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Howling Monkeys and Leaf-Cutting Ants: Comparative Foraging in a Tropical Deciduous Forest

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ABSTRACT

Foraging by mantled howling monkeys (*Alouatta palliata*) and leaf-cutting ants (*Atta colombica*) is compared with regard to plant species harvested, plant parts harvested, statistical patterns in foraging effort, seasonal variation in foraging effort, daily foraging patterns, and foliage height attacked. This comparison is possible because intensive, year-long studies of foraging by three colonies of *A. colombica* and by a group of *A. palliata* were conducted in the same study area (Hacienda La Pacifica) in the Guanacaste Province of Costa Rica. The results show that howling monkeys and leaf-cutters differ in each of the categories mentioned above, yet share many foraging patterns. Both organisms are generalist herbivores, but are also selective. Both leaf-cutters and howlers harvest a variety of plant parts including mature leaves, new leaves, fruit, and flowers, and both cut more mature leaves and fruit in the rainy season and more new leaves and flower parts in the dry season. Both organisms prefer new leaves to mature leaves if given a choice. Nevertheless, howling monkeys and leaf-cutters prefer different plant species. Of seven rank correlations between monkey and ant preferences, three were negative, and the best positive correlation was 0.100, which was not significant. In addition, based on yearly averages, howlers harvest more new leaves and fruit and fewer mature leaves than do leaf-cutters. These results are compared with recent theoretical predictions concerning feeding behavior in generalist herbivores.

THE PURPOSE OF THIS PAPER is to compare foraging in mantled howling monkeys (*Alouatta palliata*) and leaf-cutting ants (*Atta colombica*). This comparison is possible because intensive, year-long studies of foraging by three colonies of *A. colombica* and by a group of *A. palliata* were conducted in the same study area in the Guanacaste Province of Costa Rica by Rockwood (1972, 1973a, 1975, 1976) and by Glander (1975a, 1975b, 1977). While it might appear unusual to compare foraging in two such different animals, there are compelling reasons to do so. Howlers and leaf-cutters are both generalist herbivores that co-occur throughout most of the neotropics (Moynihan 1976; Weber 1966, 1972). They are generalist herbivores in the sense that they consume quantities of material from many plant species. For example, Glander (1975a) found that howlers sampled 61 of 96 (63.5%) tree species present in their home range, while Rockwood (1972, 1976) found that a colony of *A. colombica* gathered material from 47 of 70 (67.1%) woody species present in their foraging area.

At the same time, both howlers and leaf-cutters are selective. Glander (1975a, 1977) found that howlers spent 75 percent of their feeding time in only 88 of 1699 trees present in the habitat. Rockwood (1976) has demonstrated similar selectivity in both *A. colombica* and *A. cephalotes*. In three colonies of *A. colombica* studied, 80-90 percent of the mature leaves cut by each colony were selected from 10 plant

species out of the 57-62 species available in a foraging area. Similarly, in three *A. cephalotes* colonies, the top six plant species of 36-44 available to each colony accounted for 82-95 percent of mature leaves cut. Howlers and leaf-cutters both harvest flower and fruit pieces and show decided preferences for new versus mature leaves. These preferences show seasonal patterns. Finally, both species depend on mutualistic relationships for digestion of the vegetation they consume. Howling monkeys have the usual mammalian intestinal flora and depend to an unknown degree on fermentation of their food in an enlarged caecum. Colonies of *Atta* feed on a fungus which is cultured on vegetation brought into the nest by the ants.

Thus, while howling monkeys and leaf-cutting ants are not closely related in an evolutionary sense, they appear to have converged ecologically as generalist herbivores in neotropical forests. Since both howlers and *Atta colombica* forage mainly in the forest canopy they may be important interspecific competitors.

In this paper we compare foraging by these two species, determine to what degree their foraging patterns differ, and compare our results with recent theoretical predictions made about feeding behavior in generalist herbivores (Freeland and Janzen 1974; Feeny 1975, 1976; Cates and Orians 1976; Rhoades and Cates 1976).

THE STUDY AREA

Both studies were conducted along the Rio Corobici, Hacienda La Pacifica, Guanacaste Province, Costa Rica (fig. 1). La Pacifica has been the site of many ecological investigations (Janzen 1970; Fleming *et al.* 1972; Fleming 1974; Fleming and Hooker 1975; Rockwood 1973b, 1974; Frankie *et al.* 1974; Opler *et al.* 1975; Heithaus *et al.* 1975; Turner 1975; Janzen *et al.* 1976; Bradbury and Vehrencamp 1976a, 1976b), and the study area and climate have been described in detail elsewhere (Rockwood 1972, 1973a, 1975, Glander 1975a). According to Holdridge (1967) this portion of Guanacaste belongs to the Tropical Dry Forest life zone, and most tree species drop their leaves during the dry season. Riparian species tend to be evergreen or are leafless for shorter periods of time. As described by Janzen (1967), many tree species flower during the dry season in Guanacaste. Riparian species, however, are more likely to flower at the beginning of dry or wet seasons (P. Opler, pers. comm.).

