*International Journal of Primatology, Vol. 8, No. 2, 1987*

*Review Article*

# Responses of Rain-Forest Primates to Habitat Disturbance: A Review

**Andrew D. Johns**[1] **and Joseph P. Skorupa**[2,3]

*Received March 19, 1985; revised January 8, 1986*

*The survival of primates in moderately disturbed forests is determined by a complex of variables. Correlation analyses suggest that ecological features of a species may confer a basal survival ability but that details of the form of disturbance may be crucially important. Correlation analyses reveal that body size alone is a poor predictor of primate response to moderate forest disturbance. However, when the effects of diet variables are held constant, body size more strongly correlates with survival ability (smaller species surviving better). Degree of frugivory shows a significant negative correlation with survival ability at both univariate and multivariate levels of analysis. In contrast, dietetic diversity is not correlated with survival ability at either level of analysis. Together, body size and percentage frugivory explain 44% of the variation in species' responses to moderate habitat disturbance. Idiosyncratic responses of species can usually be traced to specific features of the changing environment, such as selective elimination of important food sources and, conversely, the presence of increased densities of particular food sources arising from the disturbance.*

**KEY WORDS:** primate conservation; disturbed rain forest; survival ratios; body size; frugivory; dietetic diversity.

## INTRODUCTION

A major problem facing wildlife conservation globally is the increasing rate of habitat loss or modification due to human activities. This pro-

---

[1] Sub-department of Veterinary Anatomy, University of Cambridge, Tennis Court Road, Cambridge CB2 1QS, U.K.

[2] Ecology Graduate Group, Department of Anthropology, University of California, Davis, California 95616.

[3] To whom all correspondence should be addressed.

blem is particularly pronounced in tropical broadleaf forests, which are distributed almost exclusively within the boundaries of economically stressed nations. These nations frequently regard rain forests as an economic resource to be exploited or as a waste of potentially productive land (Mergen, 1981).

Only about 4% of extant rain forest is legally protected from exploitation (Lanly, 1982; Myers, 1984). Much of this is not actually physically protected in any way and is subject to the same pressures that face surrounding forests. One important cause of forest disturbance is shifting agriculture, which may affect 33,000 to 63,000 km$^2$ of tall forest each year. About two-thirds of this area temporarily reverts to forest fallow, before eventually being cleared permanently (Melillo *et al.,* 1985). An additional 44,000 to 85,000 km$^2$ of tall forest may be selectively logged for timber each year (Myers, 1986; Lanly, 1982).

Selective timber logging normally involves the harvesting of only a certain proportion (rarely more than 10%) of the trees from an area of forest and leaving the residual stand to regenerate. Depending on the intensity of harvest and the techniques employed to cut and remove commercially valuable trees, overall destruction can range from less than 5 to greater than 70% of all trees originally within exploited areas. While it is uncertain whether typical levels of destruction (ca. 45–50%) are sustainable (UNESCO, 1978; Skorupa and Kasenene, 1984), some studies (Johns, 1983c, d; Skorupa, 1986) have indicated that survival of some primate populations is possible alongside logging operations. In view of the fact that most primate species depend on rain-forest habitat (Wolfheim, 1983) and that most of the world's rain forests will be reduced to logged or otherwise disturbed patches within 25 years, the abilities of primates to survive in such areas are of great importance in formulating conservation strategies. Not all species are likely to survive in isolated tracts of disturbed habitat, but integrative management of protected and sustainably exploited forests promises to increase substantially the size of populations that can be conserved over the long term.

This paper presents a synthesis of factors determining the ability of rain-forest primates to survive under conditions of habitat disturbance. We first analyze the extent to which intrinsic ecological variables may influence the survival of primates and then consider specific cases drawn from recent information on the actual status of wild populations in moderately disturbed forest areas.

## ECOLOGICAL CORRELATES OF SURVIVAL

### Methods

For a number of species, reported abilities to persist following habitat disturbance may be correlated with known features of the species' ecology.

Data on which the following analyses were based are given in Table I. Population *survival ratios* for each species are calculated as the mean value of

$$\frac{\text{population density in disturbed forest}}{\text{population density in undisturbed forest}}$$

where comparable data exist. Only data given by the same author(s) for both disturbed and primary forest in the same area are included. This minimizes interindividual bias in sampling techniques, differences in basal population levels, etc. However, it should be pointed out that individual authors frequently combine results from a wide range of habitat types, and single very high or very low estimates can affect the estimated mean disproportionally.

Only data from population censuses in moderately disturbed forest (selectively logged forests or forests exhibiting a small amount of agricultural encroachment) are included. Under extreme conditions of tree loss, such as those often associated with urban settlements and agricultural areas, few primates are able to survive (Johns, 1983a). Results from heavily hunted forests are also excluded from the analysis.

Correlations between primate species' survival ratios (as defined above) and specific ecological variables are analyzed here at both univariate and multivariate levels. While the response of a particular primate species to habitat disturbance is undoubtedly the outcome of a complex interaction, simple univariate correlation analyses have the advantage of employing more of the available data points than multivariate analyses do. Species for which one or more parameter values are unavailable (16 of the 37 species listed in Table I) cannot be included in the multivariate analyses employed here. However, for the remaining species ($N = 21$) multivariate analyses have the distinct advantage of allowing one to control some of the confounding interactions between variables that mask relationships in the data.

For example, a priori one would expect vulnerability due to habitat fragmentation to increase with body weight (because large resource supply areas are required to support large-bodied primates) and decrease with degree of folivory (due to the relatively high density of exploitable foliage even in disturbed forest). Yet tests of these expectations are confounded by the positive correlation between body weight and degree of folivory (Table II; cf. Clutton-Brock and Harvey, 1977; Robinson and Ramirez, 1982). To control for such complex interactions, a partial-correlation analysis was conducted (see Rodman, 1973; Isbell, 1983). Partial-correlation analysis allows the relation between two variables to be isolated from the effects of other predesignated variables by assuming that all relationships can be reasonably approximated by linear equations (Nie *et al.*, 1970). A nonparametric correlation matrix (Table II) was used as input data to minimize the bias resulting from nonlinear relations among the variables.

Many of the species dealt with here include less than 10% animal matter in their diets (based on the relative frequencies that different food classes

