PREDICTABILITY OF PLANT FOOD RESOURCES FOR MANTLED HOWLER MONKEYS AT HACIENDA LA PACIFICA, COSTA RICA: GLANDER'S DISSERTATION REVISITED

Differential use of food resources is one of the principal modes of coexistence among organisms. Groups of mantled howler monkeys (*Alouatta palliata* Gray) at Hacienda La Pacifica, Cañas, Guanacaste, Costa Rica, share an environment, tropical dry forest (see Frankie *et al.*, 1974), that is predictable ("autocorrelated") between seasons (Janzen, 1967; Jones, in press), but the degree of within-season predictability has not been evaluated. Since measures of predictability will reflect the carrying capacity of the environment at any time (see Roughgarden, 1979), howlers might be expected to use environmental cues to "track" temporal fluctuations in resource levels. In a time-varying environment such as that at La Pacifica, however, population parameters will at times "undershoot", at times "overshoot" carrying capacity and, at other times, variations in population parameters may be a function of environmental stochasticity ("discontinuity") rather than predictability.

The purpose of this note is to document variation (temporal heterogeneity) of food resources for mantled howler monkeys at La Pacifica in order to test the idea that where heterogeneity is "fine-grained" relative to generation time (T), animals will "track" the environment with behavioral and/or physiological rather than genetic mechanisms (Slobodkin and Rapoport, 1974; Emlen, 1973). A "fine-grained" environment is defined as one in which environmental variations are shorter than T (i.e., occur several times in an organism's lifetime). Based upon the census of mantled howlers at La Pacifica by Dr. Norman J. Scott, Jr. (U.S. Fish and Wildlife Service) and his assistants, including this author (reported in Malmgren, 1979), I have estimated T to be 6.27 years (Jones, in press).

Tree Abundance and Species Used for Food

The foraging strategy of *A. palliata* at La Pacifica has been described by Glander (e.g., 1975). His studies in riparian habitat showed that the diurnal and wholly herbivorous howlers spent about 24% of their yearly activity "budget" feeding. Six plant families accounted for about 75% of howler feeding time, and three of these (Anacardiaceae, Mimosaceae, and Papilionaceae) accounted for about 61% of total feeding time with about 18% of this total time spent feeding upon flowers (including buds). Glander showed that flowers, in addition to leaf flush and fruit, are a "preferred" food type for howlers who eat, for example, inflorescences of all six species of the Mimosaceae which they use for nutrients and energy. Glander (see also 1978, 1981) likewise demonstrated that five of these species (*Albizzia adinocephala*, *Enterolobium cyclocarpum*, *Inga vera* var. *spuria*, *Pithecolobium longifolium*, and *P. saman*) are among the 25 species used most often for food by howlers and that discriminative feeding may occur in response to phenological patterns within and between seasons, habitats, species, and individual trees that produce qualitative and quantitative differences among plant parts over time and space.

Glander (1975) identified every tree species used as food by one group of mantled howlers in riparian habitat at La Pacifica and classified each species by Family. The Spearman Rank correlation coefficient (r_s) between the number of species per Family used by these howlers and the number of individual trees of that Family present on the group's home range is positive (+0.79) and significant ($p<0.01$), suggesting that animals are primarily sampling from the most common Families of trees *that they use for food.*

Temporal Patterns of Food Available per Month

Glander (1975) reports the food available per month for the top 25 species used most often by his group. Food was categorized by tissue type - new leaves, flowers, and fruit the howlers' preferred diet. From Glander's data it is possible to calculate the number of species out of 25 producing new leaves, flowers or fruit each month. Table 1 presents these data. In absolute terms, there are more species producing new leaves than flowers, and flowers than fruit in each month except June, July, and August (wet season; see Frankie *et al.*, 1974) when more species are producing fruit than flowers. These calculations do not take into consideration variation in tree sizes or fluctuations in phenophases within and between months or hierarchical food preferences which might govern patterns of howler group dispersion over time (see Hubbell, 1979). Nonetheless, these data permit relative assessment of preferred plant tissue availability per month.

Table 1. The number of species producing new leaves, flowers and fruit per month for the top 25 preferred tree species (after Glander, 1975, Table 41).

Month	New Leaves	Flowers	Fruit
January	10	6	5
February	16	13	7
March	17	13	6
April	17	11	7
May	18	8	8
June	11	4	7
July	11	4	5
August	11	2	4
September	13	5	4
October	15	4	4
November	11	5	2
December	12	5	4

On average, 13.5 ± 2.9 (mean ± standard deviation) of the 25 top species are in new leaf phenophase per month, per year; 6.67 ± 3.73 species have flowers; and 5.67 ± 1.3 have fruit. The coefficients of dispersion for these phenophases are 0.62, 2.09, and 0.30, respectively. Absolute diversity of new leaves is greater across months than for flowers and fruit since more species exhibiting new leaf flush are available every month, on average. This pattern of preferred food availability may influence food choice and group dispersion in howlers, although these features of howler socioecology will also be affected by the number of individual trees per species, tree size and architecture, and food quality, as well as other factors (e.g., Schoener, 1971; D. E. Wilson, pers. comm.).

Coefficients of dispersion for new leaves and fruit are repulsed (more observations than expected around a central tendency), whereas flower dispersion is clumped (more observations than expected at tails of distribution). What do these phenomena imply for howlers? Clumping of species in flower shows that more of the 25 preferred species were in flower or not in flower than one would expect if flowering across species were independent. This effect could be explained by flowering synchrony within and between species and suggests that a similar proximate cue triggers flowering at about the same time across species across months. This cue is understood to be the cessation of rainfall in Central American forests (Janzen, 1967; Frankie *et al.*, 1974).