Rockwood (1972, 1973a, 1975, 1976) studied three colonies of *A. colombica* along the Rio Corobici from September 1970 to August 1971. Glander (1975a, 1975b, 1977) made detailed observations on one group of *A. palliata* from September 1972 to August 1973 in basically the same area. The actual areas used for foraging by the colonies of *Atta* and by the

howlers overlapped broadly. The howler group studied by Glander and colonies 1 and 2 studied by Rockwood shared a long section of forest on the east bank of the river (fig. 1B). Colony 3, however, foraged in an area not used by monkeys, and the howler foraging area included sections of forest, particularly on the west side of the river, where leaf cutter colonies did not occur. The areas of overlap corresponded roughly to Glander's area 3 (fig. 1B). Glander's total study area included 9.9 hectares of which 4.8 were riparian forest. By contrast, Rockwood's study site was approximately 2.5 hectares and was almost entirely riparian.

METHODS

In both studies, quantitative information on what the herbivores were harvesting was recorded to species whenever possible. Detailed information on the forest and a precise map of all trees larger than 15 m in height are found in Glander (1975a). Glander's data

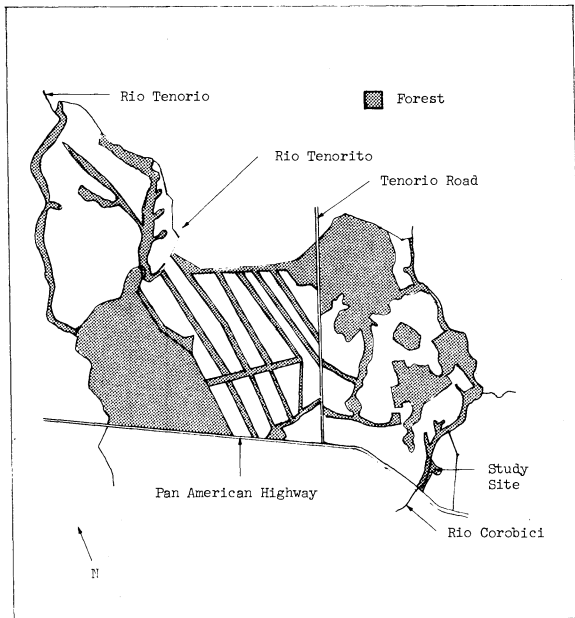


FIGURE 1A. Map of Hacienda La Pacifica near Cañas, Guanacaste Province, Costa Rica, showing location of study site. Note the location of the study site and the strips of forest to serve as windbreaks.

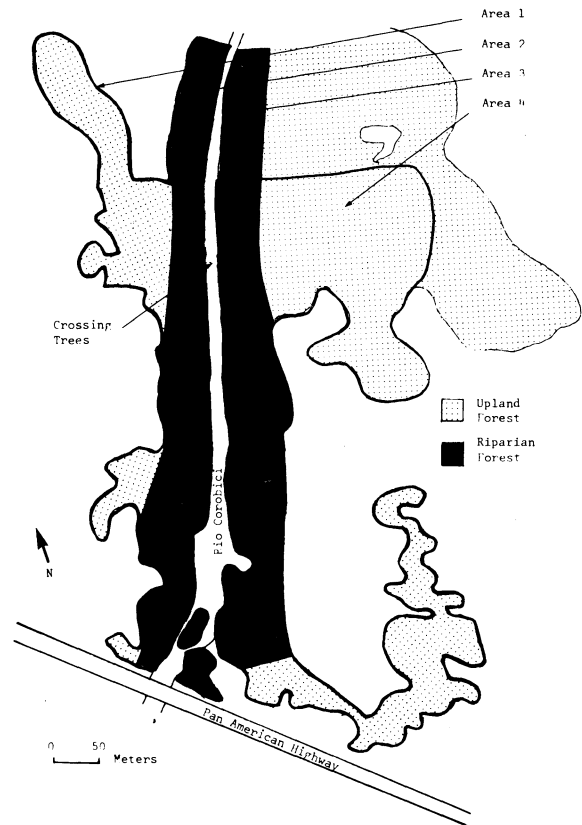


FIGURE 1B. Foraging area of howler group along the Rio Corobici. Colonies 1 and 2 of *A. colombica* foraged in area 3. Colony 3 foraged further upriver (away from Pan American highway).

on howler foraging are based largely on the daily study of randomly selected focal animals within one howler group. The number of minutes the focal animal spent eating particular plants as well as time spent in other activities were recorded. Rockwood made regular observations on three colonies of *A. colombica*. Observations were made every two days during peak foraging times, and the rate of leaf-cutting was determined for each individual plant being attacked. Using data gathered in both studies, we have compared howling monkeys and leaf-cutting ants with regard to: 1) plant species selected, using a ranking analysis; 2) statistical patterns in plant preference ranking; 3) type of plant parts harvested; 4) seasonal changes in foraging rates; 5) daily foraging patterns; and 6) canopy height used when foraging.