**Table I.** Population Survival Rates and Ecological Variables for Selected Primate Species[a]

| Family and species | Body weight (kg) | Diversity of diet (%) | | | Diversity of diet (%) | | Observed population survival rate[b] | | | Source[c] |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Foliage | Fruit, seeds, flowers | Animal matter | Top 5 species | Top 10 species | $\bar{x}$ | $N$ | Range | |
| Callitrichidae | | | | | | | | | | |
| *Saguinus fuscicollis* | 0.31 | 10 | 60 | 30 | – | – | 1.95 | 5 | 0.78-5.33 | Mittermeier and Coimbra-Filho (1977); Freese *et al.* (1977, 1982) |
| *S. midas* | 0.31 | 10 | 60 | 30 | – | – | 7.90 | 2 | 3.00-12.80 | Mittermeier and Coimbra-Filho (1977); Mittermeier *et al.* (1977b) |
| *Callithrix argentata* | 0.25 | – | – | – | – | – | 2.63 | 2 | 1.00-4.26 | Mittermeier and Coimbra-Filho (1977); Mittermeier *et al.* (1977b) |
| Cebidae | | | | | | | | | | |
| *Cebus albifrons* | 2.6 | 15 | 65 | 20 | – | – | 0.08 | 1 | NA | Freese *et al.* (1982) |
| *C. apella* | 2.6 | 15 | 65 | 20 | – | – | 0.69 | 1 | NA | Freese *et al.* (1982) |
| *Saimiri sciureus* | 0.80 | – | – | – | – | – | 1.21 | 2 | 1.19-1.23 | Mittermeier and Coimbra-Filho (1977); Freese *et al.* (1982) |
| *Alouatta seniculus* | 7.0 | 25 | 75 | 0 | 82 | 93 | 0.64 | 2 | 0.00-1.27 | Mittermeier and Coimbra-Filho (1977); Freese *et al.* (1982) |
| *Callicebus torquatus* | 1.1 | 13 | 67 | 14 | 47 | 66 | 0.15 | 2 | 0.00-0.30 | Mittermeier and Coimbra-Filho (1977); J. M. Ayres (pers. comm.) |
| *Ateles paniscus* | 8.1 | 10 | 87 | 3 | 24 | 37 | 0.00 | 1 | NA | van Roosmalen (1980) |
| *Chiropotes albinasus* | 2.8 | 1 | 90 | 9 | 39 | 56 | 0.00 | 1 | NA | J. M. Ayres (pers. comm.) |
| *C. satanas* | 2.8 | 1 | 98 | 1 | 35 | 45 | 0.00 | 1 | NA | J. M. Ayres (pers. comm.) |
| Cercopithecidae | | | | | | | | | | |
| *Cercopithecus ascanius* | 4.7 | 31 | 44 | 22 | 37 | – | 0.43 | 2 | 0.41-0.45 | Struhsaker (1975); Oates (1977) |
| *C. diana* | – | – | – | – | – | – | 0.79 | 1 | NA | Martin and Asibey (1979) |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *C. lhoesti* | – | – | – | – | – | – | 0.26 | 2 | 0.00–0.51 | Struhsaker (1975); Oates (1977) |
| *C. mitis* | 4.5 | 15 | 58 | 11 | 35 | – | 1.00 | 2 | 0.59–1.40. | Struhsaker (1975); Oates (1977) |
| *C. mona/C. petaurista* | 5.4 | 28 | 62 | 8 | – | – | 0.89 | 1 | NA | Martin and Asibey (1979) |
| *Cercocebus albigena* | 6.2 | 5 | 64 | 24 | 50 | 69 | 0.42 | 2 | 0.33–0.51 | Struhsaker (1975); Oates (1977) |
| *C. atys* | 5.5 | – | – | – | – | – | 0.68 | 1 | NA | Martin and Asibey (1979) |
| *Macaca fascicularis* | 5.0 | 16 | 57 | 23 | 38 | 56 | 1.62 | 4 | 0.32–4.16 | Southwick and Cadigan (1972); Rijksen (1978); Marsh and Wilson (1981); Salter and MacKenzie (1981) |
| *M. nemestrina* | 8.5 | 19 | 76 | 2 | – | – | 0.50 | 1 | NA | Rijksen (1978) |
| Colobinae | | | | | | | | | | |
| *Colobus badius* | 8.8 | 78 | 16 | 0 | 69 | 87 | 0.64 | 3 | 0.62–0.66 | Struhsaker (1975); Oates (1977); Martin and Asibey (1979) |
| *C. guereza* | 9.9 | 82 | 16 | 0 | 76 | 88 | 2.80 | 2 | 1.12–4.58 | Struhsaker (1975); Oates (1977) |
| *C. polykomos* | – | – | – | – | – | – | 0.81 | 1 | NA | Martin and Asibey (1979) |
| *C. verus* | 3.8 | – | – | – | – | – | 1.42 | 1 | NA | Martin and Asibey (1979) |
| *Presbytis cristata* | 6.3 | – | – | – | – | – | 2.90 | 1 | NA | Salter and MacKenzie (1981) |
| *P. hosei* | 6.3 | – | – | – | – | – | 0.33 | 1 | NA | Payne and Davies (1982) |
| *P. melalophos* | 6.1 | 37 | 62 | 0 | 25 | 35 | 0.82 | 9 | 0.24–1.33 | Southwick and Cadigan (1972); Wilson and Wilson (1976); Mohamed Khan (1978); Marsh and Wilson (1981) |
| *P. obscura* | 6.2 | 48 | 52 | 0 | 41 | 53 | 0.73 | 3 | 0.14–1.71 | Southwick and Cadigan (1972); Marsh and Wilson (1981) |
| *P. rubicunda* | 6.3 | 38 | 61 | 1 | 17 | 27 | 0.82 | 4 | 0.23–1.44 | Wilson and Wilson (1975); Payne and Davies (1982); Wilson and Johns (1982) |

Table I. Continued

| Family and species | Body weight (kg) | Diversity of diet (%) | | | Diversity of diet (%) | | Observed population survival rate[b] | | | Source |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Foliage | Fruit, seeds, flowers | Animal matter | Top 5 species | Top 10 species | $\bar{x}$ | $N$ | Range | |
| *P. thomasi* | 6.3 | 54 | 39 | 7 | – | – | 0.58 | 2 | 0.24–0.91 | Wilson and Wilson (1976); Rijksen (1978) |
| *Nasalis larvatus* | 18.0 | 90 | 10 | 0 | 96 | 99 | 0.44 | 2 | 0.13–0.74 | Salter and MacKenzie (1981) |
| Hylobatidae | | | | | | | | | | |
| *Hylobates agilis* | 5.5 | 39 | 61 | 1 | – | – | 0.17 | 1 | NA | Wilson and Wilson (1976) |
| *H. lar* | 5.5 | 34 | 62 | 10 | 28 | 44 | 1.09 | 10 | 0.61–2.17 | Southwick and Cadigan (1972); Rijksen (1978); Marsh and Wilson (1981) |
| *H. muelleri* | 6.1 | 32 | 66 | 2 | 31 | 46 | 0.70 | 4 | 0.41–1.00 | Wilson and Wilson (1975); Payne and Davies (1982); Wilson and Johns (1982) |
| *H. syndactylus* | 10.7 | 45 | 46 | 8 | 27 | 36 | 0.48 | 2 | 0.46–0.50 | Southwick and Cadigan (1972); Rijksen (1978) |
| Pongidae | | | | | | | | | | |
| *Pongo pygmaeus* | 53 | 22 | 65 | 2 | 28 | 42 | 0.18 | 1 | NA | Rijksen (1978) |
| *Pan troglodytes* | 45 | 28 | 68 | 4 | 57 | 71 | 0.26 | 1 | NA | Struhsaker (1975) |
| *Gorilla gorilla* | 125 | 86 | 4 | 0 | 71 | – | 1.17 | 1 | NA | Murnyak (1981) |

[a] Ecological variables are taken largely from Clutton-Brock and Harvey (1977), and many are approximations only. Additional data on body weights are taken from Napier and Napier (1967). Additional references consulted are as follows: *Alouatta seniculus*, Gaulin and Gaulin (1982); *Callicebus torquatus*, Kinzey (1977, 1981); *Ateles paniscus*, van Roosmalen (1980); *Chiropotes albinasus*, Ayres (1981); *Chiropotes satanas*, van Roosmalen *et al.* (1981); *Cercopithecus ascanius*, Struhsaker (1978); *Cercopithecus mitis*, Struhsaker (1978); *Macaca fascicularis*, MacKinnon and MacKinnon (1980a); *Presbytis melalophos*, MacKinnon and MacKinnon (1980a); *Presbytis obscura*, MacKinnon and MacKinnon (1980a); *Presbytis rubicunda*, A. G. Davies (in prep.); *Presbytis thomasi*, Rijksen (1978); *Nasalis larvatus*, Salter and MacKenzie (1981); *Hylobates agilis*, Gittins (1979); *Hylobates muelleri*, D. Leighton (in prep.); *Pan troglodytes*, Wrangham (1977).

[b] Population survival is calculated as (population density in disturbed forest/population density in undisturbed forest).

[c] This table was assembled from sources published prior to early 1983. Although additional results from more recent reports are reviewed in the text, they are not included in the statistical analyses.

**Table II.** Spearman Rank-correlation Matrix Used as Input Data for Partial-Correlation Analysis

| | *S* ratio[a] | Body weight | % folivory | % frugivory | Diversity[b] |
|---|---|---|---|---|---|
| *S* ratio | 1.000[c] | 0.134 | 0.599 | −0.638 | 0.081 |
| Body weight | – | 1.000 | 0.591 | −0.396 | 0.247 |
| % folivory | – | – | 1.000 | −0.817 | 0.260 |
| % frugivory | – | – | – | 1.000 | −0.297 |
| Diversity | – | – | – | – | 1.000 |

[a] Ratio of primate abundance in disturbed and undisturbed forest habitat (see text).

[b] Dietetic diversity as measured by the percentage of the diet made up by the five most utilized food species.

[c] Spearman rank correlations were calculated using data from Table I for the 21 species with complete variable sets.

are observed to be ingested). As a result, percentage foliage and percentage fruit (including seeds and flowers) in the diet are often mirror-image representations of diet type. Here, percentage folivory is used to characterize primate diets except where percentage frugivory per se is a variable of interest [following Clutton-Brock and Harvey (1977); see Sailer *et al.* (1985) for a critique of this approach]. Since definite hypotheses are being tested—e.g., that vulnerability to habitat disturbance increases with body weight and dietetic diversity and decreases with folivory—all probabilities reported are one-tailed.