The repulsed distributions of new leaves and fruit are more difficult to interpret than the clumped distribution for flowers, although repulsion does imply that new leaves and fruit are more evenly dispersed across months since about the same number of species exhibit new leaves or fruit over time. Although the clumped distribution of flowers imply that they are a highly predictable food source to howlers *when they are available*, it is not clear whether the relatively even dispersion of new leaves and fruit translates into temporal predictability for howlers. It is likely that one advantage to organisms of foraging on a traditional home range would be an increase in relative stability gained from fine-tuned adjustment to the phenological rhythms of a constant set of trees (see Jones, 1983).

A coefficient of variation (CV) was calculated for the number of months preferred food (new leaves, flowers, and fruit) was available for the 25 favored species. Not every preferred tree species is used for each of the three phenophases. New leaves, flowers, and fruit displayed CV's of 0.30 (8.6 ± 2.6 months), 0.87 (5.3 ± 4.6), and 0.47 (6.3 ± 2.98), respectively. Apparently, the availability of flowers fluctuates more and new leaves and fruit, less, per month than either new leaves or fruit, consistent with the analysis of monthly species diversity as a function of tissue type already reported.

Glander's (1975, Table 41) results on tree phenologies also permit an evaluation of the relative degree of temporal clumping or randomness of new leaves, flowers and fruit for each species. A "runs test" (Siegel, 1956) was performed on the pattern of availability of each preferred phenophase for each of the 25 favored tree species. Sixteen "runs" (8 new leaves, 6 flowers, and 2 fruit) for 14 species could not be evaluated due to insufficient frequency of "runs". Twenty-five "runs" (9 new leaves, 11 flowers, and 5 fruit) of phenophases for 16 tree species exhibited a random pattern of plant tissue availability for one or more of the three preferred phenophases. Ten "runs" (1 new leaves, 5 flowers, and 4 fruit) of 9 of the 25 favored tree species exhibited significant clumping in time ($p<0.05$). That one or more phenophases of the 16 top tree species exhibited a random distribution in time and of 9, a clumped distribution in time, indicates that uncertainty and resource clumping are constant components of the local conditions in which howlers work to survive and reproduce (e.g., Wittenberger, 1980).

Conclusions

A reanalysis of Glander's (1975) data leads to the conclusion that howler populations at La Pacifica are influenced by both predictable and unpredictable factors related to the dispersion of their preferred food, within and between seasons. Emlen (1973) proposes that organisms in a "fine-grained" environment, such as that of the howlers in Guanacaste, will respond to temporal heterogeneity with behavioral and physiological responses and a monomorphic genotype. Malmgren (1979) has shown that howler genotypes are highly monomorphic, implying a "generalist" strategy (Emlen, 1973). Numerous studies document the rich array of behaviors (e.g., Jones, 1995) and physiological responses (e.g., Glander, 1978) displayed by howlers. Studies of the temporal heterogeneity of *A. palliata* and other taxa are important to basic as well as conservation ecology, since an increase in temporal heterogeneity with habitat fragmentation may lead to mortality, negative population growth, and eventual extinction. This observation implies that evolved strategies to the conditions described in this note are eventually limited in their ability to cope with environmental change.

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NOTES ON A DISTRIBUTIONAL RIVER BOUNDARY AND SOUTHERN RANGE EXTENSION FOR TWO SPECIES OF AMAZONIAN PRIMATES

Despite over twenty years of intensive field research in the Neotropics, new species of large mammals, particularly primates, are still being discovered today (e.g., Ferrari and Queiroz, 1994; Lorini and Persson, 1990; Mittermeier *et al.*, 1992). However, from a conservation viewpoint, new distribution records for endangered and threatened species are as important, for example, the significant population of giant otter, *Pteronura brasiliensis*, recently encountered in eastern Bolivia (Taber *et al.*, in prep.). As further regions of the vast Amazonian basin are explored it is vital to recognise the scientific and conservation importance of publishing sightings of rare and endangered species, particularly if localities represent range extensions.

Recent analysis has demonstrated the importance of river boundaries as limiting factors for the distribution of Amazonian primates (Ayres and Clutton-Brock, 1992). Intuitively, the low water width and annual discharge of a given river are important factors to consider when assessing the similarity of primate communities on each bank, since both are likely to affect the river-crossing ability of a given primate species. Ayres and Clutton-Brock (1992) measured the width of a river during the dry season at the midpoint of the river's length, and found that body size and the ability to colonize *várzea* (white-water inundated) or *igapó* (black-water inundated) forest habitats seem to be the most important interspecific differences in how rivers affect different primate species' distributions.

The following observations were made whilst conducting mammalian surveys and ecological research at "Lago Caiman" (13° 35.64' S, 60° 54.74' W) in the Flor de Oro region of the Noel Kempff Mercado National Park, between September 1991 and December 1992, and again from February to December 1995. This protected area is situated on the edge of the Brazilian Shield in north-eastern Santa Cruz Department, Bolivia. The eastern limit of the park is the Guaporé/Iteñez river which is also the border with neighbouring Brazil. At Flor de Oro the dry season river width is between 100-150 m.

In early April 1992, two primates, identified as white-faced bearded saki monkeys (*Chiropotes albinasus*) were observed in *igapó* forest at the river's edge in Brazil (13° 32.63' S, 60° 56.49' W). Both individuals had a striking red colouration around the nasal and genital areas. This species was not encountered again during this field season, probably because it predominantly occurs in *terra firme* forest, with only occasional reports