RESULTS

SPECIES USED.—Although leaf-cutting ants and howling monkeys are both generalists and use small quantities of material from many plant species, they are both selective in terms of plant species attacked and type of material harvested within a species (Rockwood 1976, Glander 1975a). Nevertheless, their preferences were rather different. Glander (1975a, table 40) identified 24 primary food species for howlers based on the number of times a species was visited by the howler troop, the number of individuals of the

species present in the range, and the number of trees actually used by the howler troop. For comparison we identified a "top 24" from table 6 of Rockwood (1976). These 24 species were visited at least five times by a colony of *A. colombica* (based on 50 observations, all at least four days apart) and were cut at a mean observed rate of 30.0 laden ants per minute or better by one of the three colonies studied. When these top 24 species are compared, only seven species are common to both lists (table 1). The other 17 species were largely ignored by either the ants or the monkeys. Even the seven species in common were used differently by the two herbivores in terms of plants parts harvested (table 1). It should be noted, however, that four other species preferred by the monkeys were palatable to colonies of *Atta cephalotes* in Guanacaste (*Bursera simaruba*, *Luehea speciosa*, *Manilkara achras*, and *Spondias mombin*, Rockwood 1976), and that three species preferred by *A. colombica* (*Acacia farnesiana*, *Cassia biflora*, and *Polygonatum punctatum*) are shrubs or herbs, normally not available to monkeys.

In order to analyze these apparent differences in food plant selection more precisely, we returned to the original data (Glander 1975a, Rockwood 1972) and ranked plant species in terms of use by colonies of *A. colombica* and by the *Alouatta* group. Rock-

TABLE 1. A comparison of the 24 primary food species used by the howling monkey troop and a "top 24" food species for the three colonies of *A. colombica* studied. Data are based on Glander (1975a) and Rockwood (1976). The symbols following Latin names indicate the type of material harvested from each species (Le=mature leaves, NI=new leaves, Fl=flower parts, Fr=fruit, Pe=petioles, Pu=pulvini).

Group of <i>Alouatta palliata</i>	Colonies of <i>A. colombica</i>
<i>Albizzia adinocephala</i> —NI, Fl	<i>Acacia farnesiana</i> —Le
<i>Anacardium excelsum</i> ^a —NI, NI Pe, FlPe	<i>Anacardium excelsum</i> —NI, Fl
<i>Andira inermis</i> —NI	<i>Annona holosericea</i> —Le, NI
<i>Astronium graveolens</i> —Le, NI, Pe	<i>Bombacopsis quinata</i> —Le, NI
<i>Bursera simaruba</i> —Le, NI, Fl	<i>Cassia biflora</i> —Le
<i>Cecropia peltata</i> —NI, Fr, Pe	<i>Chlorophora tinctoria</i> —Le
<i>Enterolobium cyclocarpum</i> ^a —Le, NI, Fl	<i>Cordia deamii</i> (=collococca)—Le, NI
<i>Ficus glabrata</i> —NI	<i>C. dentata</i> —Le
<i>Inga vera</i> var. <i>spuria</i> —Le, NI, Fl	<i>Enterolobium cyclocarpum</i> —Le, NI
<i>Licania arborea</i> ^a —NI	<i>Eugenia salamensis</i> —Le, NI, Fr
<i>Lonchocarpus hondurensis</i> —NI, Fl	<i>Genipa caruto</i> —Le
<i>L. minimiflorus</i> —NI, Fl	<i>Guarea luxii</i> —NI
<i>Luehea candida</i> —Fl	<i>Hippocratea volubilis</i> —NI
<i>L. speciosa</i> —Fl	<i>Hymenaea courbaril</i> —NI
<i>Manilkara achras</i> (= <i>Achras zapota</i>)—Fl, Fr	<i>Licania arborea</i> —NI
<i>Mastichodendron tempisque</i> ^a —Fl, Fr, Pe	<i>Mangifera indica</i> —NI, Fr
<i>Muntingia calabura</i> —Le, NI, Fl, Fr	<i>Mastichodendron tempisque</i> —Le, NI
<i>Pithecolobium longifolium</i> ^a —NI, Fl	<i>Pithecolobium longifolium</i> —NI
<i>P. saman</i> ^a —Le, NI, Fl, Fr	<i>P. saman</i> —NI, Fl
<i>Pterocarpus robri</i> —NI	<i>Polygonatum punctatum</i> —Le
<i>Schizolobium parabybum</i> ^a —Fl, Fr	<i>Sloanea ternifolia</i> —NI, Fl
<i>Spondias mombin</i> —Le, NI, Fl, Fr, Pu	<i>Schizolobium parabybum</i> —Le
<i>Trichilia cuneata</i> —Le	<i>Swietenia humilis</i> —NI
<i>Zanthoxylum setulosum</i> —Le, NI, Fl	<i>Species one</i> (vine)—Le

^aPlant species common to both lists.

wood's data were yearly totals of rates of leaf-cutting per plant, combined by species. Glander's data consisted of yearly totals by plant species of daily observations on the number of minutes spent eating leaves, or other plant parts, from individual trees by focal animals. In all cases fruit, flower, and leaf-eating were combined. The differences in ranking were then analyzed and the Kendall Coefficient of rank correlation (Sokal and Rohlf 1969) computed for each comparison (table 2). Only plant species present in those foraging areas being compared were used in this analysis.

