altmann and Altmann 1970; Scholz and Kappeler 2004; Campos and Fedigan 2008), swamps (Doran-Sheehy et al. 2004), areas of geophagy (Krishnamani and Mahaney 1999; Pages et al. 2005), and sleep sites (Dietz et al. 1997; Anderson 1998; Di Bitteti et al. 2000). When these resources are limiting within a groups home range, animals are expected to concentrate their ranging around these sites. During periods of when groups are using small parts of their home range regularly the home range size could stay the same but should show an uneven pattern of use around these sites. If these sites are very limiting groups may adopt an energy saving strategy and ranging can both become restricted and even shift the home range (Scholz and Kappeler 2004).

Group size has historically been a factor closely associated with home range size (Clutton-Brock and Harvey 1977; Waser 1977; Janson and Goldsmith 1995). A home range must encompass all the resources a group needs and increasing the number of individuals will increase the overall energetic demands of the group. With increasing numbers of individuals in a group there should be higher levels of feeding competition (e.g. Janson 1988; Terborgh and Janson 1986) which might lead to significant fitness costs to larger groups even in folivorous primates (van Schaik 1983; Borries et al. 2008). Higher levels of feeding competition should lead to larger home ranges; because groups must travel further to obtain the same amount of nutrients per group member. This effect should be present in folivores if they are feeding on depleteable patches (Isbell 1991; Gillespie and Chapman 2001; Chapman et al 1995; Snaith and Chapman 2005). If food resources are truly found in superabundant patches then increasing group size should have little impact on home range size.

The number of receptive females within a group has not traditionally been investigated as a factor contributing to variation seen in home range size and use pattern. Female choice can have a significant influence on mating success (Paul 2002) and could also change ranging patterns, should females make travel decisions (Stanford 1992). In species with a high risk of infanticide, it could be to the females benefit to mate with extra group males (Hrdy 1979; Hausfater 1984). Such a paternity confusion could be one way of females lowering the future risk of infanticide similar to females who have longer receptive periods mating with as many males in their group as possible (Borries et al. 2001). The presence of receptive adult females could increase both the size of a home range but also increase the use of peripheral areas.

Intergroup encounters are another factor that may have an effect on home range use patterns and they have been shown to be important in some primate species (Struhsaker 1975; Waser 1977; Stanford 1991; Watts 1991). Although for different reasons both males and females may avoid extra group males and/or other groups. Male fitness is dependent on access to females (Trivers 1972) and males have been shown to try to limit the amount of contact that the receptive females have with rivals (Kitchen et al. 2004). Thus, males should try to avoid extra-group males or other groups when females are receptive. Females on the other hand should avoid other groups if young infants are present particularly in species in which infanticide is common. Therefore both males and females should avoid intergroup encounters when dependent offspring are present but only males should actively avoid encounters when females are receptive (while receptive females might try to contact other groups; see above). Groups would be expected to utilize their core areas more than peripheral areas. Many primate species, however, have interbirth intervals that exceed one year so there may be receptive females and females with dependent offspring at the same time. Overall an increase in intergroup encounters should influence the home range usage. However groups should have an adaptive response to the composition of groups that they meet (Ydenberg et al. 1988). Groups or males that have the potential to overthrow the dominant male should illicit the greatest response (Wich and Sterck 2007). Young males, within another group or solitary, should have the greatest potential for displacing group males so responses would be dependent on the composition of the group encountered.

To test hypotheses concerning ranging behavior in folivorous primates I have tested what ecological and behavioral variables account for variation in home range size and the pattern of its use. Phenology, diet, activity, temperature, rainfall, group size, waterhole use, the number of receptive adult females, and intergroup encounter are the independent variables used to predict variation in home range size and the diversity of its use. To test these variables a highly adaptable folivorous primate was used: the Hanuman langur.

Study Species

Hanuman langurs are widespread across the Indian subcontinent ranging from an elevation of 4,000 m (Sayers and Norconk 2008) to sea level and have been studied at over 30 locations (reviewed in Koenig and Borries 2001). They are known to be very flexible and inhabit areas as diverse as semi-desert, open park woods, moist deciduous forests, and mountain forests (Roonwal and Mohnot 1977) which makes them ideal for studying variation in habitat use because of their flexibility. Their ability to thrive in varied environments is likely due to their diverse diet. While labeled folivores there is considerable variation in the diet between months and animals heavily supplement their diet with fruit, seeds, flowers, and other items (Stanford 1991b; Podzuweit 1994; Koenig and Borries 2001).

Hanuman langurs show great diversity in their social organization and social system has been thought to reflect certain ecological conditions. Groups size ranges from 11 to 64 members and the number of resident males ranges from 1-14 (Newton 1988; Moore 1984). Group compositions can vary spatially and temporally as well between single male and multimale. Studies from 29 hanuman langur sites have shown that male composition ranges from 100% single male at certain sites to 100% multimale at others with considerable range in between (Oppenheimer 1977; Bishop 1979; Koenig and Borries 2001). While many factors may contribute to this phenomenon, several attempts to address the issue have concluded that the number of group males is correlated with the number of group females (Newton 1988). The presence of either system is most likely a result of variation in the ability of males to monopolize females (Emlen and Oring 1977; discussion in Koenig and Borries 2001). Those sites where it is feasible to monopolize females one male groups dominate and visa versa. Females are normally philopatric with males dispersing at adolescence. Males may form all male bands or disperse directly into another group with a short or no transition phase. Male residency patterns may vary including full time residency, influx during breeding seasons, and frequent transfer near the end of their reproductive careers in multimale groups (Borries 2000).

Home ranges in Hanuman langurs vary considerably between sites. Reported values for home range size vary between 19 (Sugiyama 1964) and ~1,275 (Curtin 1975) hectares. Population densities are also quite different between sites ranging from 121 (Starin 1978) and ~2 (Curin 1975) (for review of home range and densities see Kirkpatrick 2007). This is not particularly surprising given the extreme range of habitats used by the Hanuman langur.

Goals

In this project I investigated some proximate reasons for variation in both the size and use of monthly Hanuman langur home ranges near Ramnagar, Nepal. I accomplished this by totaling grid square use of two groups to create monthly home range size. Using the values of cell use I then compared these values to measures of temperature, rainfall, phenology, activity, diet, group size, number of receptive females, and the intergroup encounters. The predictive power of these variables will give an indication of their significance in determining range size and the patterns of use. Many studies have found correlations between some of these variables and home range size and use but none to my knowledge have combined behavioral and ecological factors. Also, few studies have gone beyond correlational analyses and explored the predictive power of these variables.

Predictions for these variables are shown in Tables 1 and 2. It is expected that all ecological variables except mature leaves and specifically used locations (geophagy and water holes) will lead to larger home range sizes. Warmer temperatures should allow animals to range further and higher rainfall, which is coupled with higher food availability, should both increase size and evenness of use. If langurs are feeding on patchy resources (young leaves, fruits, and flowers) these too would lead to larger home ranges and more diverse ranging. When langurs are feeding on mature leaves at high levels it predicted that groups would use a reduced portion of their home range heavily. When groups must return to a specific location (waterholes and areas of geophagy) ranging is predicted to be concentrated on those areas even if total range size does not decrease. Intergroup encounters could have either a positive or a negative influence on range size and its use depending on animal’s response. If groups restrict their ranging to avoid encounters then range size should be small and Shannon’s index low. If encounters cause groups to move further to avoid encounters then this would increase range size and the diversity of use. Activity variables are harder to predict because these do not take direction of movement into account and individual animals can be moving while the total group is not. When animals are feeding less it is expected that groups will be their inactivity will increase but their overall range size will also be large and have a higher Shannon’s index.

Materials and Methods

Study Site and Langur Population

The study site was a 12.6 km² part of the forest located near the town of Ramnagar, in the south of Nepal (latitude 27°44’N, longitude 84°27’E; Figure 1). The forest is a Sal (*Shorea robusta*, Diperocarpaceae) dominated monsoon forest with large seasonal fluctuations in temperature and precipitation (Koenig et al. 1997). It included 125 total tree and climber species, 105 of which were identified to the genus level (Wesche 1995). There were four major forest types identified (Wesche 1997) including Sal-forest (two types), Tropical Deciduous Riverain Forest, and East Nepal Tropical Evergreen Forest (definition of forest types in Stainton 1972).

Climate at Ramnagar is seasonal with large fluctuations in both temperature and rainfall throughout the year. Temperature ranged between 5 and 42.5°C overall but with large differences in the range between the two main seasons. The warm monsoon season (May-October) had higher average temperatures and a smaller temperature range (15.0-42.5°C) while during the drier winter period there was a much larger range (5-42°C). Temperature was recorded using a continuous thermohygrographic instrument. From this recording the temperature every two hours were extracted along with average, minimum, and maximum daily measures. Rainfall also varied greatly between seasons. Wet season months averaged 9.38 mm (287.7 mm/month) of precipitation per day while dry season months averaged only 0.55 mm per day (16.6 mm/month). Rainfall was collected using a commercial rain gauge. Figure 2 gives an ecological climate diagram (Walter 1984) of temperature and rainfall variation throughout the year.

During the study period (July 1991- April 1996) there were at least 290 langurs present within 19 bisexual groups. Group composition throughout the study was 72% multimale multifemale and the remaining 28% were single male multifemale (Koenig and Borries 2001). There were 1-6 males per group (average= 2.6) and 1-15 females (average= 6.7).

Focal Groups

For the current data from two study groups were used because they covered multiple months and years. P group was systematically observed between July 1991 and May 1996 while O group was observed between January 1994 and April 1996. Group P was the smaller group with 15.8 individuals and O group contained 22.7 individuals on average. All group members were recognized as individuals and were fully habituated to human observation. Group P averaged 7.5 females (range: 4-10) and 2.6 males (range: 2-7) while O group averaged 14.3 females (range: 13-15) and 4.4 males (range: 3-8). Both groups ranged in an extensive grid system (> 3 km^2) in which grid trees were marked every 64 m resulting in grid cells of 0.4 hectare (Figure 3).