Clearly, the data base can serve only to indicate trends because there are many confounding variables that cannot be controlled. The degree of disturbance involved will vary to a considerable extent, as will the time interval since disturbance. In many cases the species' populations may be hunted occasionally, either in primary or in disturbed forest or both (although results from regularly hunted areas are excluded). Both censusing techniques and the time spent arriving at estimates of density also vary to a great extent. It is supposed that surveys include different vegetation types within rain forest proportional to their abundance: censuses conducted along river courses, for example, will overestimate species which prefer more open, secondary habitats (*Saimiri* spp. in the Neotropics and *Macaca fascicularis* in Southeast Asia). Such surveys are excluded from the analyses where they can be detected.

While these inherent defects of any literature-generated data base will weaken the apparent relationships between ecological traits and a species' vulnerability to habitat disturbance, there is no reason to suppose that they could be responsible for producing a relationship where none existed (Clutton-Brock and Harvey, 1977, 1984; Johnson, 1981). The results of a well-controlled recent case study (Skorupa, 1986) independently corroborate the general trends generated from this literature review, leading us to concur with Martin's (1981) opinion 'that it is overly pessimistic to rule out any firm conclusions about the relationship between primate behaviour and ecology merely because (intraspecific) variability exists."

## RESULTS

From an analysis of the available data, the folllowing overall trends are apparent.

### *Body Weight*

There is no simple correlation between survival ratios and body weights of primate species ($r_s = 0.207$, $P > 0.10$) (Fig. 1).

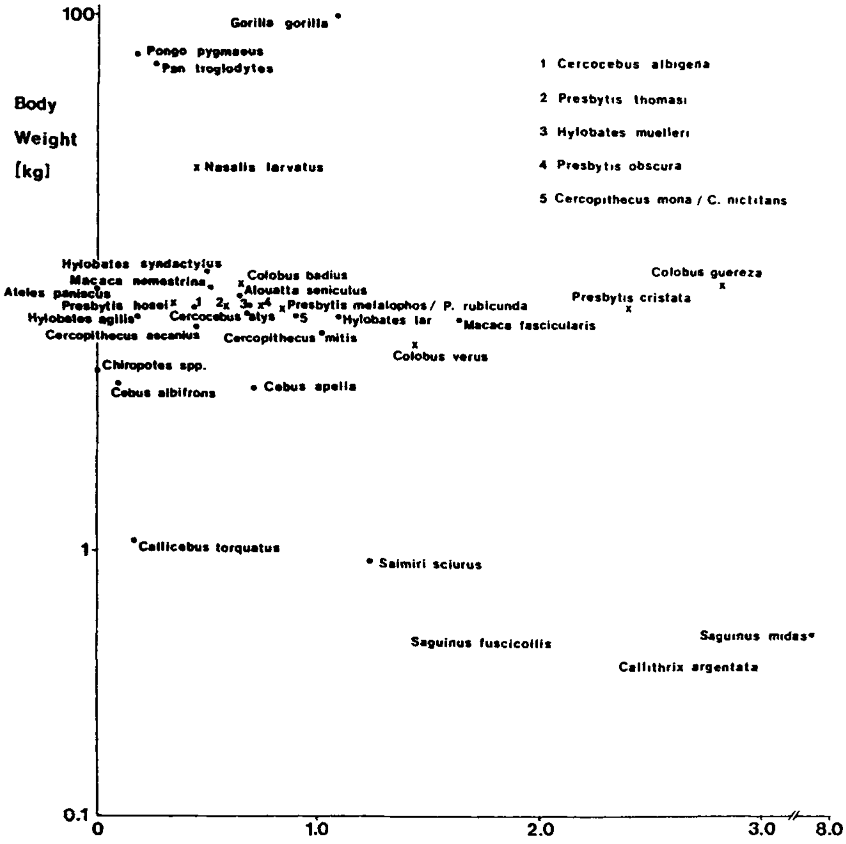

Fig. 1. Primate species survival ratios plotted against body weight (logarithmic scale). Colobines are indicated by an x; noncolobines, by a filled circle.

When the effects of diet type and dietetic diversity (measured as the percentage of the diet made up by the five most used food species) are controlled, body weight shows a weak negative correlation with survival ratios ($r = -0.333, p = 0.08$). Thus, within any given dietary strategy, large-bodied species are generally more sensitive to forest disturbance than smaller-bodied species. Failure to control dietary variables obscured this relationship in the univariate analysis.

### *Dietary Diversity*

Dietary diversity may influence prospects for survival because disturbed forest develops a different plant species composition, and the seasonal availability of food types may require primates to subsist periodically on a monotonous diet (Struhsaker and Oates, 1975). Measures of dietetic diversity will reflect both the degree of feeding specialization and the diversity of vegetation available, although the latter is unlikely to be a controlling factor in most undisturbed rain forests. There is, however, no simple correlation between survival ratios and dietary diversity, as measured by the percentage of a species' diet occupied by the 5 and by the 10 most used food species ($r_s = 0.093$, $P > 0.25$; $r_s = 0.006$, $P > 0.45$) (Fig. 2).

When the effects of diet type and body weight are controlled, dietetic diversity (as measured by the percentage of the diet made up by the five most used food species) shows no correlation with survival ratios ($r = -0.060$, $P = 0.40$). This result agrees with the univariate analysis: both suggest that dietetic diversity is largely facultative rather than obligate or, alternatively, that the measure of dietetic diversity used here is not biologically significant to primates. However, as Clutton-Brock and Harvey (1977) point out, few studies provide the data necessary for testing alternative measures of dietetic diversity.

### *Diet Type*

In disturbed forest there is a tendency for the relative availability of fruit and foliage food resources to differ from that in primary forest (Johns, 1983a). The abundance of suitable fruit may decrease, whereas the availability of new leaves may not. Thus the degree of folivory/frugivory shown by primate species may be important in determining the survival ability in disturbed forest.

There is a negative simple correlation between the percentage of fruit and flowers in the diet (in primary forest) and survival ratios ($r_s = -0.534, p < 0.01$) (Fig. 3). There is no simple correlation between the percentage of foliage

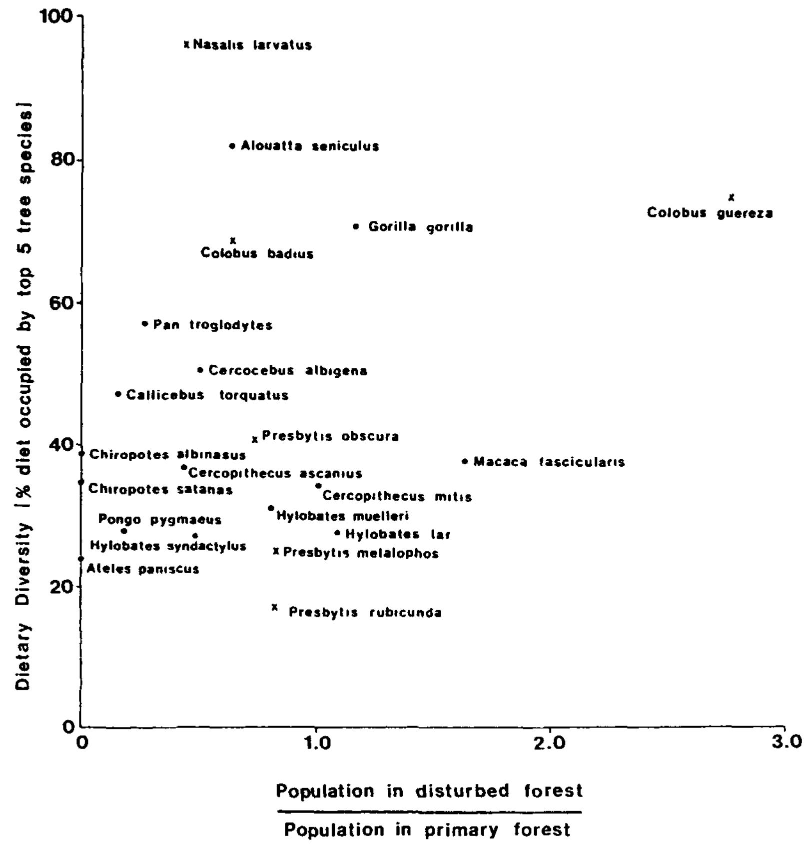

Fig. 2. Primate species survival ratios plotted against dietary diversity. Colobines are indicated by an x; noncolobines, by a filled circle.

in the diet and survival ratios ($r_s = 0.148$, $P > 0.20$), but this may be explained by the confounding influence of very small-bodied species (ca. $< 1$ kg body weight) that, as a general rule, substitute arthropods in place of foliage as a source of protein—presumably to meet the metabolic constraints imposed by small body size (Kay, 1984). If callitrichids are excluded from the analysis [callitrichids feed on a significant proportion of insects even in undisturbed forest (Hladik and Hladik, 1969)], the correlation becomes significant ($r_s = 0.537$, $p < 0.01$).