TABLE 2. Kendall coefficient of rank correlation, T, between plant species preferences of howling monkeys and colonies of *A. colombica*. (See text)

Plant preferences of <i>A. colombica</i> as compared with those of <i>Alouatta</i> group	Coefficient of rank correlation, T	Probability that rank correlation arose by chance p
1. Colony 1	0.094	0.35
2. Colony 2	-0.012	0.92
3. Colony 3	-0.043	0.72
4. All three colonies combined	0.084	0.35
5. Colony 1	-0.053	0.62
6. Colony 2	0.029	0.81
7. Colonies 1 and 2 combined	0.100	0.33

Several different ranking analyses were used (table 2). In analyses 1, 2, and 3, colonies 1, 2, and 3 of *A. colombica* were ranked individually against the combined data for the howler group over its entire foraging range. In analysis 4, data from all three *Atta* colonies were combined and plant preferences ranked against these same howler data. Two of these correlations were negative, and in all cases the probability that the rankings arose by chance was 0.35 or greater.

We then used the detailed map presented in Glander (1975a), identified exactly which trees were present in the foraging areas of colonies 1 and 2, and found the total howler feeding time per individual tree in table 25 of Glander (1975a). These data were then combined by species, and new rankings were devised for howler utilization of trees based on the specific foraging areas of colonies 1 and 2, and 1 and 2 combined (correlations 5-7, table 2). The best correlation is the last, 0.110, but it is still far from significant.

For comparison, the Kendall coefficients of rank correlation among colonies 1, 2, and 3 are presented in table 3. Correlations range from 0.186 (colony 1 versus colony 2) to 0.308 (colony 1 versus colony 3). The probability that these rankings arose by chance is

less than 0.100 in all cases, but only two are significant at the 0.05 level. It must be remembered that in table 3 the colonies being compared used different, non-overlapping, foraging areas with resultant differences in tree species compositions, whereas the correlations in table 2 compare monkey and ant utilization of almost identical foraging areas. We conclude, then, that the monkey and ant preferences at the plant species level are very different.

TABLE 3. Kendall coefficients of rank correlation based on plant species preferences between pairs of *A. colombica* colonies. (See text)

Colonies compared for plant preferences	Coefficient of rank correlation, T	Probability that rank correlation arose by chance p
1 and 2	0.186	0.091
1 and 3	0.308	0.013
2 and 3	0.256	0.039

STATISTICAL PATTERNS IN RANK ANALYSIS:—As part of the analysis of a one-month study of colonies of *A. cephalotes*, Hubbell and Rockwood (1977) plotted the log of the number of plant parts harvested against the rank of these species as determined by amount cut. The results showed a nearly perfect geometric progression with species rank. However, when data for longer periods of time were examined, they no longer fit a geometric, but began to show a log-normal distribution instead (Hubbell and Rockwood 1977).

We examined the *A. colombica* data in a similar way. First we plotted the log of total vegetative fragments cut for the year versus rank. As can be seen from figure 2, the data do not fit a straight line as one would expect for a geometric distribution of amount cut. The observed patterns tend toward a log-normal distribution and are consistent with the data of Hubbell and Rockwood for *A. cephalotes*.

Next we used Glander's (1975a) data and plotted the log of observed foraging time versus species rank for all plant species used by the howlers (fig. 3). In this case the data do fit a straight line, especially the first 30 ranked species.

A related way of presenting the *Alouatta* data is to plot the cumulative fraction of total observed foraging time against species rank (fig. 4). The nth point on the graph is the cumulative fraction of total time spent foraging up to and including the nth ranked species. A negative exponential equation, $C_n = 1 - e^{-an}$, where n = species rank, a is a fitted constant, and e is the base of natural logarithms, describes the data quite well. In this case a = 0.120.

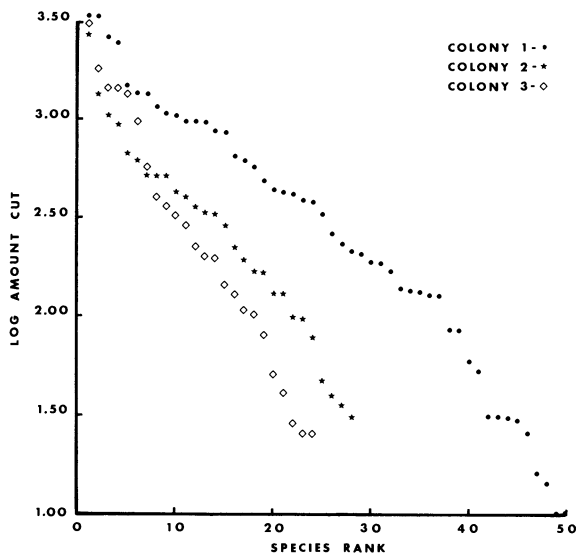


FIGURE 2. Log of total vegetative parts cut by each of three colonies of *A. colombica* for all plant species used versus plant species rank.