Phenology

Measures of phenology were gathered at the midpoint of each month by using a crown density method (Koelmeyer 1959). The whole sample consisted of 307-317 trees and climber from 63 species including many langur foods (known from focal sampling of individuals; Podzuweit 1994) but also non-food species. If available a species was represented by a maximum of 10 individual plants except Sal, which was represented by 20 trees. Each month each individual plant was measured on a 4 fold scale for abundance of mature leaves, young leaves, fruits (ripe and unripe), and flowers. For this analysis these data were transferred into a presence-absence measure and for each month the percentage of trees and climbers bearing a specific phenophase was calculated. The resulting percentages were arcsin transformed before the use in any statistical analysis.

Intergroup Encounters

Intergroup encounters were recorded on an all-occurrence basis (Martin and Bateson 1993) and consisted of any instance where visual contact was made with another group or individuals and the focal group seems to perceive that other groups/individuals were present. Encounters were coded as follows: 0) no intergroup interactions the entire day, 1) meetings with another group, 2) meetings with adult or subadult males (single male from bi-sexual group males or all-male band), 3) meeting with another group and an adult male on the same day or meeting more than one group in the same day. Data was entered as an ordinal variable during analysis.

Receptive Females

Receptive females were labeled as those females observed copulating. Following Sommer et al. (1992), the receptive period was defined as sexual behavior on consecutive days not interrupted by more than 2 days. The receptive period could be limited to one day if it was accompanied by copulations. In addition, in this analysis females that solicited matings but were not in a receptive period were also included in the analysis. Solicitation usually consisted of the females presenting their anogential region to the male and then shaking their head side to side vigorously (Hrdy 1977). The number of receptive adult females will be labeled #RAF throughout the analysis.

Drinking

During some months of the dry season (e.g., March and April) there were few waterholes available for the langurs to drink from. Use of these specific locations may have affected the ranging pattern. Thus, generally, whenever the langurs were seen drinking this (and the place) was noted down in an ad libitum fashion (Martin and Bateson 1993). For the analysis each day within the month was coded for presence-absence (1-0) of drinking and a proportion calculated for each month. This gave a score where months with many visits to the water holes having a value closer to 1.

Diet and Activity

Both diet and activity were recorded via instantaneous focal animal sampling (Martin and Bateson 1993). All adult individuals within the group were observed according to a preset sequence determined at random and food/ activity type was noted either every 30 seconds or 1 min. Individual focal samples lasted for 30 min or 1 hour. Food types were classified as mature leaves, young leaves (including buds), flowers (all reproductive parts), fruits (both ripe and unripe), insects (spiders, caterpillars), geophagy and stone licking, and other. Data was averaged over each month for a given group. Activity was split into four categories: moving, inactive, feeding, and social (grooming). Altogether a total of 545 focal animal months was used in the analysis (P: 341; O: 204).

Data from P group comes from 2 study periods (Aug 91-May 93 and Jan 95-Apr 96) and data from O group was taken intermittently from Jan 93-Apr 96). Males and females are not equally represented in the sample. However, because, no differences in behavior was found in a previous analysis (Chalise 1995), data were pooled regardless of sex. Because the values are represented as percentages, all values were arcsin transformed before analysis.

Monthly Habitat Use

Habitat use was analyzed based on the use of a grid system shown in Figure 3 encompassing 370 squares of 0.4 hectares each. To establish grid square use 30 min scan samples (Martin and Bateson 1993) were performed and all grid squares with at least one group member present were noted. These values were summed per month and used in analysis. Groups P and O are shown within their home range in Figure 3. Group P was followed for 1028 days over 58 months while group O was followed 722 days over 28 months. The number of days per month ranged between 5 and 31. On average 23.5 and 23.7 scans were performed per day for groups O and P respectively (Table 3 and 4).

Statistical Analysis

To determine if habitats are chosen out of proportion to their availability, a Mann-Whitney U test was performed in SPSS 13.0 to see if animals are using grid squares within valleys out of proportion. This measure of habitat is the only measure available to determine habitat preference post hoc and only P group will be analyzed in this way. Secondly a G-test was preformed with expected values to test this relationship as well. Several variables were compared between groups including group size, home range size, and Shannon's index to test for significant differences between groups using a two tailed T-test.

Because some of the variables are likely to be correlated (e.g., ecology, diet, activity) data reduction was conducted before being used in a regression analysis. All dietary variables were subjected to a principle component analysis (PCA) and components with eigenvalues over 1.0 (for exceptions see results) were included in the regression. The same process was repeated for activity variables as well. A PCA was also used to reduce certain ecological variables. This included measures of temperature (max., min., and average), rainfall, and all phenological variables.

Monthly habitat use was measured in two ways. For home range size, the quadrant use was totaled for each month and the different grid squares were then counted to give the total number of quadrants entered. To investigate the diversity of range use, the Shannon index of diversity (Shannon and Weaver 1949) was also calculated per month. This value gives a representation of how diverse quadrant use was throughout the month. The formula for Shannon's index is:

$$H' = -\sum_{i=1}^{S} p_i \ln p_i$$

S represents the number of total grid squares. The relative use of each grid square (p_i) is calculated by finding the proportion of number of times each gird square is used divided by the total number of grid squares used during that month (n_i / N). A low value for Shannon's index indicates that groups are ranging in a concentrated percentage of their monthly home range while using other areas disproportionally less. A high Shannon's index means that groups are using each grid square more evenly. The highest index possible occurs when the group uses every square in equal numbers.

In order to investigate the best predictor(s) of home range size and diversity of use multiple stepwise regression analyses were performed using SPSS 13.0. Two analyses were performed per group. Both the number of quadrants entered and the Shannon index of diversity were used as the dependent variables within the multiple stepwise regressions. Independent variables within the regression consisted of the PCA factors for diet, activity, and ecology along with group size, intergroup encounters, and the number of receptive females.

Results

Figures 4 and 5 show the cumulative number of new grid cells entered throughout the study period. After a steep increase, P group did not enter many new grid cells from the ninth month of observation onwards, i.e., the cumulative number seemed to have reached an asymptote. O group, however, steadily increased its home range over the first 24 months of study never reaching an easily recognizable asymptote. Only after two years the curve finally leveled off, there was no increase in the number of grid cells entered. It should be noted that data for Figures 4 and 5 come from the entire study period at Ramnagar while only those months where diet and activity variables were collected are included within subsequent analyses.

Descriptive statistics for groups P and O are given in Tables 3 and 4 respectively. Group P entered more quadrants on average (P= 253.05; O= 214.81) and had a higher Shannon's Index of diversity than O group (P= 5.142; O= 4.999). Home range size was not significantly different but approached significance (p=.101, two tailed paired T-test) and Shannon's index also approached significance between group P and group O (p=.060, two tailed paired T-test). Group size was also significantly different between groups (p<.001, two tailed T-test) with the smaller group, P.

Principal Component Analysis of Activity, Diet, and Ecology

Activity Variables

When activity variables were entered into a PCA analysis each group returned two components what accounted for high levels of variation (P= 82.97%; O= 85.15%) shown in Table 5. For component 1, feeding (P= 0.914; O= -0.975) and inactivity (P= -0.977; O= 0.940) had the highest loadings in both groups but had opposite signs. Grooming was positive in both groups but was not consistently related to feeding or activity and moving had the lowest loadings in both groups. Component 1 appears to account most of the variation in feeding and inactivity with differing affects of grooming between focal groups.

Component 2 has little consensus in the loadings between groups, both in the sign and the value. The outstanding factor for Component 2 (Table 6) is the high loadings for moving (P= 0.974; O= 0.872). Component 2 is therefore primarily concerned with fluctuations in the amount of moving by groups P and O.

Figures 6 and 7 shows scatter plots of activity Components 1 and 2 for both groups P and O. Group P shows high levels of moving and moderate to high levels of feeding during the winter months (Nov-Feb) but in group P during February they are highly inactive. The warmer months show greater loading on inactivity and grooming in general for both groups.

Dietary Variables

PCA analysis revealed two very similar significant components from the 8 dietary variables entered into analysis for both groups. Total variance accounted for in Group P (77.35%) and O (62.38%) was high for each group (Table 7). In P and O the first component accounted for 28.43% and 36.27% respectively and had similar loadings in the component matrix (Table 8). Mature leaves (P= -0.882; O= -0.825) and other (P= -

0.698; O= -0.806) had the largest negative loadings while young leaves (P= 0.671; O= 0.755) and fruits (P= 0.592; O= 0.657) had the greatest positive loadings (Table 8). Between groups all variables in the component matrix had the same sign except insects and flowers. Component 1 appears to account for variation in feeding behavior upon leafy foods and to a lesser extent fruits.

Component 2 has slightly different matrix than Component 1 as shown in Table 8. Similar to Component 1 mature leaves has a negative loading and young leaves a positive. The greatest loadings, however, are for fruits (P= -0.690; O= -0.492), flowers (P= 0.488; O= 0.747), and geophagy (P= 0.772; O= 0.657). Component 2 still accounts for some variation in mature and young leaves but it is primarily concerned with the other two major plant parts and specifically used locations. Group P had 4 components with eigenvalues over 1.0 but only the first two were used because the first 2 components of each group matched closely. Also, eigenvalues for components 3 and 4 were closer to 1.0 and far below the eigenvalues for any other components (<1.734) (Table 7).

A plot comparing Component 1 and 2 is shown in Figures 8 and 9. Dry months cluster along the negative end of Component 1 when animals are feeding on mature leaves. March and April, warm dry months, are grouped together at the top of Component 2 in group P when animals are engaging in more geophagy then during other periods. The period of greatest leaf eating comes during April and May which is represented in Figures 8 and 9 as well. Other months are grouped with less distinction and seem to be centered during periods of interplay between mature leaf consumption and other factors.

Ecological Variables

Ecological variables returned two components with similar loadings for each group. These two components accounted for high levels of variance in the ecological variables (P= 85.38%; O= 87.81) and had large eigenvalues (Table 9). Component 1 had very high loadings for all measures of temperature (>0.929, Table 10). Young leaves was also positively loaded at high levels (P= 0.950; O= 0.955). Percentage of fruit (P= 0.660; O= 0.609), % flower (P= 0.615; O= 0.584), and rainfall (P= 0.573; O= 0.567) all had more intermediate yet still positive loadings as well. The percentage of mature leaves was the only factor in the matrix for Component 1 that had negative loadings (P= -0.409; O= -0.498).