When the effects of dietetic diversity and body weight are controlled, diet type is very strongly correlated with survival ratios. The equal but opposite second-order partial-correlation coefficients for folivory ($r = 0.651$, $P = 0.0015$) and frugivory ($r = -0.649$, $P = 0.0015$) again emphasize the

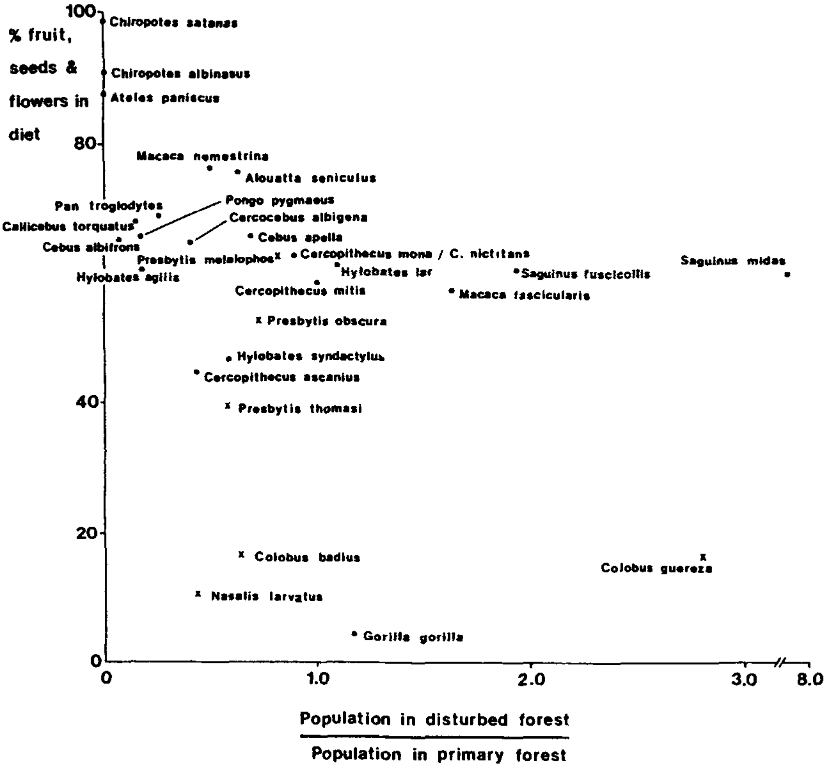

Fig. 3. Primate species survival ratios plotted against diet type (percentage fruit, seeds, and flowers in diet). Colobines are indicated by an x, noncolobines, by a filled circle.

mirror-image nature of these alternative measures of dietary preference for our particular sample of data points.

Since leaves substitute for animal prey as body size increases (Gaulin and Konner, 1977; Terborgh, 1983, p. 152; Chivers and Hladik, 1984), we should ideally split our species into frugivore/folivores versus frugivore/insectivores and then separately test the correlation of folivory and insectivory with survival ratios within each group. This would be particularly important if the dispersion and abundance of insects were suspected to be fundamentally different from the dispersion and abundance of foliage in disturbed forests (D. Leighton, personal communication). Unfortunately, the sample size for frugivore/insectivores in Table I is too small to assess the relation between insectivory and survival ratios. After intensive study of several frugivore/insectivores, however, Terborgh (1983, pp. 154, 213) concluded that fruit, not animal prey, was the most important ordering constraint on habitat utilization. Throughout the interpretation of the following analyses, the reader should bear in mind that most of the data points are for Old World primates; if Neotropical primates are fundamentally more insectivorous (cf. Terborgh, 1983, pp. 150–152), and if insectivory influences survival ratios differently than folivory, the results would apply best only to Old World primates.

### *Predictive Power*

The foregoing interspecific comparisons suggest that *large-bodied frugivores* are the class of primates most vulnerable to habitat disturbance. This is consistent with observations for species in the genera *Pan, Pongo, Ateles,* and others (cf. Wolfheim, 1983; see below). Furthermore, Terborgh and Winters (1980) arrived at a similar conclusion with regard to tropical bird faunas. However, multiple regression of survival ratios on $\log_e$ body weight and percentage frugivory explains only 44% of the total variation in survival trends [$F_{3,25} = 8.26$, $P < 0.01$; S ratio $= 23.5 - 4.40 \log_e \mathrm{wt}\ (\mathrm{g}) - 0.019\%$ frugivory $+ 0.218\ [\log_e \mathrm{wt}\ (\mathrm{g})]^2$; regression calculated using the Minitab program (Ryan *et al.,* 1981)]. While the amount of variation explained by body weight and percentage frugivory is statistically significant, it is nonetheless an insufficient basis for reliable prediction of the outcome of individual cases.

## DISCUSSION

In a recent worldwide survey of primate conservation status, Wolfheim (1983) proposed that body size should be a strong predictor of a primate species' survival ability. This follows rules applied to other rain-forest taxa (e.g., by Willis, 1974). Wolfheim pointed out that body size potentially affects conservation status in a multitude of ways. Larger primates need more food and larger foraging areas and tend to occur at lower densities than ecologically similar small species do. Large species mature later and reproduce more slowly than small species. Large species tend to be preferred by hunters (cf. Robinson and Ramirez, 1982) and, therefore, are subject to heavy hunting pressure. From an evolutionary perspective, Wolfheim (1983) notes that larger mammals within a given phyletic line tend to be more recently derived and specialized forms [in accordance with Cope's law (Ricklefs, 1979, pp. 418–420)] and, therefore, should be more vulnerable to "habitat reduction."

Body size alone, however, may not be a good predictor of species' abilities to adapt (Lovejoy *et al.,* 1984). Karr (1982) reaches the same conclusion for the undergrowth avifauna of Barro Colorado Island. Our review indicates that the effects of body size approach statistical significance only when the effects of diet type are controlled for. The fact that small primate species generally survive moderate habitat disturbance well and are frequently able to exist in close association with humans [e.g., *Tarsius spectrum* (MacKinnon, 1979); *Miopithecus talapoin* (Gautier-Hion, 1971); *Cebuella pygmaea* and *Saguinus* spp. (Mittermeier and Coimbra-Filho, 1977)] is due less to body size per se than to the dietary constraints concomitant with small body size (Kay, 1984), at least when hunting is not an important factor. To the extent that diets reflect phyletic lineage (e.g., Colobinae vs Cercopithecinae), controlling for the effects of diet constitutes a de facto stratification along phyletic lines. Consequently, that the larger species within dietary groupings tend to be more vulnerable than the smaller species is consistent with Cope's law and provides support for Wolfheim's (1983) evolutionary argument.

In contrast to body size, diet type is a statistically significant correlate of survival even at a univariate level of analysis and proves to be an even stronger correlate when the effects of confounding parameters are controlled. Accordingly, the response of primates to selective logging and other forms of moderate habitat disturbance can be expected to be mainly a reaction to changed distributions and abundances of different food types, although other factors may also be important. The abundance of food – i.e., the extent and rate at which disturbed forests regenerate exploitable foods – is probably crucial, and regeneration of foliage is likely to occur before the reappearance of fruit resources.

There is, however, an inherent deficiency in the data base for diet types because species values for degree of frugivory are based on studies of *single* populations, which are often well removed from the populations providing data for survival ratios (see Table I). It is naive to assign a single number to represent a species' degree of frugivory, since such a trait can be expected to vary according to specific environmental conditions (within anatomical and physiological limitations). While it is conceivable that the strong negative correlation between degree of frugivory and species' survival ratios is merely an artifact of a crude data base, it is more reasonable to suppose that the correlation would be stronger were the data base more precise (Clutton-Brock and Harvey, 1977, 1984; Johnson, 1981).