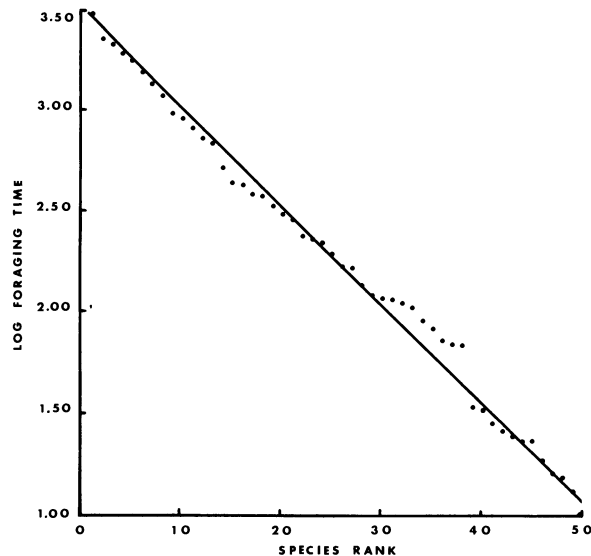


FIGURE 3. Log of total observed foraging time versus species rank for all plant species used by the howler group.

The relationship between the negative exponential of figure 4 and the geometric of figure 3 has been described in Hubbell and Rockwood (1977). In short, if the howler group's foraging time is represented by a time unit equal to one, then the monkeys devote a fraction, K , of that unit to the first-ranked species. They then devote the same fraction, K , of the remaining time to the second-ranked species, and so on. The foraging time devoted to each ranked species is thus the series K , $(K)(1-K)$, $(K)[1-(K)(1-K)]$, As shown in Hubbell and Rockwood (1977), $K = 1 - e^{-a}$, and in this example, with $a = 0.120$, then $K = 0.113$.

May (1975) has shown that ranked data of this sort tend to fit a log normal distribution for statistical reasons. The fact that the ranked *Alouatta* data do not fit a log normal, but rather a geometric distribution, leads one to suppose that there is a biological reason. This mathematical observation is merely a curiosity, however, unless it leads to predictions concerning howler foraging. Such predictions must take into account the social organization of howler groups and the fact that older individuals probably provide a reservoir of knowledge about the habitat and the location of preferred resources. Such knowledge of the availability of safe foods in both time and space could produce the mathematical pattern described above. For the present we simply note that the ranked *Atta* data fall into the log normal pattern whereas the *Alouatta* data produce a geometric distribution.

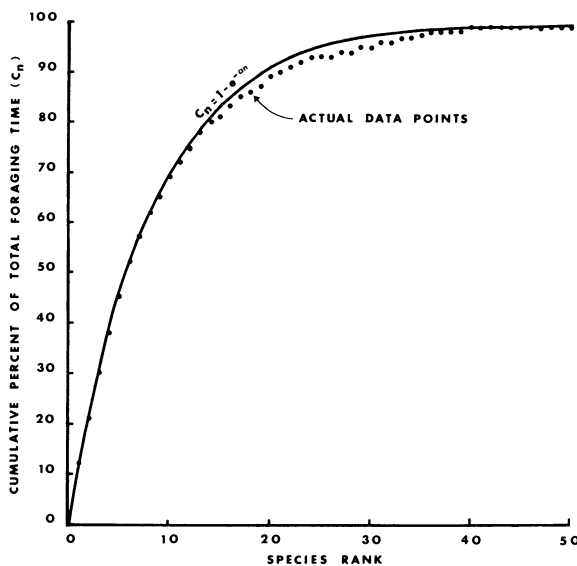


FIGURE 4. Cumulative percent of total time spent foraging by the howler group on all plant species used up to and including the n th ranked species, versus species rank. $C_n = 1 - e^{-an}$ where n is species rank and a is a fitted constant equal to 0.120. See text for further explanation.

TYPES OF VEGETATION CUT:—Both Rockwood (1972, 1975) and Glander (1975a) classified the type of vegetation selected according to the following: mature leaves, new leaves, fruit parts, and flower parts. The proportion of foraging effort devoted to the four categories is presented by month for leaf-

cutters and howlers in table 4. The proportions are based on foraging rates in terms of observed laden ants per minute and observed time spent feeding for *Atta* and *Alouatta*, respectively. Glander (1975a) also presented data on time spent eating leaf pulvini and petioles, but these data have been omitted from this analysis.

Seasonal changes in type of material cut by colonies of *Atta* or harvested by *Alouatta* groups in Guanacaste have been discussed elsewhere (Rockwood 1975; Glander 1975a, 1977). For the purpose of this paper we have chosen to define the wet season as June-November and the dry season as December-May (table 5). This approach is slightly different from that of Glander (1975a) where May was included as a wet-season month. Obviously there are problems with defining seasons on a calendar basis. The definition used here has the advantage of including two months of transition from wet to dry season (December-January), two months of mid-dry season (February-March), and two months of transition dry-wet season. (April-May). During these months many spe-

cies, especially in the riparian forest, flower and/or produce new leaves (Janzen 1967; P. Opler, pers. comm.).

The Corobici howler group and the leaf-cutter colonies followed identical seasonal patterns with regard to the four phenophases compared. Both monkeys and ants harvested more mature leaves and fruit in the wet season, and concentrated foraging efforts on new leaves and flowers during the dry season (table 5). Nevertheless, howlers and leaf-cutters differ in emphasis. For example, howling monkeys devote much less of their annual foraging effort to mature leaves than do colonies of *A. colombica* (0.227 vs. 0.482, yearly means).