Ecology Component 2 showed very different loadings from Component 1 (Table 9). Mature leaves and rainfall had the greatest positive values [(P= 0.822; O= 0.826) and (P= 0.720; O= 0.745) respectively]. Important negative loadings belonged to flower (P= -0.612; O= -0.674) and fruit (P= -0.347; O= -0.471). This component has an increased influence of mature leaves and rainfall compared to Component 1 while a decreased effect of temperature and young leaves.

Figure s 10 and 11 shows how Component 1 and Component 2 interact during the study period. These plots are markedly similar between groups and show a cluster of the dry cold months (Nov-Feb) at the left of the plot. This coincides with high levels of mature leaves in Component 1 and moderate levels of influence in Component 2. Values during spring months (Mar-Apr) are heavily influenced by temperature and young leaves in Component 1 and with the presence of flowers in Component 2. Summer months (May-Oct) have high levels of rainfall and mature leaves and are strongly influenced by Component 2.

Predictors of home range size and diversity of use

PCA variables, group size, number of receptive females, days per month (N), drinking at waterholes, and intergroup encounters were analyzed using a multiple stepwise regression with both the number of quadrants used and the Shannon index of diversity as the dependent variable.

This kind of an analysis might strongly depend on the number of days with which a group was observed in a given month. Thus, when the number of days per month was a significant predictor, months with low number of days observed were removed until the effect was absent. Subsequently, the analysis was run with the reduced data set. This effect did not occur in O group but was present in P and all months with fewer than 25 days were removed from analysis.

P Group

Regression of the number of quadrants entered in P group revealed that ecological factor 2 was the single greatest predictor of home range size per month, accounting for 35.8% (Table 12) of the variation in quadrant use. This component has high positive loadings for rainfall and presence of mature leaves and is negatively correlated (Table 11) with the number of quadrants used per month. The second best predictor (21.4%) of home range size was ecological factor 1 (Table 12). Factor 1 was positively correlated with quadrants used (Table 11) and has high positive loadings for temperature and young leaf presence (Table 10). The only negative loading in ecology factor 1 was mature leaves which complement the fact that ecology 2 was the greatest predictor in the regression and was negatively correlated with mature leaves. The last predictor for P group was the number of receptive females present in the group. This factor was negatively correlated with home range size (-0.446: Table 11) and accounted for 12.7% (Table 11) of the variation found in home range size. Altogether, high amounts of rain and mature leaves as well many receptive females are linked to smaller home range size, whereas higher temperatures and many young leaves to larger home ranges. Total variance accounted for in this analysis was 69.9% (Table 12).

Analysis of the Shannon index of diversity had rather different results. The number of receptive adult females was negatively correlated with the Shannon index (-0.626: Table 11) and was its greatest predictor (39.2%: Table 13). In other words, group P was using its home range less diversely when there were more receptive females. The second best predictor was ecological variable 1 (Table 13) which was positively correlated with the Shannon's index and accounted for 14.7% of the variation seen. Thus, with higher temperatures and more young leaves, the home range was used more diversely. Total variation accounted for by these two measures was 53.8% (Table 13).

O Group

Regression analysis of both O group's total home range size and diversity of use each had only one significant variable. Activity variable 1 was the single significant predictor for the number of quadrants entered and accounted for 37.2% of the variation shown (Table 15). These two factors are positively correlated with a score of 0.610 (Table 14). When the diversity of home range use was analyzed, activity 1 was again the single best predictor (25.2%: Table 16) and positively correlated (0.502: Table 14).

Activity factor 1 has high positive loadings for inactivity and high negative loadings for feeding. Thus, during periods of low feeding time, the home range was larger and used more diversely. Overall cumulative percentage of variance was much lower for O group when compared to P group.

Discussion

The results presented here generally showed that ecological variables can be strong predictors of home range size and use (Bennett 1986; Boinski 1987). However, demographic/ reproductive variables can be important as well (Strusaker 1975; Waser 1977; Watts 1991). In addition, results derived from individual groups may not necessarily represent general trends for a population or a species (Delfer 1996; Chapman et al. 2002; Dela 2007).

P was the only group to have any variation in the results of the regression analysis. Ecological variables dominated the analysis of total home range size. Between the two ecological variables the presence of mature leaves was always negatively correlated with home range size. Conversely the presence of young leaves was positively correlated. Ecology 2 and Ecology 1 have rather strong explanatory power and account for 57.2% of the variation in home range size (Table 12). Aside from temperature in Ecology 1, the main contributors to this pattern are the presence of leafy foods. So, in P group, ranging is partially dependent on the presence of young leaves in the environment but to a greater degree is negatively correlated with the presence of mature leaves. The fact that animals are shifting their ranging behavior to exploit a patchy and nutritionally valuable resource would refute the assumption that folivores are only using large, ubiquitous, and non-depletable patches and the predictions that stem from this assumption (Milton and May 1976; Clutton-Brock and Harvey 1976; Wrangham 1980). Travel costs are increased but so are benefits from feeding on young leaves. Variation in Shannon's Index was also partially explained by ecological factors. Ecology 1 is significant and accounts for 14.7% of the variation in Shannon's Index. So the presence of mature and young leaves help determine home range use but with less significance than in determining home range size. Increasing temperature was also correlated with larger home ranges and more diverse use of those ranges. Rainfall was positively correlated in one factor (Ecology 2) and positively correlated in another (Ecology 1) so rainfall is probably not an important influence in determining home range size or use but is more closely tied to changes in food availability which is an important factor.

The number of receptive females present in group P was the best predictor for variation in Shannon's index and the third best predictor for variation in home range size. Receptive females were negatively correlated with both measures (Table 11) so groups were using a smaller home range and using restricted areas heavily during periods with many receptive females. Males would be expected to keep their group in the core area of their range to exclude extra-group males from copulating with receptive females (Kitchen et al. 2004). Females were not expected to avoid extra-group males when receptive but only when they had dependent offspring that would be at risk of infanticide if group males were overthrown. Group males have been shown to distinguish potentially fertile females (Borries et al. 1999; Ostner et al. 2006) and they may take female receptivity into account when making travel decisions and try to avoid other groups when females are receptive to increase their probability of paternity. If this is true it would represent an attempt to guard females from extra-group males at the group level. It would be expected that this behavior would have more influence in larger groups with more females but O group showed no effect. Perhaps the increase in group size forced the larger group to continue ranging further to satisfy energetic demands even when females were receptive.

Because Ramnagar is seasonal, the timing of reproductive events are closely tied to the ecology of the area (Koenig et al. 1997) and the number of receptive adult females is correlated with the two measures of ecology. Females are receptive during the end of the monsoon season when mature leaves are more abundant than any other food resource so this effect could have confounded results. However it appears that the presence of receptive females has an influence on ranging behavior which, to my knowledge, has not been shown before in a primate which lives in permanently cohesive groups.

Results of the regression analysis in O group had confusing results at first glance because Activity 1 is the best predictor for both total range size and the use of that range. Activity factor one had high positive loadings for inactivity and high negative loadings for feeding. The high levels of variation that this factor accounts for is perplexing until you look at the correlation matrix in Table 14. Activity 1 has high positive correlations with both Diet 1 and Ecology 1. Both of these factors have negative loadings for the use and presence of mature leaves and positive loadings for the use and presence of young leaves. So the activity patterns seen and their high predictive power could be an effect of variation in ecological and dietary factors. Considering these correlations, O group has results more comparable with P group.

This result becomes clearer when you consider the seasonal habitat at Ramnagar and the corresponding changes in food availability. Individual's caloric intake at Ramnagar increases dramatically during the summer months (Koenig et al. 1997) when food availability is high. Groups are required to move further to reach patchy, high quality resources but the actual feeding time needed upon reaching those sites is lower than during dry months (Koenig et al. 1997). Because animals can intake significantly more calories in a shorter period of time, inactivity is expected to increase as feeding decreases (Boinski 1987; Newton 1992; Sayers and Norconk 2008). During dry periods when food availability is low, animals fallback on mature leaves which are lower in value and they must feed longer to meet energetic demands in a more restricted and heavily used section of their home range**.** Langurs at Ramnagar are, however, losing weight during these periods (Koenig et al. 1997) and rely on energy reserves created during the wet season. The presence of these high quality resources and their distribution are influencing activity budgets which are accounting for variation in home range size and use patterns.

No dietary factors accounted for significant levels of variation for either total home range size or evenness of use. This is surprising because the utilization of specific dietary variables have been shown to correlate with ranging patterns in several primate taxa (Raemaekers 1980; Bennett 1986; Strier 1987; Garber 1993; Olupot et al 1997; Goldsmith 1999; Di Fiore 2003; Doran-Sheehy et al. 2004; Wallace 2006). While most dietary variables were positively correlated with both dependent variables, no correlation coefficient was greater than ±0.546 (Table 11 and 14). Diet 1 and Ecology 1 are significantly correlated (P=0.829; O=0.850) and Diet 2 and Ecology 2 are moderately correlated (P= -0.565; O= -0.579) which supports the documented tendency for Hanuman langurs to employ a generalist feeding strategy (Koenig and Borries 2001; Sayers and Norconk 2008). When both ecological variables were removed from the analysis, however, dietary variables were still not significant in either group. Regression of dietary variables only (PES unpublished) showed that, for the Shannon's index, neither variable was a significant factor indicating that food preference has little influence on the diversity of range use in the langurs at Ramnagar. Range size, in the same analysis, showed low predictive power for Diet 1 in both groups P and O.