Evidence that the diet/survival correlation is a real biological phenomenon and not an artifact of the data base is provided by an intensive standardized study of a seven-species primate community in Kibale Forest, Uganda (Skorupa, 1986, 1987). The diets of most Kibale primates have been well studied using uniform methods (e.g., by Struhsaker, 1978). In a series of study plots located in selectively logged forest, the biomass density of frugivorous Kibale primates averaged 59% lower than in undisturbed forest, while the biomass density of folivorous primates declined by an average of only 39%. Additional evidence is provided by Lovejoy *et al.* (1986), who report that *Alouatta seniculus* can survive in 10-ha isolates of Amazonian rain forest "because of their folivory." They note further that such "frugivorous primates" as *Ateles paniscus, Chiropotes satanas,* and *Cebus apella* all fail to persist in such small patches of rain forest.

Given the strong effect of diet type, failure to detect an effect of dietary diversity is somewhat surprising. It may be that under conditions of relatively light disturbance, there is little change in primate food diversity (Isbell, 1983; Johns, 1983a), so that even if dietary diversity does affect survival ability, its effects would be evident only at more severe levels of disturbance than those reported in the studies providing the data base employed here.

The low predictive power of the ecological parameters examined here is due partly to the imprecision of a literature-generated data base and partly to the large number of factors potentially influencing survival (such that no single factor is overwhelmingly dominant). Species-specific ecological and behavioral idiosyncracies, which are difficult to represent mathematically, are undoubtedly important. It is worthwhile to examine actual reported responses of individual species to demonstrate why differences occur.

## FIELD OBSERVATIONS

The conservation status of rain-forest primates has recently been reviewed by Wolfheim (1983). This work contains few references after 1978, however, and most detailed work on the ability of rain-forest primates to survive under conditions of habitat disturbance has been carried out after that date.

It is clear that the responses of primates to forms of habitat disturbance less severe than outright loss (i.e., converting forested into nonforested lands) are dependent upon a complex set of variables giving rise to many local permutations. Thus, for some taxa, the available data appear contradictory (see Table I), and various conclusions can be drawn, depending on the emphasis afforded to particular studies.

A number of important factors will influence the survival abilities of primates at particular sites. The level of actual damage caused to the forest is a fundamental influence, but the ratio of disturbed to primary forest, the proximity of primary forest, and the time since the disturbance occurred are also vitally important. Some of these more subtle influences on primates may be illustrated with reference to selected field studies.

### Neotropical Species

Few studies of Neotropical primates provide quantitative data on the abilities of primates to survive conditions of moderate habitat disturbance.

Recent studies providing some data are those of Ayres and Milton (1981), Freese *et al.* (1982), and Branch (1983). Robinson and Ramirez (1982) review certain characteristics of species that promote survival or extinction in hunted or fragmented forest but offer no original data. The only field study that concentrates on this issue is that of Johns (1986a).

Information is available on a range of Neotropical species (Tables III and IV), but it should be recognized that most data result from short-term surveys. The patchiness of distribution of many Neotropical primates, even in continuous forest, may be a major confounding feature. Many species are also very wide-ranging, and their encounter during brief survey programs will be dependent on chance environmental or other stochastic factors.

The inability of *Chiropotes s. satanas* to survive in heavily logged forest is due largely to the felling for timber of important food trees, which are rare species in the forest (Ayres, 1981; Johns, 1985a). This is an important pressure which cannot be predicted without a knowledge of local timber trade and detailed feeding behavior of primates (another example of this is given below: disproportionate removal of figs, *Ficus* spp., in Asian and African forests). The effect upon *C. s. satanas* is sufficiently drastic that only lone animals persist even 2 years after logging: the rest have already disappeared. Similar conditions of disturbance would be expected to affect *C. albinasus* in the same way: Branch (1983) does not specify the conditions of selective logging that provide a higher estimate than in primary forest, but much of the region where her surveys were carried out has been logged only very lightly for a single rare tree, *Aniba duckei* (Lauraceae), which is not a food source for the primates.

Another pithecine, *Pithecia albicans,* survives well in logged forest, principally because it is much less selective than *C. s. satanas.* Its feeding strategy is quite different; it splits into small foraging units and feeds on a wide range of fruits, arils, seeds, leaves, and probably insects. This ability enables *P. pithecia* to persist even in degraded forest fragments (Oliveira *et al.,* 1986).

Small-bodied frugivore/insectivores respond as expected from analysis of dietary parameters. Species of *Saguinus* are often common in disturbed habitat, even in cleared and regenerating forests (see Freese *et al.,* 1982; Ayres, 1983). The exception to this trend, low densities of *S. midas* at Gorupí F. R., is puzzling. *Leontopithecus* have been reported to be reliant on tree holes as refuge sites (Coimbra-Filho, 1977), but recent studies suggest that they can actually persist in highly degraded forest and colonize 10- to 15-year-old regenerating scrub (Dietz, 1985).

Species of *Callicebus* (excepting *C. torquatus*) and *Callithrix* are often found in secondary forest but not in adjacent primary forest, as is the case with *Callicebus moloch* at Ponto da Castanha: it occurs only on the fringe of tall forest (cf. Kinzey, 1981; Ryland, 1981). *Callicebus torquatus* tends to replace *Callicebus moloch* in tall forest, although the latter may occur at disturbed sites within otherwise tall forest (e.g., tree-fall areas). Species of *Cebus* are usually well able to persist in disturbed areas, including crop

**Table III.** Primate Densities in Primary and Disturbed Forests in Eastern Amazonia

| Area | Tapajós N.P.[a] | | | Remansinho, Tucurui Lake[b] | | Gorupi F.R.[b] | | |
|---|---|---|---|---|---|---|---|---|
| Vegetation type | *Terra firme* forest | | | *Terra firme* and *igapo* forests | | *Terra firme* forest | | |
| Trees extracted/hectare | | < 1 | | | ~10 | | 1-2 | ~10 |
| Total damage (%) | | ? | 100 | | 60 | | 10 | 50 |
| Time since logging | Primary | > 10 years | "Secondary" | Primary | 1 year | Primary | 2 years | 2 years |
| Species (density, groups/km²) | | | | | | | | |
| *Saguinus midas* | –[c] | – | – | 3.1 | 3.6 | 3.0 | 1.5 | 0.4 |
| *Callithrix humeralifer* | 0 | 0.4 | 3.6 | – | – | – | – | – |
| *Callicebus moloch* | 0 | 0 | 0.6 | 0 | 0 | – | – | – |
| *Saimiri sciureus* | 0.1 | 0 | 0 | 0 | 0 | – | – | – |
| *Cebus apella* | 1.9 | 4.3 | 1.1 | 2.3 | 2.4 | 1.8 | 0.5 | 0 |
| *C. albifrons* | 0 | 0 | Present | – | – | – | – | – |
| *Pithecia hirsuta* | 0 | 0.4 | 0.7 | – | – | – | – | – |
| *Chiropotes albinasus* | 0.9 | 1.4 | 0 | – | – | – | – | – |
| *C. s. satanas* | – | – | – | 0.8 | 0 | 1.0 | 0.5 | Solitaries only |
| *Alouatta belzebul* | 0.7 | 0.4 | 0 | 2.3 | Present | 11.7 | 2.3 | 2.2 |
| Distance surveyed (km) | 34.1 | 14.7 | 8.5 | 18.4 | 12.0 | 20.7 | 22.9 | 45.5 |

[a] Data from Branch (1983) were converted to estimates of density using detection distances provided by the author (results combine several survey sites).

[b] Data from Johns (1986a).

[c] (–) Outside the geographical range of this species.