Both howlers and leaf-cutters prefer new to mature leaves in many plant species (Rockwood 1975, 1976, Glander 1975a, table 4). However, howlers either have a stronger preference, or are able to locate new leaves more consistently than are *Atta* colonies, or perhaps both. During 10 of 12 months, howlers devoted more foraging effort to new leaves than did *Atta* colonies (table 4). On a seasonal basis,

TABLE 4. Monthly analysis of proportion of foraging effort devoted to four types of vegetation by three colonies of *A. colombica* and the Corobici *A. palliata* group. Monkey data exclude pulvini and petioles. Fruit includes fruit stems.

Month	<i>Atta</i> mean foraging rates	Mature leaves		New leaves		Fruits		Flowers	
		<i>Atta</i>	<i>Alouatta</i>	<i>Atta</i>	<i>Alouatta</i>	<i>Atta</i>	<i>Alouatta</i>	<i>Atta</i>	<i>Alouatta</i>
Sept. ^a	—	—	0.202	—	0.477	—	0.287	—	0.034
Oct.	328.4	0.754	0.249	0.067	0.442	0.170	0.078	0.009	0.231
Nov.	249.7	0.771	0.265	0.152	0.326	0.011	0.124	0.067	0.285
Dec.	224.6	0.631	0.421	0.142	0.448	0.070	0.065	0.157	0.066
Jan.	223.3	0.259	0.147	0.622	0.668	0.039	0.011	0.079	0.174
Feb.	196.9	0.136	0.092	0.370	0.633	0.000	0.119	0.494	0.157
March	186.4	0.093	0.055	0.398	0.463	0.019	0.190	0.491	0.292
April	238.3	0.124	0.069	0.451	0.434	0.000	0.261	0.425	0.237
May	306.8	0.262	0.129	0.573	0.311	0.005	0.180	0.160	0.380
June	323.5	0.706	0.392	0.240	0.233	0.010	0.176	0.044	0.198
July	141.3	0.757	0.314	0.073	0.291	0.140	0.226	0.029	0.169
August	263.8	0.809	0.391	0.084	0.202	0.094	0.407	0.013	0.000
Yearly Mean	2678.0	0.482	0.227	0.288	0.410	0.051	0.177	0.179	0.185
		0.499 ^b	0.202 ^c	0.288 ^b	0.448 ^c	0.051 ^b	0.143 ^c	0.161 ^b	0.206 ^c

^aInsufficient data available for *Atta*.

^bCorrected for foraging rate differences (see column one).

^cBased on data from the entire year rather than a mean of the monthly proportions.

TABLE 5. Seasonal comparison of proportion of foraging effort devoted to four phenophases by the *Atta* colonies and the *Alouatta* group. Data from Table 4. Wet season includes June-November, dry season is defined as December-May.

Season	Mature leaves		New leaves		Fruits		Flowers	
	<i>Atta</i>	<i>Alouatta</i>	<i>Atta</i>	<i>Alouatta</i>	<i>Atta</i>	<i>Alouatta</i>	<i>Atta</i>	<i>Alouatta</i>
Wet (June-Nov.)	0.759	0.302	0.123	0.329	0.071	0.216	0.032	0.153
Dry (Dec.-May)	0.251	0.152	0.426	0.493	0.022	0.138	0.301	0.218

howlers and leaf-cutters both concentrated on new leaves during most of the dry season. However, during May while leaf-cutters continued to cut a large quantity of new leaves, howlers divided their effort among new leaves, flowers, and fruit. During the wet season (June-November) when leaf-cutters apparently found little to cut other than mature leaves, howlers were still able to find significant quantities of new leaves and fruit. On a yearly basis, howlers spent 41.0 percent of their foraging time eating new leaves, and this activity ranked first among the four categories (table 4).

Frugivory was considerably more important to howlers than to leaf-cutters. Howlers spent significant amounts of time eating fruits, especially in the months of April through September, and a high of 40.7 percent of foraging time devoted to fruits was recorded in August. Leaf-cutters, however, never spent more than 17.0 percent of their monthly foraging effort on fruit collection. On a yearly basis, the monkeys spent three times more effort on fruit harvesting than did the ants. Nevertheless, fruit collection ranked last for both ants and monkeys (table 4).

Colonies of *Atta* depend heavily on flower parts during the dry season (table 5). During February through April between 40 and 50 percent of foraging time is devoted to flower part collection (table 4); this is considerably reduced during the remainder of the year. The *Alouatta* group also spends significant amounts of time foraging for flower parts, and the yearly averages for *Atta* and *Alouatta* are almost identical (table 4). The howlers, however, show no typical seasonal pattern. Of the six months in which howlers devoted approximately 20 percent or more of their foraging time to flower eating, three are in the wet season and three are in the dry season (table 4). It would appear that howlers may be able to exploit opportunistically rare and/or short-lived flower crops whenever they occur. Leaf-cutters apparently must exploit more common and longer-lived resources. A tropical flower crop is likely to be seen by a group of howlers and exploited, whereas leaf-cutter scouts do not have an all-encompassing, large-scale view of their environment.