It appears that at Ramnagar groups are using an energy minimizing strategy during periods of low food availability. This strategy is present in both the reduction of home range size during periods of reliance on mature leaves and in the increase in feeding behavior in O group. Digestion time must increase to break down low quality food and total food intake must also increase in an effort to satisfy energetic demands. Home range size, in P group, is significantly reduced during periods when mature leaves are present at high levels and the opposite when young leaves are more abundant (Table 12). This is not particularly surprising given the morphological adaptations that Hanuman langurs possess. But the fact that the presence of young leaves accounts for an increase in home range size suggests that simple categories such as "folivore" do little in predicting primate ranging behaviors. The dispersed and patchy food sources used by the langurs of Ramnagar seem to exert a significant influence on ranging behavior that mirrors the affects of fruit availability in frugivores (Raemaekers 1980; Bennett 1986; Strier 1987; Garber 1993; Olupot et al 1997; Goldsmith 1999; Di Fiore 2003; Doran-Sheehy et al. 2004; Wallace 2006). Mature leaves can be viewed as a staple fallback food (Marshall and Wrangham 2007) that is relied upon when preferred foods, young leaves, are absent (Koenig and Borries 2001).

The use of specific locations within the group’s home range did not play a significant role either. The habitual use of areas of geophagy and year round water holes is thought to constrain home range size and the evenness of its use because sites must be revisited often (Altmann and Altmann 1970; Scholz and Kappeler 2004; Campos and Fedigan 2008). Diet 1 accounted for most of the variation in geophagy but correlations with range size and use differed in sign (Tables 11 and 14). From these values it appears that P group is not constrained to areas of geophagy and actually travel further on days when these sites are utilized. O group’s slight negative correlations between Diet 2 and both range size and Shannon index would suggest that groups are traveling shorter distances when using these areas of geophagy at a high level, but the relationship is weak at best. It appears that the langurs at Ramnagar are not affected by geophagy at high enough levels to seriously change their ranging patterns. Geophagy peaks during the spring months when groups are feeding primarily on young leaves which have been shown to increase travel so the effect of soil eating might be negated. The location of these sites could also explain this trend if they are not far enough away from the group’s core area to significantly increase overall ranging patterns. Drinking at year round water holes was positively correlated with home range size and use for both groups P and O (Table 11 and 14). This refutes the hypothesis that groups would center their home range use around these areas during drought periods (Altmann and Altmann 1970; Scholz and Kappeler 2004; Campos and Fedigan 2008). Ecology 2, which has high positive loadings for rainfall, is negatively correlated with visits to the water hole which suggests that groups are visiting this site less when rainfall is more plentiful, however. Because groups still visit this site throughout the year, even during the monsoon period, the effect of this variable during the dry seasons might be lost within the year round variation. Perhaps analysis of only the dry season would reveal a significant influence of visitation to permanent water holes.

Group size was never a significant factor in any analysis. While there is a significant difference in the size of the two focal groups the variation within groups was not strong enough to affect total range size or use. Groups had moderate fluctuation in group size (P= 13-20; O= 21-25) but this had no predictive power. While average group size was significantly different, the smaller group (P) had, on average, larger home range sizes and a greater Shannon's index. These differences, too, were significant. This could be a result of differences in home range quality and distribution of resources throughout the range. Comparisons of group size between groups could be performed by combining both P and O in a regression analysis but this has not been preformed.

Intergroup encounters were not a significant factor in any analysis. In P group they were negatively correlated with home range size and very weakly positively correlated with the Shannon index (Table 11) while in O group intergroup encounters were positively correlated with both measures of home range (Table 14). The lack of predictive power and similarity in correlations could be a result of the coding used to classify these encounters. The classifications used were very broad and the same code might have incorporated two very different encounters. Also the demography of the neighboring groups was not controlled for in the analysis. If focal group's reactions are dependent on the threat level of the other group/males (Ydenberg et al. 1988; Wich and Sterck 2007) then this effect would not be clear in the results. Truly testing this hypothesis would require a much more detailed approach in cataloging intergroup encounters based on a finer scale of measure of treat level.

There are many possible reasons for the differences seen between the two focal groups (Chapman et al. 2002). Group P was influenced by both ecological factors and the presence of receptive adult females. This group had a both a larger sample size and a more even spread between months while O group had several months only represented once. Affective sample sizes, once months with less than 25 days were removed from P, were close (P= 19; O= 16) but PCA results were created before the removal of these months. It should be noted that when months with less than 25 days were removed from O group there was no change in the significant variable, Activity 1. Home range quality and distribution are other unmeasured variables that could have differed between the two groups. There are high levels of overlap, however, between these two groups and each group also overlapped with other, non focal, groups. Total overlap throughout the study period for P group was 48.8% and 44.3% for group O and this overlap area encompassed both the water hole and the area of geophagy. Because of this extensive overlap, it seems unlikely that differences in habitat quality are driving the differences seen in ranging quality, but this hypothesis cannot be tested at this time.

The applicability of this model should be approached with caution. There are other measures of diversity that could have been used other than Shannon's index which may have produced different results. Also, while most major historical influences on ranging and habitat use are addressed this model might not work for all primate species. For example, predictive power for species with a fission-fusion social system would likely be low because of the highly variable ranging patterns between sexes and variation in group composition. In highly seasonal environments the effect of shifts in rainfall, temperature, and food availability could overwhelm the travel decisions made based on behavioral and other ecological variables. This effect however is justified because of the documented effects of ecology on Hanuman langur behavior and life history traits

(Koenig et al. 1997; Borries et al. 2001). Application of this model in other (tropical) environments could illuminate behavioral regulation of home range size and use because groups are less constrained by environmental pressures. Regression analysis of folivore groups living in a less seasonal environment might show a stronger connection between ranging patterns and leafy food availability and other behavioral factors.

Conclusion

1. The ecology of the study area held the greatest predictive power when compared to total home range size with 57.2% of variation accounted for P group. The presence of leafy foods appears to be the greatest factor in determining overall range size, along with temperature. The interplay of ecological and dietary factors is most likely responsible for the high predictive power of activity variables in O group. Utilizing an energy minimizing strategy sets limits on range size and is reflected in the activity budgets of individual langurs. The presence of receptive females was significant in one group accounting for 12.7% of the variation in home range size.
2. How groups utilized their home range showed a greater importance for social variables in P group. The presence of receptive females was the greater predictor of use patterns and groups did not range as far as when females were receptive. Males seem to be restricting ranging during these periods to ensure paternity.
3. Diet factors had no significant predictive power in this analysis. This is perhaps because of the generalist foraging strategy of Hanuman langurs.
4. Groups are restricting home range size when foraging on mature leaves but forest Hanuman langurs are also feeding selectively on young leaves. Groups are increasing their home range size and the evenness of its use when exploiting this resource. This ranging pattern is typical in frugivorous primate species but evidence in folivorous primates has been mixed. During periods of low food availability, groups fallback on mature leaves and range size and the evenness of use decreases.
5. The total home range size may be a function of ecological conditions and their corresponding effects on activity budgets but the actual use of the home range could be more influenced by social decisions than previously though. This result was only seen in one group, however, and results have to be treated with caution.

Tables

Table 1: Predictions for factors with increasing home range size

Variable	Increasing HR size	Variable	Increasing HR size	Variable	Increasing HR size
Temperature	+	Mature Leaves	-	Inactive	-
Rainfall	+	Young Leaves	+	Feeding	+
Specific Locations	±	Fruits	+	Moving	+
Group Size	+	Flowers	+	Grooming	-
IGE	±	Insects	+		
Receptive Females	+	Geophagy	±		

Table 2: Predictions for factors with increasingly Shannon's Index

Variable	Increasing SI	Variable	Increasing SI	Variable	Increasing SI
Temperature	+	Mature Leaves	-	Inactive	-
Rainfall	+	Young Leaves	+	Feeding	-
Specific Locations	-	Fruits	+	Moving	+
Group Size	+	Flowers	+	Grooming	-
IGE	±	Insects	+		
Receptive Females	+	Geophagy	-		

Table 3: Descriptive Statistics, Group P

	N	Min.	Max.	Mean	Std. Dev.
N	19	25	31	28.68	1.857
# Quad	19	186	341	253.05	40.529
Total cells	19	1201	2332	1803.11	323.946
Shannon index	19	4.815	5.4189	5.142	0.163
# scan samples	19	18.60	26.00	23.50	2.08
Group Size	19	13.0	20.0	15.461	2.258
IGE	19	0.037	0.778	0.363	0.213
Rain	19	0.000	21.465	5.485	7.192
T mean	19	12.794	30.846	22.949	5.958
T max	19	18.846	38.563	30.441	6.131
T min	19	8.583	24.575	17.834	6.043
Drink	19	0.111	0.667	0.363	0.168
#RAF	19	0.000	1.875	0.361	0.659
ML	19	0.144	67.019	26.416	23.594
YL	19	0.559	69.892	25.619	20.627
Fruit	19	0.977	83.099	20.984	22.401
Flower	19	0.000	37.814	10.346	13.338
Insect	19	0.000	18.961	1.037	4.342
Geophagy	19	0.000	18	4.12	6.236
Drink	19	0.000	0.715	0.176	0.191
Other	19	1.010	38.147	11.296	10.676
% moving	19	1.973	7.428	4.469	1.550
% grooming	19	0.042	15.651	5.761	4.220
% feeding	19	15.957	49.597	30.750	11.732
% inactive	19	34.015	79.264	59.020	14.684
% ML	19	49	100	85.77	16.683
% YL	19	9.491	99.331	49.494	34.893
% Fruit	19	18.310	34.667	23.720	4.689
% Flower	19	3.729	29.932	15.607	9.493

Table 4: Descriptive Statistics, Group O

	N	Min.	Max.	Mean	Std. Dev.
N	16	21	31	28.31	2.726
# Quad	16	151	291	224.81	49.490
Total cells	16	1356	2448	1898.50	310.918
Shannon index	16	4.666	5.314	4.999	0.227
# scan samples	16	20.90	26.10	23.70	2.03
Group Size	16	21.0	25.0	22.358	1.269
IGE-2	16	0.071	0.692	0.352	0.189
Rain-2	16	0.067	20.728	6.359	7.877
T mean	16	13.267	30.631	22.752	5.968
T max	16	20.473	38.331	30.0658	6.116
T min	16	8.577	24.683	18.049	6.042
Drink	16	0.333	0.806	0.506	0.141
#RAF	16	0.000	2.065	0.738	0.736
ML	16	1.139	83.960	41.936	28.685
YL	16	0.000	61.494	19.385	21.796
Fruit	16	1.999	80.699	21.648	19.767
Flower	16	0.000	43.021	7.539	11.803
Insect	16	0.000	4.614	0.484	1.162
Geophagy	16	0.000	9.979	2.415	2.724
Drink	16	0.000	0.740	0.250	0.218
Other	16	1.980	14.911	6.343	3.696
% moving	16	2.597	5.892	4.512	0.974
% grooming	16	1.918	8.939	5.729	1.917
% feeding	16	22.371	52.014	36.105	11.723
% inactive	16	38.557	69.195	53.653	11.085
% ML	16	12.162	99.331	48.688	32.421
% YL	16	4.068	29.932	13.296	9.042
% Fruit	16	16.776	34.667	22.7941	4.934
% Flower	16	49.000	99.671	87.102	16.534