**Table IV.** Primate Densities in Primary and Disturbed Forests in Western Amazonia

| Area | Ponta da Castanha[a] | | | E. Peru (Cocha Cashu and Samiria)[b] | | Mamiraua Lake[a] | |
|---|---|---|---|---|---|---|---|
| Vegetation type | *Terra firme* forest | | | *Terra firme* and *igapo* forests | | *Várzea* forest | |
| Trees extracted/hectare | | 3-5 | | | "Light" | <0.1 | 4.6 |
| Total damage (%) | | 61 | 80 | | ? | <1 | 5 |
| Time since logging | Primary | 11 years | Cultivated mosaic | Primary | <35 years | Continuing | Continuing |
| Species (density, groups/km²) | | | | | | | |
| *Saguinus mystax* | 5.7 | 8.0 | 2.0 | –[c] | – | – | – |
| *S. fuscicollis* | 0 | 0 | 0.05 | 1.8 | 2.5 | – | – |
| *Callicebus moloch* | 0.1 | 0.4 | 2.3 | 0.7 | 0 | – | – |
| *C. torquatus* | 1.0 | 1.2 | 0.1 | 0 | 0 | – | – |
| *Saimiri sciureus* | 0.5 | 1.4 | 1.2 | 2.1 | 1.8 | – | – |
| *S. vanzolinii* | – | – | – | – | – | 1.4 | 0.7 |
| *Cebus apella* | 1.0 | 2.1 | 0.4 | 3.6 | 2.5 | 1.1 | 0.6 |
| *C. albifrons* | 0.6 | 1.0 | 0.3 | 2.4 | 0.2 | – | – |
| *Pithecia albicans* | 1.7 | 4.6 | 0.4 | – | – | – | – |
| *P. ?monachus* | – | – | – | 0 | 1.8 | – | – |
| *Cacajao calvus* | – | – | – | – | – | 0.4 | 0.6 |
| *Alouatta seniculus* | 0.3 | 0.05 | 0.05 | 4.8 | 6.1 | 3.2 | 10.7 |
| *Ateles paniscus* | 0.1 | 0.1 | – | 3.2 | 0 | – | – |
| *Lagothrix lagotricha* | 0.2 | 0.05 | – | 0 | 0.7 | – | – |
| Distance surveyed (km) | 554.3 | 170.1 | 560.1 | 30.9 | 55.2 | 67.6 | 63.1 |

[a] Source: Johns (1986a).

[b] Source: Freese *et al.* (1982). Results are pooled from a number of observers. (Most of the data presented by Freese *et al.* derive from heavily hunted forests and are not considered here.)

[c] (–) Outside the geographical range of this species.

mosaics, where they may become agricultural pests (Defler, 1979). In many areas a large proportion of their diet is palm fruit (Freese and Oppenheimer, 1981; Terborgh, 1983; J. M. Ayres, personal communication); palms are not timber trees and are often left standing in agricultural areas since the fruit is also edible by humans. The apparent absence of *C. apella* from logged forest at Gorupí F. R. was unexpected but may have been due to hunting. (It was the species of primate preferred as a food item, although it was shot only if no other game was available.) Small opportunistic species of such genera as *Cebus* and *Pithecia* are able to feed on fruit from some of the early colonizing trees, notably *Inga* spp. (Leguminosae), and this ability aids their survival in disturbed areas (Johns, 1985b).

Among large-bodied species, survival is typically related to hunting pressure. Where *Alouatta* spp. are not hunted they often survive in some numbers, but their densities are not as high as in primary forest (Mittermeier and Coimbra-Filho, 1977; Ayres and Milton, 1981). The other large Neotropical frugivore/folivore, *Brachyteles arachnoides,* may also persist even in highly degraded habitat if it is not hunted (Fonseca, 1985).

While the large food sources favored by *Ateles paniscus* and *Lagothrix lagotricha* were not cut as timber trees at Ponta da Castanha, some were lost through incidental destruction; in the agricultural mosaic most were lost through forest clearance and were not present in regenerating growth. These large primates were able to enter disturbed forest from adjacent primary forest but would not be expected to persist in completely disturbed areas. (They were recorded in logged forest at Ponta da Castanha but were never further than 200 m from primary forest.) Where they do use disturbed areas, foraging units tend to be smaller.

The importance of details of the destructive effects of habitat disturbance can be illustrated by the following example. Logging at Ponta da Castanha was carried out at an extraction level of 3-5 trees/ha, which is comparable to results from seasonally flooded *Váreza* forest in the same part of Amazonia, where the extraction level was 4.6 trees/ha (Johns, 1986a). The primate fauna differs between the sites (Table IV), but it is noticeable that the large-bodied species were abundant in logged *Váreza.* That the specialist frugivore *Cacajao c. calvus* was present at a higher density in logged than in primary forest is unexpected. The explanation lies in the type of disturbance. Cut trees are floated out of the forest in the flooded season and there is no need to use heavy machinery; consequently, there are no logging roads and little incidental destruction occurs. The overall loss of perhaps 5% of the total trees does not seriously affect *C. c. calvus,* as a loss of only a few trees does not affect *Chiropotes albinasus* (Branch, 1983). A high number of fruit trees along the census trail caused a probable overestimation of numbers of *C. c. calvus,* and also of *Alouatta seniculus,* in logged forest in this example. Why the smaller species should be less numerous is not clear, since these genera are normally highly resilient to disturbance (see above). As is always the problem with small amounts of survey data, the serendipity of encounters may be the most important factor influencing the data.

## Southeast Asian Species

Most work on the responses of primates to habitat disturbance, especially selective logging, has been carried out in Southeast Asia. The principal studies are by Wilson and Wilson (1975), Payne and Davies (1982), and Wilson and Johns (1982) for Borneo; Wilson and Wilson (1976) and Rijksen (1978) for Sumatra; and Southwick and Cadigan (1972), Marsh and Wilson (1981), and Johns (1981, 1983a, 1985c, 1986b,c) for Peninsular Malaysia. Some of these studies have quantified the type of forest disturbance (Table V and VI).

Throughout Southeast Asian forests, the principal trees cut for timber are species of the Dipterocarpaceae, typically a dominant family occupying up to 30% of the total tree biomass but providing almost no food for primates. Logging is normally carried out at moderate to high densities (the average yield is generally over 50 $m^3$ha). Shifting agriculture is less common than plantation agriculture or permanent smallholdings, except in western Borneo. Few data are available concerning cultivated mosaics, but the only species that appears to persist under such conditions is *Macaca fascicularis* (Southwick and Cadigan, 1972).

The large frugivore *Pongo pygmaeus* is typically much reduced in abundance following habitat disturbance, although this may be due to some extent to avoidance of the presence of humans (Wilson and Wilson, 1975); *P. pygmaeus* is a nonterritorial species and has the option of long-distance movement in this regard (cf. Johns, 1985c). Payne and Davies (1982) mention that this species congregates in small unlogged reserves within logging areas at times of active tree felling, but may recolonize disturbed forests after a number of years. Surveys indicate that it is rare in even quite old logged forests, however, perhaps because of a reliance on upper-canopy food trees (Table VI; cf. Davies, 1986).

*Macaca* spp. are largely frugivorous but opportunistic and thus survive better than would be expected for more specialized frugivores. Several species have been reported to be more common in disturbed than in primary forest [e.g., *M. fascicularis* (Marsh and Wilson, 1981)]. In some cases, this may be due to the development of crop-raiding habits, common among *M. nemestrina* in Sumatra and *M. nigra* in Sulawesi (Wilson and Wilson, 1976; MacKinnon, 1979).

**Table V.** Primate Densities in Primary and Disturbed Forests in Peninsular Malaysia

| Area | Sungai Tekam[a] | | | | Lesong F.R.[b] | | | Pasoh F.R.[b] | |
|---|---|---|---|---|---|---|---|---|---|
| Vegetation type | Hill dipterocarp forest | | | | Lowland dipterocarp forest | | | Lowland dipterocarp forest | |
| Trees extracted/hectare | | ~18 | ~18 | ~18 | | "Light" | "Intensive" | | "Intensive" |
| Total damage (%) | | ~50 | ~50 | ~50 | | ? | ? | | ? |
| Time since logging | Primary | 1-2 years | 3-4 years | 5-6 years | Primary | 6 months | 5 years | Primary | 25 years |
| Species (density, groups/km$^2$) | | | | | | | | | |
| *Hylobates lar* | 2.5 | 1.8 | 3.8 | 1.5 | 1.8 | 2.0 | 1.2 | 4.3 | 1.2 |
| *Presbytis melalophos* | 3.4 | 3.0 | 4.9 | 3.4 | 6.5 | 1.0 | 3.9 | 4.2 | 4.6 |
| *P. obscura* | 0.5 | 1.8 | 3.0 | 0.8 | 3.8 | 1.8 | 5.0 | 3.6 | 3.7 |
| *Macaca fascicularis* | 0 | 0 | 0.2 | 0 | 0 | 0 | 7.7 | 2.0 | 4.6 |
| *M. nemestrina* | 0.2 | 0.5 | 0 | 0.2 | 0 | 0 | 0 | 0 | 0 |
| *Nycticebus coucang*[c] | 25.1 | 6.0 | 26.5 | 5.3 | | | | | |
| Distance surveyed (km) | Range mapping | 45.0 | 30.0 | 30.0 | 30.0 | 17.6 | 28.8 | 70.2 | 24.8 |
| | | 10.0[c] | 9.0[c] | 9.0[c] | | | | | |

---

[a] Source: Johns (1986b, unpubl.).