In summary, howling monkeys spend most of their time eating new leaves. The remainder of their effort is split about evenly among certain mature leaves, flowers, and fruits. Leaf-cutters, on the other hand, spend the largest part of their foraging time harvesting mature leaves. New leaves and flowers are of seasonal importance. Fruit parts are a minor source of forage. Seasonally, mature leaves made up more than 75 percent of the ants' wet-season cuttings. New

leaves were the most important part of the diet for howlers during both the wet and dry seasons, and for ants during the dry season (table 5).

OTHER FORAGING DIFFERENCES:—Rockwood (1975) found that *A. colombica* colonies displayed significant seasonal differences in amount of material harvested by the ants (table 4). Significant bursts of activity occurred at the beginning of the dry and rainy seasons when many plant species were putting out new leaves or flowering. Glander (1975a), however, found less variation in monthly averages of time spent feeding by howlers. Based on focal animals, Glander (1975a) found that the percent feeding time varied from a low of 20.9 for April to a high of 26.8 for January. The yearly average was 22.2. When wet and dry season averages were compared, feeding time was 24.4 percent for the dry season and 22.9 percent for the wet season. This seasonal difference is accentuated for males when the data are broken down by sex (24.8% dry season, 22.7% wet season). Females are more consistent in their feeding patterns throughout the year (Glander 1975a). None of these differences are statistically significant. It would appear, then, that howling monkeys are affected less by the dry season than are colonies of *Atta*, which sharply decrease their foraging activities during the mid-dry season and sometimes lose large numbers of workers (Rockwood 1973a, 1975). In fact, the dry season may be less stressful for howlers than is the wet season (Glander 1975a).

Comparisons also can be made with regard to daily foraging patterns and foliage height attacked. Rockwood (1975) showed that colonies of *A. colombica* were predominantly diurnal, but there were significant amounts of nocturnal foraging during the dry season. Conversely, Glander (1975a) found that howler groups, like most monkeys, foraged during the day and rested at night. With regard to foliage height, leaf-cutters feed on a variety of herbs, shrubs, and understory as well as canopy trees, while howlers generally attack canopy trees and rarely forage on shrubs.

DISCUSSION

These data show that while the Corobici howling monkeys and leaf-cutting ants share many foraging patterns, there are also distinct differences. Both organisms are selective in spite of being generalist herbivores. Both harvest a variety of plant parts including, but not limited to, mature leaves, new leaves, fruit, and flowers. The amount of each of these phenophases harvested varies seasonally, and both monkeys and ants cut more mature leaves and fruit in the rainy

season, and more new leaves and flower parts in the dry season. Both organisms show preference for new leaves when there is a choice (Glander 1975a, Rockwood 1975). Nevertheless, these two herbivores show differences in 1) plant species harvested, 2) plant parts harvested, 3) statistical patterns in data on foraging effort versus plant rank, 4) seasonal variation in foraging effort, 5) daily foraging patterns, and 6) height of foliage attacked. Phrased in traditional ecological terms, their feeding niches are clearly distinct.

A number of factors lie behind these differences. The plant species selected by a generalist herbivore will be determined by a combination of nutritional requirements, ability to detoxify defensive compounds in leaves and other plant parts, and the availability of alternate foods. The fungus cultured by *A. colombica* will certainly have different requirements and have different abilities to detoxify defensive compounds in the food than the digestive system of a mammalian herbivore such as the howling monkey. Thus it is not really surprising that the plant species harvested by leaf-cutters and howlers were so different. Moreover, the fact that howlers preferred a combination of new leaves, flowers, and fruit to mature leaves is not as surprising as their ability to find these items so consistently, especially during the dry season. Mature leaves make up less than 20 percent of the howler diet during the dry-season months of January-May, but were 25 percent or greater for all other months except September. Since mature leaves of many species are tougher, high in fiber, and contain digestibility-reducing compounds such as tannins, resins, and silicon (Feeny 1976, Rhoades and Cates 1976), Glander (1975a) has suggested that the rainy season, when the monkeys consume more mature leaves, is a time of stress for the Corobici howlers. By contrast, although the leaf-cutters respond to new leaf production by increased foraging rates during the early dry season (Rockwood 1975), they were apparently unable to cut large amounts of new leaves or flower parts during the remainder of the dry season. Since foraging rates declined significantly during the dry season and mortality of workers was very high (Rockwood 1973a, 1975), the dry season was definitely the period of stress for *A. colombica*.

On a yearly basis, both leaf-cutters and the *A. palliata* group spent less than 50 percent of their foraging effort collecting the most abundant resource, mature leaves. Even when mature leaves of a particular species are chosen, Glander (1975a, 1977) found that the monkeys often select leaves from a particular individual of that species while ignoring conspecifics. For example, mature leaves were ingested from

six individual *Gliricidia sepium* trees while the mature leaves of 146 others were ignored. Recent chemical tests indicate that these individual trees lack certain alkaloids present in the other members of this *Gliricidia* population. This is a case of intraspecific variation in chemical defense, similar to cases described by Gates (1975) and by Mothes (1976).