Table 5: Total Variance Explained by PCA of Activity variables

Group P				Group O			
	Initial Eigenvalues				Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %	Component	Total	% of Variance	Cumulative %
1	2.321	58.022	58.022	1	2.175	54.369	54.369
2	0.998	24.948	82.971	2	1.231	30.782	85.151

Table 6: Component Matrix for PCA of Activity Variables

	Component			Component	
Group P	1	2	Group O	1	2
arcsin moving	0.209	0.974	arcsin moving	0.143	0.872
arcsin grooming	0.699	-0.181	arcsin grooming	0.566	0.591
arcsin feeding	0.914	-0.126	arcsin feeding	-0.975	0.187
arcsin inactive	-0.977	-0.038	arcsin inactive	0.940	-0.294

Table 7: Total Variance Explained by PCA of Diet variables

	Group P				Group O		
	Initial Eigen values				Initial Eigen values		
Component	Total	% of Variance	Cumulative %	Component	Total	% of Variance	Cumulative %
1	2.274	28.425	28.425	1	2.902	36.274	36.274
2	1.734	21.674	50.099	2	2.088	26.105	62.379
3	1.122	14.020	64.119				
4	1.058	13.228	77.346				

Table 8: Component Matrix for PCA of Diet variables

	Component					Component	
Group P	1	2	3	4	Group O	1	2
arcsin ML	-0.882	-0.222	-0.008	0.041	arcsin ML	-0.826	-0.290
arcsin YL	0.671	0.316	0.089	-0.432	arcsin YL	0.755	0.349
arcsin fruits	0.592	-0.690	0.099	-0.034	arcsin fruit	0.657	-0.492
arcsin flowers	0.231	0.488	0.128	0.550	arcsin flower	-0.355	0.747
arcsin insects	-0.045	0.051	0.768	0.452	arcsin insects	0.656	0.266
arcsin geophagy	0.342	0.772	-0.194	0.038	arcsin geophagy	0.055	0.657
arcsin drinking	0.191	-0.205	-0.670	0.577	arcsin drinking	0.093	0.722
arcsin other	-0.698	0.479	-0.105	-0.167	arcsin other	-0.806	0.240

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Table 9: Total Variance Explained by PCA of Ecological variables

Group P				Group O			
	Initial Eigenvalues				Initial Eigenvalues		
Component	Total	% of Variance	Cumulative %	Component	Total	% of Variance	Cumulative %
1	5.010	62.631	62.631	1	4.941	61.767	61.767
2	1.820	22.753	85.384	2	2.083	26.039	87.806

Table 10: Component Matrix for PCA of Ecological variables

	Component			Component	
Group P	1	2	Group O	1	2
Rainfall	0.573	0.720	Rainfall	0.567	0.745
T mean	0.980	0.087	T mean	0.971	0.139
T max	0.973	-0.022	T max	0.971	0.040
T min	0.944	0.289	T min	0.929	0.333
arcsin %YL	0.950	0.202	arcsin %YL	0.955	0.195
arcsin %flower	0.615	-0.612	arcsin %flower	0.584	-0.674
arcsin %fruit	0.660	-0.347	arcsin %fruit	0.609	-0.471
arcsin %ML	-0.409	0.822	arcsin %ML	-0.498	0.826

Table 11: Pearson Correlations for Group P

	# Quad	S.I.	Gr Size	IGE	Drink	#RAF	Diet 1	Diet 2	Act. 1	Act. 2	Ecol 1	Ecol 2	N
# Quad	1.000	0.852***	-0.268	0.009	0.570*	-0.446(*)	0.464*	0.378	-0.171	-0.065	0.467*	-0.598**	0.202
Shannon index	0.852***	1.000	-0.205	-0.188	0.529*	-0.626**	0.254	0.300	-0.170	0.052	0.160	-0.543*	0.375
Group Size	-0.268	-0.205	1.000	0.444(*)	-0.534*	0.279	0.003	0.490*	0.194	-0.001	-0.144	-0.059	-0.099
IGE	0.009	-0.188	0.444(*)	1.000	-0.261	0.613**	0.480*	0.116	-0.070	-0.584**	0.590**	0.236	0.055
Drink	0.570	0.529*	-0.534*	-0.261	1.000	-0.576*	0.235	0.177	-0.176	0.215	0.187	-0.619**	0.055
#RAF	-0.446(*)	-0.626**	0.279	0.613**	-0.576*	1.000	0.160	-0.280	-0.063	-0.400(*)	0.323	0.533*	-0.155
Diet 1	0.464*	0.254	0.003	0.480*	0.235	0.160	1.000	-0.049	-0.258	-0.704***	0.829***	-0.184	-0.014
Diet 2	0.378	0.300	0.490*	0.116	0.177	-0.280	-0.049	1.000	0.143	0.387	-0.101	-0.565*	0.022
Activity 1	-0.171	-0.170	0.194	-0.070	-0.176	-0.063	-0.258	0.143	1.000	0.384	-0.476*	-0.021	-0.029
Activity 2	-0.065	0.052	-0.001	-0.584**	0.215	-0.400(*)	-0.704***	0.387	0.384	1.000	-0.783***	-0.431(*)	-0.186
Ecol 1	0.467*	0.160	-0.144	0.590**	0.187	0.323	0.829***	-0.101	-0.476*	-0.783***	1.000	-0.007	0.113
Ecol 2	-0.598**	-0.543*	-0.059	0.236	-0.619**	0.533*	-0.184	-0.565*	-0.021	-0.431(*)	-0.007	1.000	0.062
N	0.202	0.375	-0.099	0.055	0.055	-0.155	-0.014	0.022	-0.029	-0.186	0.113	0.062	1.000

(*) p<0.10, * p<0.05 , ** p<0.01, *** p<0.001

Table 12: Model Summary of Group P Quadrant Entered Regression

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.598(a)	0.358	0.320	33.422	0.358	9.469	1	17	0.007
2	0.756(b)	0.572	0.519	28.118	0.214	8.018	1	16	0.012
3	0.836(c)	0.699	0.639	24.351	0.127	6.333	1	15	0.024

a Predictors: Ecol 2

b Predictors: Ecol 2, Ecol 1

c Predictors: Ecol 2, Ecol 1, #RAF

Table 13: Model Summary of Group P Shannon Index Regression

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.626(a)	0.392	0.356	0.1304	0.392	10.958	1	17	0.004
2	0.734(b)	0.538	0.481	0.1171	0.147	5.081	1	16	0.039

a Predictors: #RAF

Table 14: Pearson Correlations for Group O

	# Quad	S.I.	Gr Size	IGE	Drink	#RAF	Diet 1	Diet 2	Act. 1	Act. 2	Ecol 1	Ecol 2	N
# Quad	1.000	0.960***	0.073	0.327	0.270	0.425	0.546*	-0.059	0.610*	0.172	0.389	0.106	0.523*
Shannon Index	0.960***	1.000	0.015	0.289	0.209	0.373	0.369	-0.100	0.502*	0.293	0.214	0.160	0.464(*)
Group Size	0.073	0.015	1.000	0.265	0.183	-0.251	-0.159	0.054	-0.057	-0.196	-0.182	-0.077	-0.585*
IGE	0.327	0.289	0.265	1.000	0.274	0.542	0.171	0.195	0.698**	-0.208	0.507*	0.470(*)	0.063
Drink	0.270	0.209	0.183	0.274	1.000	0.097	0.214	0.073	0.191	-0.029	0.183	-0.083	0.167
#RAF	0.425	0.373	-0.251	0.542*	0.097	1.000	0.516*	-0.414	0.622*	-0.114	0.562*	0.691**	0.512*
Diet 1	0.546*	0.369	-0.159	0.171	0.214	0.516	1.000	0.000	0.670**	-0.254	0.850***	-0.122	0.629*
Diet 2	-0.059	-0.100	0.054	0.195	0.073	-0.414	0.000	1.000	0.169	-0.226	0.313	-0.579*	0.070
Activity 1	0.610*	0.502*	-0.057	0.698**	0.191	0.622	0.670**	0.169	01.00	0.000	0.828***	0.327	0.513*
Activity 2	0.172	0.293	-0.196	-0.208	-0.029	-0.114	-0.254	-0.226	0.000	1.000	-0.322	0.173	0.053
Ecol 1	0.389	0.214	-0.182	0.507*	0.183	0.562*	0.850***	0.313	0.828***	-0.322	1.000	0.000	0.607*
Ecol 2	0.106	0.160	-0.077	0.470(*)	-0.083	0.691**	-0.122	-0.579*	0.327	0.173	0.000	1.000	0.047
N	0.523*	0.464(*)	-0.585*	0.063	0.167	0.512	0.629*	0.070	0.513*	0.053	0.607*	0.047	1.000