[b] Source: Marsh and Wilson (1981). Results are pooled from several observers.

[c] Detected during night censusing.

Table VI. Primate Densities in Primary and Disturbed Forest in Borneo

| Area | Bole Kecil/Malabuk[a] | | Silabukan/Bakapit[a] | | Sepaku River[b] | |
|---|---|---|---|---|---|---|
| Vegetation type | Hill dipterocarp forest | | Hill dipterocarp forest | | Lowland dipterocarp forest | |
| Trees extracted/hectare | | 10 | | 8 | | 8 |
| Total damage (%) | | ? | | ? | | 50 |
| Time since logging | Primary | 15 years | Primary | 19 years | Primary | 1 year |
| Species (density, groups/km²) | | | | | | |
| *Pongo pygmaeus* | 3.0 | Present | Present | 0 | 0 | 0 |
| *Hylobates muelleri* | 2.9 | 1.1 | 2.4 | 2.3 | 5.5 | 7.4 |
| *Presbytis rubicunda* | 4.5 | 1.1 | 0.9 | 1.3 | 1.9 | 1.9 |
| *P. aygula/P. hosei* | 0.7 | 0 | 3.6 | 1.3 | 0 | 0 |
| *Macaca fascicularis* | 0 | 0 | 0 | 0 | 1.9 | 0 |
| *M. nemestrina* | 0.7 | 0 | 0 | 3.8 | 0 | 0 |
| Distance surveyed (km) | 16.8 | 11.1 | 13.9 | 11.7 | 7.4 | 10.8 |

[a] Source: Payne and Davies (1982), results for sites matched by altitude and proximity.

[b] Source: Wilson and Wilson (1975).

[c] (–) Outside the geographical range of this species.

Frugivore/folivores (*Hylobates* spp. and *Presbytis* spp.) are typically able to survive well under conditions of logging, but few species survive in agricultural mosaics. The lesser degree of persistence of Sabahan species is probably due to hunting: Peninsular Malaysian primates are rarely hunted for food. It has been suggested that *Hylobates* spp. may be limited by the disproportionate removal of strangling figs, *Ficus* spp. (Moraceae), in logged forest: these figs are commonly attached to large timber trees, such as dipterocarps (Leighton and Leighton, 1983), and are felled together with them. Where figs are a very important food source for primates, as in parts of North Sumatra, their loss may indeed reduce the carrying capacity of logged forest (Rijksen, 1978), but in most areas figs are eaten opportunistically and their loss appears less important (e.g., Johns, 1983a). The main feature enabling primate frugivore/folivores to survive in disturbed Southeast Asian forests is their ability to change their diet and feeding behavior to a considerable extent (Berenstain, 1986; Johns, 1986c). The largely frugivorous *H. lar*, for example, is able to survive mostly on leaf material in logged forest, despite the low incidence of leaves in its diet in undisturbed forest. This ability to change diet and feeding behavior is not, of course, measured by the dietary parameters used here.

Insectivore/frugivores are present in the form of small-bodied prosimians, all of which appear to survive well under conditions of disturbance (for the same reasons that favor callitrichids in the Neotropics). Some species show very patchy distributions, however, and this can create ambiguous results—as in the case of *Nycticebus coucang* at Sungai Tekam (Johns, 1986b), where (nonterritorial) females were apparently congregating in areas with high densities of particular food resources.

. The main caveat that should be added is that there is often differential hunting pressure between primary and logged forests in non-Moslem parts of Southeast Asia. On Siberut Island, for example, resident species appear able to persist in forest logged less than 10 years before at a moderate density (15 trees/ha) but are much reduced in logged forests close to human habitations (Watanabe, 1981). Logging roads make useful hunting trails.

Another caveat to be considered is that the time that has passed since logging is likely to affect the carrying capacity of the forest. The critical period for many primates, when the fewest fruits will be available, is the period directly following logging, but stresses exerted at this time may affect parameters such as birth rates rather than population densities (directly) and may not show up in population samples for many years (e.g., Marsh and Wilson, 1981; Johns, 1983b). Unfortunately, long-term data are not yet available from a single site, and any trends are masked by basal population differences between sites. Continuing studies at Sungai Tekam in Peninsular Malaysia and at Danum Valley in Sabah may provide useful data in this respect.

Table VII. Primate Densities in Primary and Disturbed Forests in Africa

| Area | Kibale Forest, Uganda (Ituri community)[a] | | | | Bia Rainforest Area, Ghana (Upper Guinea–East community[b]) | | |
|---|---|---|---|---|---|---|---|
| Vegetation type | Medium-altitude mixed forest (*Parinari* type) | | | | Lowland mixed forest (*Celtis-Triplochiton* type) | | |
| Trees extracted/hectare | | ~5 | ~7.5 | ~6 | | ? | |
| Total damage (%) | | ~25 | ~45 | >50 | | ? | ~100 |
| Time since logging | Primary[c] | 9.5–11 years | 10–13 years | 11–16 years | Primary[c] | <2 years | Young regrowth-cultivation mosaic |
| Species (groups detected/10 km censused) | | | | | | | |
| *Cercocebus albigena* | 1.5 | 1.3 | 0.4 | 0.3 | — | — | — |
| *C. atys* | —[d] | — | — | — | 0.3 | 0.2 | 0.2 |
| *Cercopithecus diana* | — | — | — | — | 1.8 | 1.2 | 0.7 |
| *C. lhoesti* | 0.7 | 0.3 | 0.1 | 0.1 | — | — | — |
| *C. mitis* | 3.3 | 2.4 | 3.1 | 2.1 | — | — | — |
| *C. petaurista/C. mona* | — | — | — | — | 3.9 | 3.3 | 2.6 |
| *C. ascanius* | 5.7 | 8.7 | 2.6 | 2.4 | — | — | — |
| *Colobus verus* | — | — | — | — | 1.1 | 0.8 | 0.1 |
| *C. badius* | 10.8 | 8.8 | 4.3 | 3.1 | 0.6 | 0.1 | 0.0 |
| *C. polykomos* | — | — | — | — | 1.7 | 1.6 | 1.0 |
| *C. guereza* | 1.0 | 6.2 | 7.3 | 6.7 | — | — | — |
| *Pan troglodytes*[e] | 1.9 | 0.9 | 0.4 | 0.1 | Present | Present | 0.0 |
| Distance surveyed (km) | 108 | 75 | 104 | 150 | 235 | 202 | 193 |

[a] Source: Skorupa (1986, 1987). Forest in which there was no hunting and detection rates were corrected for differential visibility in closed and open forest.

[b] Source: Martin and Asibey (1979). Area with moderate hunting and severe logging (Hall and Swaine, 1981, p. 75). Detection rates are uncorrected.

[c] Here the term primary is used to imply only that the canopy is high and more or less closed (i.e., mature-phase forest).

[d] (—) Outside the geographical range of this species.

[e] Detection rates for *Pan troglodytes* are in units of *individuals* detected per 10 km censused.

## African Species

Few field-workers in Africa have intensively examined the status of primates in disturbed forest habitats. Only Martin and Asibey (1979) and Skorupa (1986, 1987) provide community-level data derived from a reasonable sampling intensity (Table VII), while studies by Harcourt (1981), Murnyak (1981), Tutin and Fernandez (1984), and Kano (1984) provide comparable data for particular focal species. At least one community-level investigation in progress promises to provide a third African case study (Howard, 1986; Kisubi, in preparation), and Davies (1986) recently completed a series of brief surveys in the Gola Forest Reserves (including logged areas) of Sierra Leone. Early studies, such as those by Gartlan and Struhsaker (1972), Struhsaker (1975), and Oates (1977a), dealt with habitat disturbance only as a peripheral issue and, therefore, allocated minimal effort for sampling disturbed habitats. Nonetheless, most of the conclusions drawn from those early studies have been confirmed by more intensive follow-up research (Skorupa, 1987). Finally, there are a host of studies that provide generally relevant information but few details (e.g., Kingdon, 1971; Rucks, 1976; Harding, 1983).