The preference for new leaves displayed by both howling monkeys and leaf-cutters is consistent with Feeny's (1976) predictions regarding herbivore response to the types of chemical defense found in what he calls apparent and unapparent plants. Apparent plants are large, perennial, usually woody species, "bound to be found" by their herbivores. The mature leaves of apparent plants should contain compounds such as those referred to earlier (tannins, resins etc.), which serve to reduce the growth rates of herbivores. These are called quantitative defenses, and Feeny states that such defenses are generally associated with low nutritive value for herbivores and tough leaves.

Feeny calls plants which are hard to find, in time and/or space, "unapparent" to herbivores. He states that these plants are often r-selected in the sense of MacArthur and Wilson (1967) and are often ephemeral, herbaceous plants.

Feeny proposes that unapparent plants are protected by "qualitative" defensive compounds. While these chemicals are effective in relatively small concentrations and are easy to produce, they are, however, susceptible to counter-adaptation and have little inhibitory effect on the growth and fitness of adapted herbivores. Increased feeding pressure from herbivorous enemies is likely to select for the production of different defensive compounds rather than more of the same kind. This idea is supported by the wide variety of defensive compounds found among early successional plants and unapparent herbs (Feeny 1976). Cardiac glycosides, cyanogenic glycosides, many kinds of alkaloids, coumarins, and other compounds are found among such plants. Levin (1976) has found that alkaloids are more common in early successional plants and occur twice as commonly among annuals as in perennials.

Young foliage of apparent plants, however, resembles the leaves of unapparent species in many ways (Feeny 1976). New leaves are often a nutritious food for herbivores, for they are higher in nitrogen and water per unit weight than mature leaves, and lack physical toughness. New leaves are not defended by the components of quantitative defense since tannin, resin, silicon, and fiber content are usually low and increase with leaf age. New leaves

may depend on being unapparent in time and/or space or they may contain small amounts of the same potent toxins which occur in the foliage of unapparent plants. Not surprisingly, qualitative defenses such as alkaloids are highest in newly expanded leaves (Robinson 1968, McKey 1974). Some plants may have a "double-barreled" defense; that is, new leaves may be defended by qualitative defenses such as cyanogenic glycosides while mature leaves are defended by tannins (a quantitative defense). This is the case in fronds of the braken fern, *Pteridium aquilinum* (Lawton 1976).

If one assumes that the Corobici forest plants are largely apparent and use the type of chemical defenses proposed by Feeny (1976), what is the optimal foraging strategy for generalist herbivores such as howling monkeys and leaf-cutting ants? This is a complex question without an exact answer. Generalist herbivores show wide variation in their degree of adaptation to possible food plants. Qualitative defenses may inhibit feeding altogether. On the other hand, digestibility-reducing compounds found in apparent plants will force herbivores feeding upon them to grow slowly, if at all (Feeny 1976, Scriber 1975, Futuyma 1976). Rhoades and Cates (1976) state that generalists should be repulsed by both qualitative toxins and by quantitative defenses. They predict that generalists will prefer mature tissues since they are lower in specific toxins, even though they are difficult to digest. But as Freeland and Janzen (1974) and Feeny (1976) point out, generalist herbivores, especially mammals, are capable of tolerating a wide variety of toxic compounds provided they are ingested in small quantities when first encountered. Once the proper detoxification enzymes are induced in the liver, kidney, or other organs, mammalian herbivores can feed on increasing amounts of foods containing the particular toxin (Freeland and Janzen 1974). The amount of defensive chemicals found in unapparent tissues is unlikely to deter most mammalian generalists,

though there are exceptions. Among mammals, then, new leaves are likely to be preferred to mature leaves in many cases. Other generalist herbivores may also follow this pattern.

In the tropical dry forest of Guanacaste, *Atta* and *Alouatta* preferred the new leaves of many plant species. These species were almost all apparent plants. Many plants were not attacked by one herbivore or the other, and many other plants were attacked by neither. The detoxification systems of the monkeys and the ants' fungus are obviously very different since they share few preferred plant species. Both herbivores follow an extensive sampling program, but forage mainly from a restricted list of plant species. Thus both colonies of *A. colombica* and groups of *A. palliata* conform well to Freeland and Janzen's (1974) model of an expected foraging strategy for a generalist herbivore.

Finally, Cates and Orians (1975) and Rhoades and Cates (1976) have predicted that generalists should also prefer early successional (unapparent) plants. This prediction is consistent with Feeny's (1975, 1976) ideas. Cates and Orians (1975) found that two species of generalist slugs preferred the tissues of early successional plants, and evidence from the present study lends support to this view. Colonies of *Atta* attack certain early successional woody understory plants such as *Cassia biflora* with vigor, and colony density may be higher in successional forests as compared to mature forests in Costa Rica and Panama (Rockwood 1973a, 1976, and field notes, Haines 1978). Howling monkeys are found in all stages of forest growth, but group density was found to be much higher in secondary forests than in mature forests in Colombia (Scott *et al.* 1976). Thus secondary forest will apparently support larger numbers of both *Atta* and *A. palliata* than mature forests. This conclusion suggests that more "usable" vegetation is present per unit area for both of these generalist herbivores.

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