(*) $p<0.10$, * $p<0.05$, ** $p<0.01$, *** $p<0.001$

Table 15: Model Summary of Group O Quadrant Entered Regression

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.610(a)	0.372	0.327	40.594	0.372	8.295	1	14	0.012

a Predictors: Activity 1

Table 16: Model Summary of Group O Shannon Index Regression

					Change Statistics				
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate	R Square Change	F Change	df1	df2	Sig. F Change
1	0.502(a)	0.252	0.199	0.2030	0.252	4.721	1	14	0.047

a Predictors: Activity 1

Figures

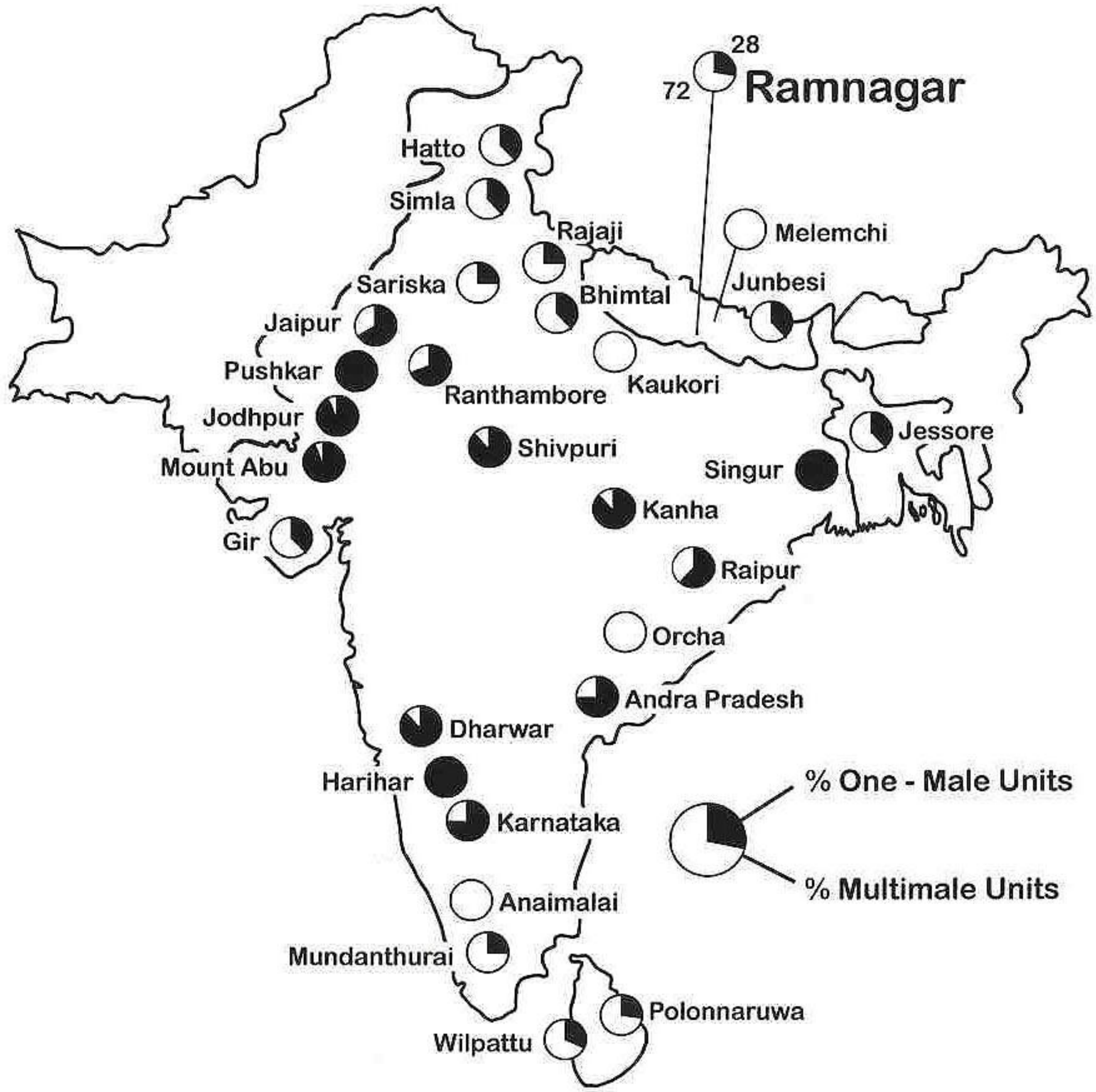

Figure 1: Locations where Hanuman langurs have been studies. Ramnagar is located in the south of Nepal and is bolded above. Pie charts show the social structure of groups at each site. (Figure taken from Koenig and Borries 2001)

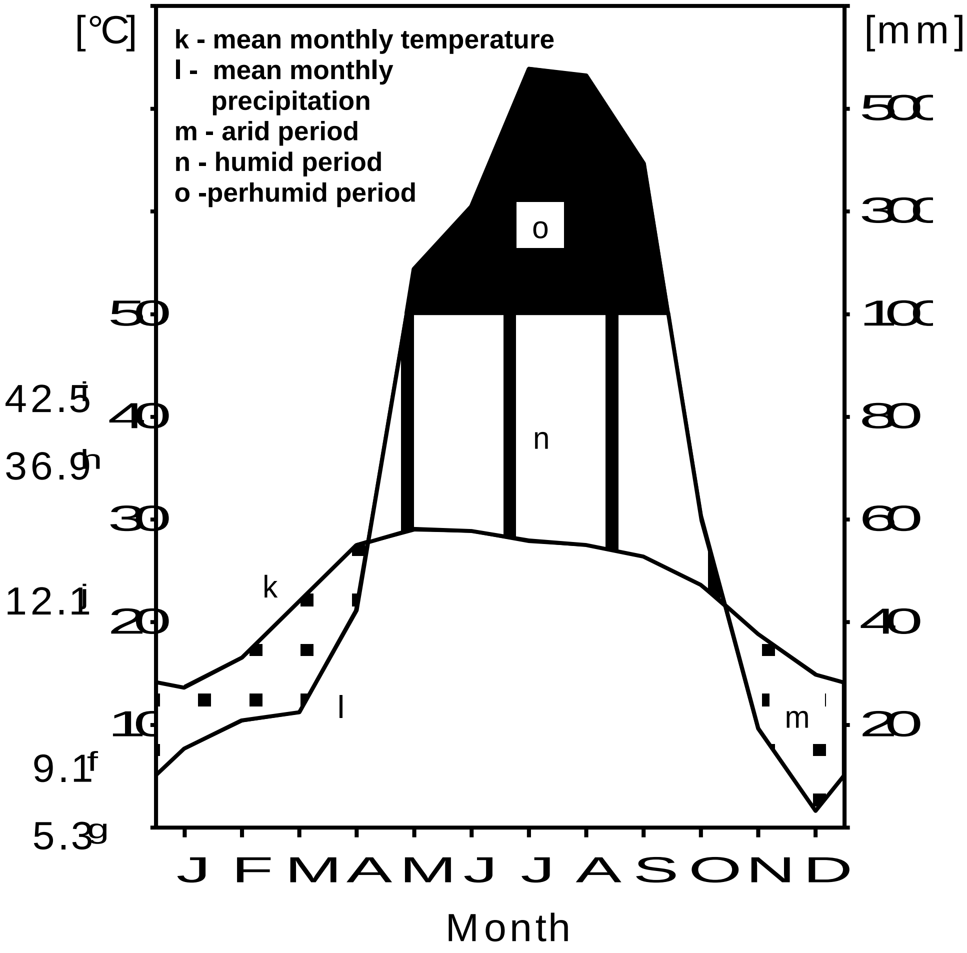

Figure 2: Yearly fluctuations in rainfall and temperatures at Ramnagar. Notice the highly seasonal monsoon season between May and October when the environment is classified as perhumid. April and November are classified as humid and the remaining 4 months are arid (Figure taken from Koenig et al. 1997; keys according to Walter 1990).

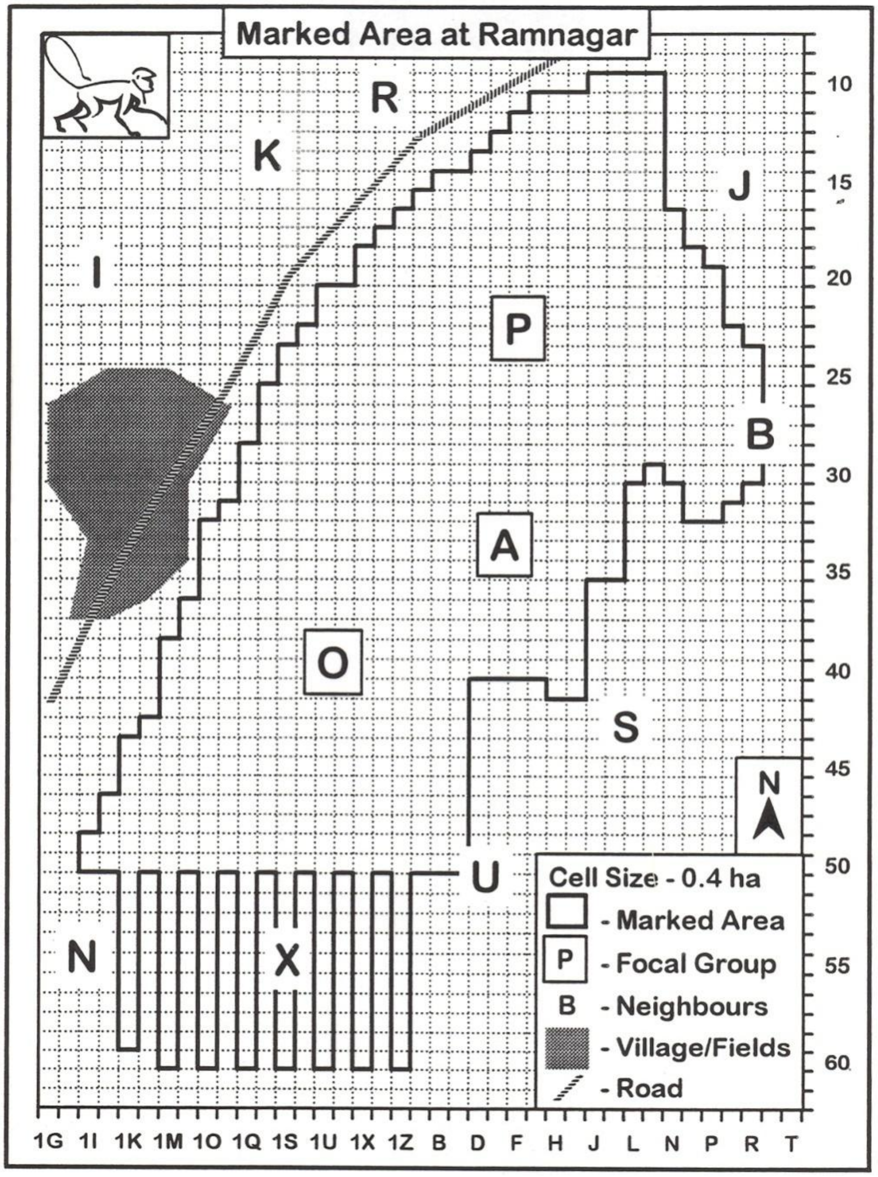

Figure 3: Grid network at Ramnagar, Each grid square is 64m². Focal groups P and O are shown near the center of their home range. .Groups interact primarily with neighboring groups. Figure courtesy of A. Koenig.

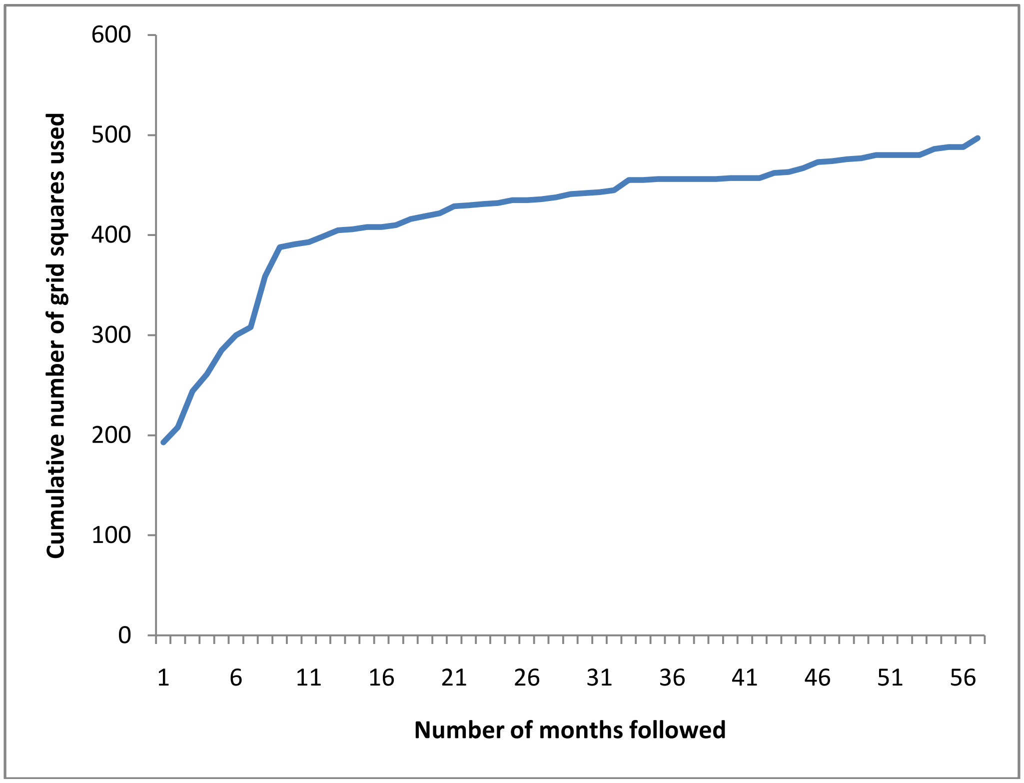

Figure 4: Cumulative number of grid cells entered by Group P derived from scan samples, Jul 1991- Apr 1996.

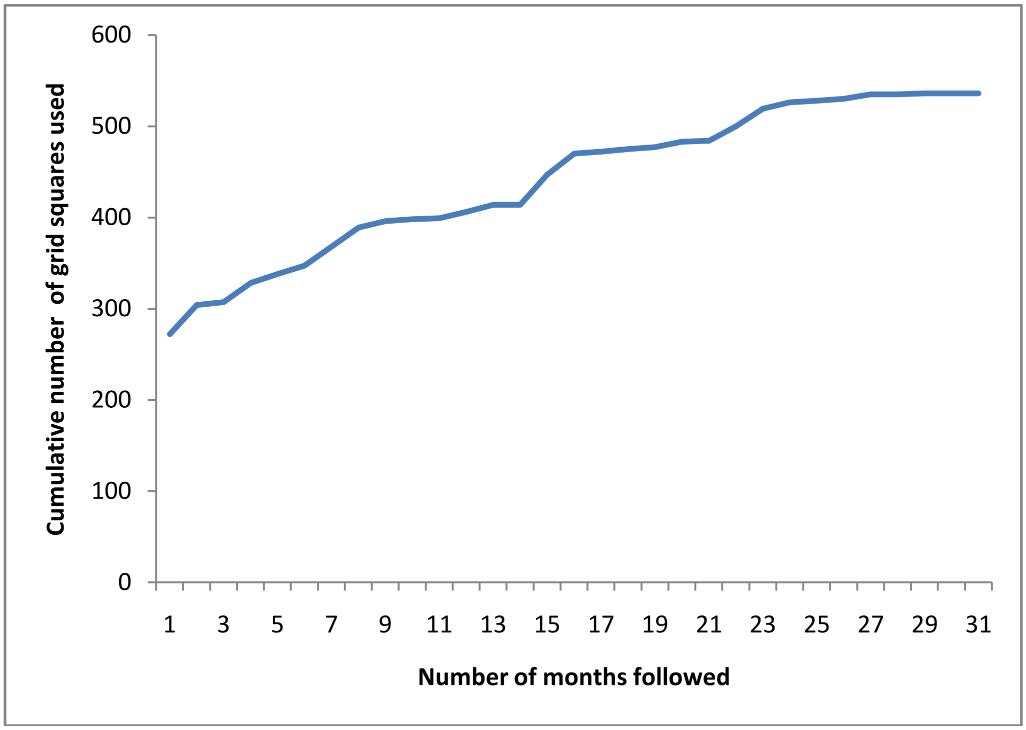

Figure 5: Cumulative number of grid cells entered by Group O derived from scan samples, Sep 1993-Apr1996.

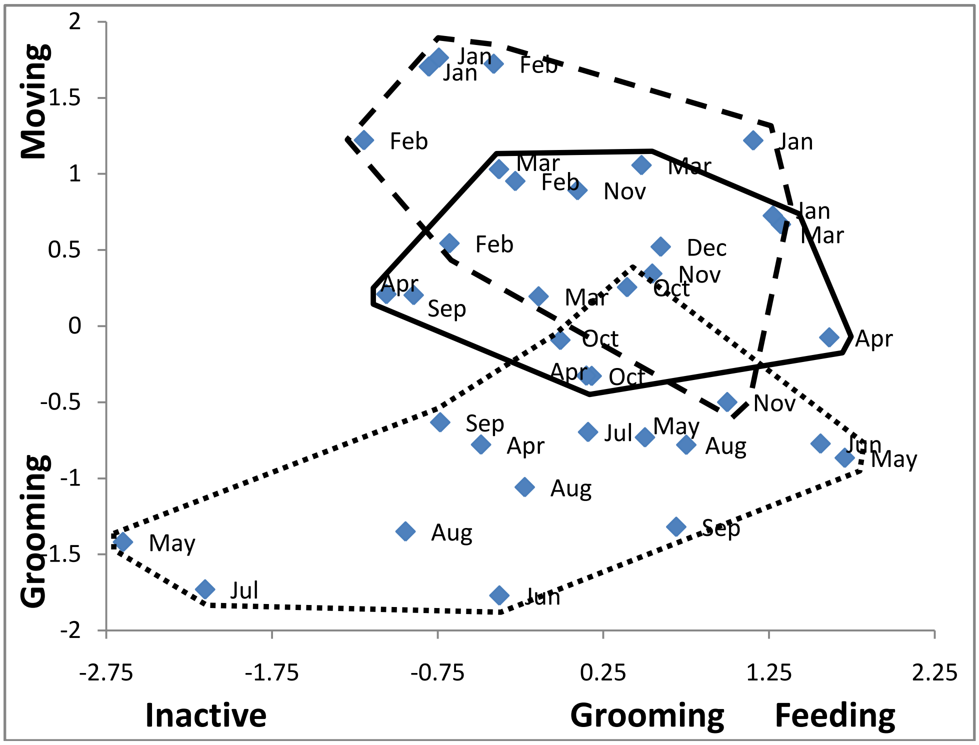

Figure 6: Scatter plot of Activity components 1 and 2 for group P. Activity 1 is on the x axis and Activity 2 is on the y axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

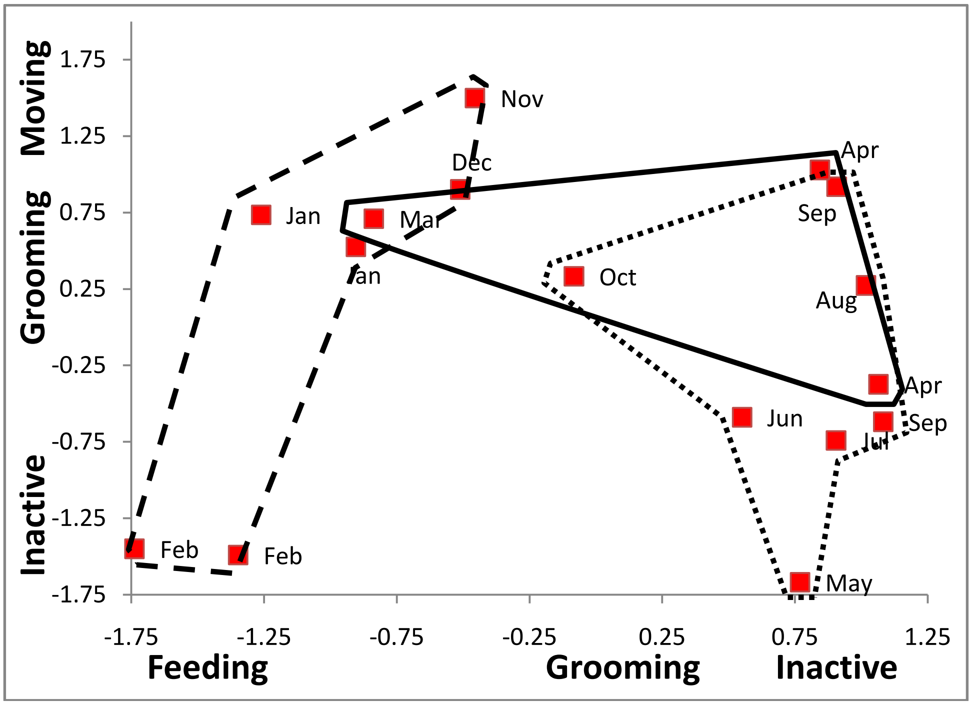

Figure 7: Scatter plot of Activity components 1 and 2 for group O. Activity 1 is on the x axis and Activity 2 is on the y axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

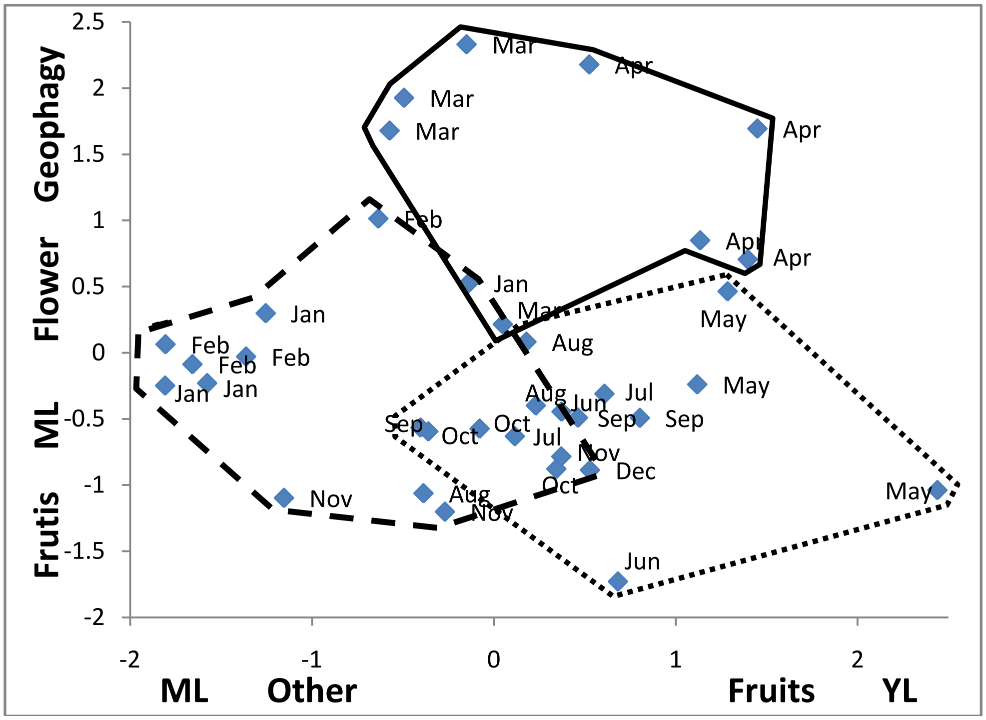

Figure 8: Scatter plot of dietary components 1 and 2 for group P. Diet 1 is on the x axis and Diet 2 is on the y axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

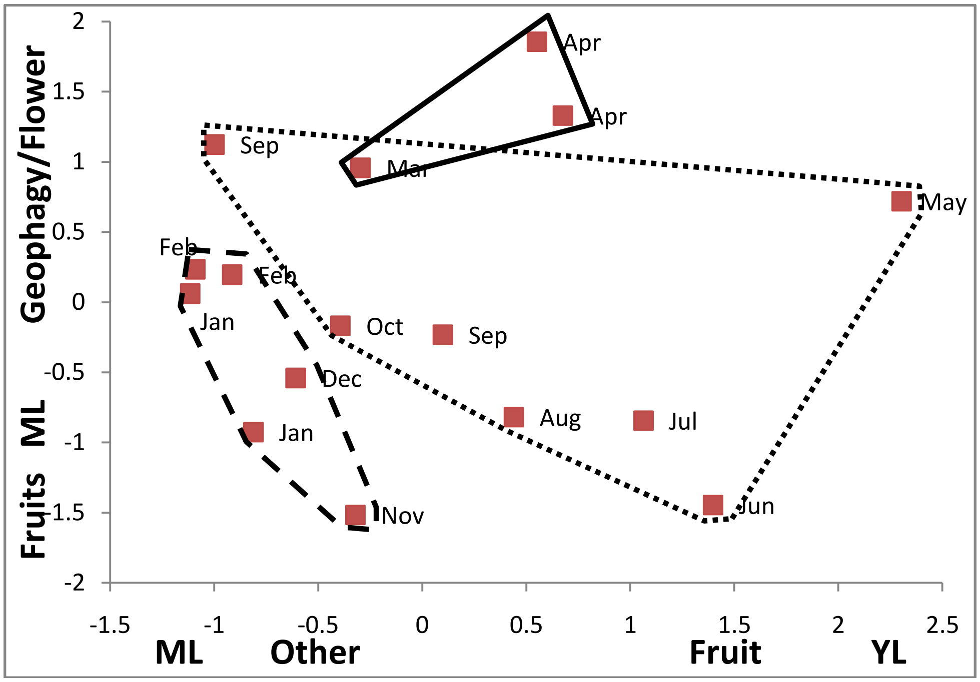

Figure 9: Scatter plot of dietary components 1 and 2 for group O. Diet 1 is on the x axis and Diet 2 is on the y axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

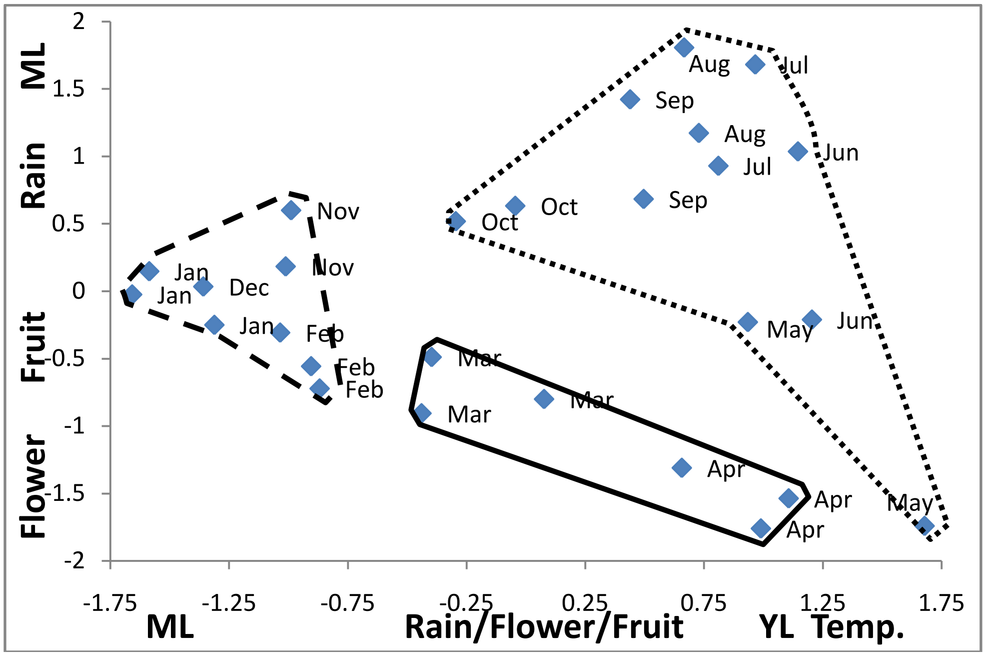

Figure 10: Scatter plot of ecological components 1 and 2 for group P. Ecology 1 is on the x axis and Ecology 2 is on the y axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

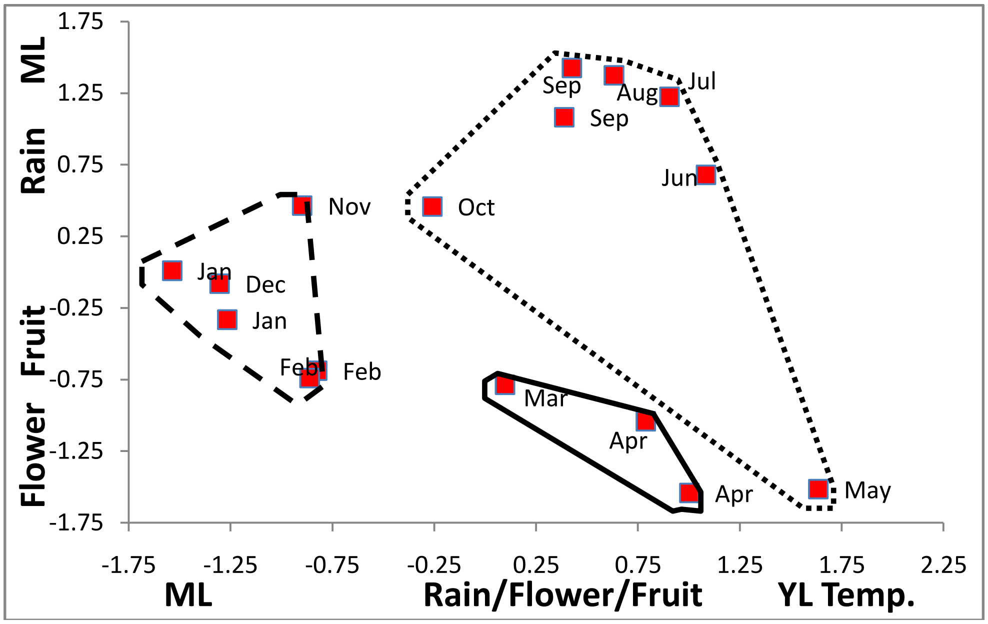

Figure 11: Scatter plot of ecological components 1 and 2 for group O. Ecology 1 is on the x axis and Ecology 2 is on the y axis. Polygons include dry cold months (Nov- Feb; dashed line), dry warm months (Mar-Apr; solid line), and warm wet months (May-Oct; dotted line).

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