Commercial-scale logging activity greatly expanded following World War II (Hall and Swaine, 1981; Adams, 1985) and was focused primarily on a group of species marketed as "African mahogany" (primarily, but not strictly, from the family Meliaceae). However, domestic trade has always been less selective and varies tremendously from region to region in its magnitude relative to harvesting for the international trade. Unlike the dipterocarps of Southeast Asian forests, commercially exploited species in Africa tend to be important food trees for one or more species of co-occurring primates (e.g., Struhsaker, 1975; Rucks, 1976; Martin and Asibey, 1979). Although extraction rates rarely exceed 3-5 trees/ha or 25 $m^3$/ha, the incidental damage associated with capital-intensive mechanized harvesting techniques can significantly reduce primate food supplies (Skorupa, 1986). Furthermore, logging is often followed by clearing for agriculture, frequently resulting in a cropland/regenerating forest mosaic (Jeffrey, 1978).

The large frugivore *Pan troglodytes* is capable of ranging over hundreds of square kilometers (Baldwin *et al.*, 1982) and of occupying a wide diversity of habitat types (Teleki and Baldwin, 1979). This has prompted some observers to conclude that *P. troglodytes* densities exhibit no pattern with respect to habitat type (Teleki and Baldwin, 1979) or that open forest is the preferred habitat (Kortlandt, 1983). Case studies, however, consistently indicate that *P. troglodytes* persists in disturbed forest at much lower densities than in closed forest of similar botanic affinities (Struhsaker, 1975; Tutin and Fernandez, 1984; Skorupa, 1986). Short-term surveys can be particularly misleading when applied to wide-ranging phenological nomads such as

*P. troglodytes.* While the closely related *Pan paniscus* is known to utilize secondary forest, it remains doubtful that large tracts of secondary forest, isolated from access to primary forest, would support normal densities (Kano, 1984).

In contrast, the large folivore *Gorilla gorilla* appears to thrive in disturbed forest (Harcourt, 1981; Murnyak, 1981; Tutin and Fernandez, 1984), where the abundance and diversity of preferred foods may be maximized. However, a mosaic dominated by regenerating forest, but still including patches of primary forest, may constitute the optimal habitat (Murnyak, 1981).

The *Cercopithecus* monkeys of Africa vary widely in their abilities to persist in disturbed forest, and several cases illustrate how responses are often idiosyncratic. *Cercopithecus mitis* is an extreme generalist, seemingly equally capable of utilizing fruit, insect, and foliar foods. It is not surprising, then, that *C. mitis* densities were not strongly correlated in any way with several measures of forest structure (Skorupa, 1986). At Kibale Forest, *Cercopithecus lhoesti* seems to be associated with closed forest (Skorupa, 1986), although within closed forest they are most often sighted near patches of secondary growth. Thus, mosaic habitat may again constitute the optimal type, something similar to what Kano (1984) reports for *Pan paniscus,* a mosaic dominated by mature forest. However, even within Uganda, Butynski (1985) found *C. lhoesti* most abundant in the bamboo zone of the Impenetrable (Bwindi) Forest, while Howard's (1986) preliminary findings indicate a preference for logged habitat in the Kalinzu Forest. Moreover, Howard finds all forest primates at Kalinzu to be roughly three to five times more abundant in logged habitat, including the generalist *C. mitis.* Apparently much of the contrast in results from Kibale and Kalinzu may be due to an abundance of the colonizing tree *Musanga leo-errerae [cecropioides]* (Moraceae) at Kalinzu. It grows in place of *Trema orientalis [guineensis]* (Ulmaceae), the common early-colonizing tree found at Kibale but, unlike *Trema,* produces abundant large fruits that are a favorite food for cercopithecine monkeys (Howard, 1986).

*Cercopithecus ascanius* may be particularly sensitive to variation in fig tree (*Ficus* spp.) densities [Skorupa (1986); cf. Terborgh (1983, p. 84) for *Saimiri*]. If this is true, then the highly variable descriptions of the *C. ascanius* response to habitat disturbance (e.g., Kingdon, 1971; Suzuki, 1971; Struhsaker, 1975; Albrecht, 1976; Skorupa, 1986; Howard, 1986) may reflect site-specific variation in human practices— depending, for example, on whether fig trees are poisoned during silvicultural treatments (i.e., liberation or refinement thinning) or whether fig timber is valued locally (cf. Eggeling and Dale, 1952, p. 237; Marsh *et al.,* 1986). *Ficus* is one of the largest genera of trees in Africa (cf. Hall and Swaine, 1981, p. 30), comprising species of many ecotypes [although most are mature forest species (Hall and Swaine, 1981, p. 352)]. Undoubtedly, the particular mix of colonizing versus mature-forest species varies from forest to forest, and this may influence the suitability of closed versus open forest for *C. ascanius*. Complicating matters further, individual fig trees within a species vary immensely in their response to canopy opening, with a few individuals becoming much more productive while most individuals show little response (Primack *et al.*, 1984). The chance inclusion or exclusion of an unrepresentative number of the "responders" along a census route can lead to qualitatively different impressions of *C. ascanius* densities. To the extent that fig trees are "key species" for many frugivorous forest primates (e.g., Leighton and Leighton, 1983; Terborgh, 1983, pp. 235-237, 1986; Marsh *et al.*, 1986), the above considerations are widely relevant.

Due to the generally alert nature of *Cercopithecus* monkeys (Struhsaker, 1981, p. 295), and their abilities to conceal themselves (Kawai *et al.*, 1975), they are less susceptible to hunting than most African primates. For example, *C. erythrotis* survives on the island of Fernando Po (Bioko) in areas subjected to intense hunting (Butynski, personal communication). Likewise, *C. mona (campbelli)* and *C. petaurista* survive in heavily hunted areas of Ghana (Martin and Asibey, 1979) and Sierra Leone (Davies, 1986). Nevertheless, *Cercopithecus* densities can be depressed greatly by hunting (e.g., *C. diana*), and throughout much of the continent it is very difficult to separate the effects of hunting from the effects of habitat disturbance (Asibey, 1978). On the basis of data collected in the Gola Forest Reserves of Sierra Leone, Davies (1986) suggests that response to logging disturbance accounts for much less of the between-site variation in primate densities than is accounted for by between-site variation in hunting pressure.

Africa's folivorous colobine monkeys also illustrate the importance of idiosyncrasies. *Colobus guereza* is typically more abundant in logged habitat, but this response does not appear to be related to food supplies, at least if we assume that their monotonous reliance on *Celtis* and *Markhamia* is unaltered in logged forest (Skorupa, 1986). *Colobus guereza* may simply be a "light-loving" species of primate. Energy obtrained via insolation may be a critical adjunct to *C. guereza*'s ability to persist on a low-quality diet (Watkins *et al.*, 1985), as Young (1982) has suggested for howler monkeys (*Alouatta* sp.). *Colobus guereza*'s principal food trees are typically found in the understory, as are guerezas themselves (Oates, 1977b), and this zone is heavily shaded in closed canopy forest.

*Colobus badius*, in contrast, is most abundant in undisturbed forest (Struhsaker, 1975; Asibey and Martin, 1979; Davies, 1986). While *C. badius* does not seem to be linked to any one or two key species of tree for food, it does depend on a very specialized diet (as evidenced by failure to maintain *C. badius* successfully in captivity, while *C. guereza* is commonly kept in captivity). Apparently, the optimal dietary mix is the crucial consideration for *C. badius*, and at Kibale *C. badius* densities were strongly correlated with a particular suite of food trees that were most abundant in the mature-forest study plot (Skorupa, 1986). Jeffrey (1978) also suspected that the decline of *C. badius* in the logged forests of West Africa was due at least partly to its specialized diet.

*Colobus satanus* is reported to be vulnerable to any form of habitat disturbance (McKey, cited by Oates, 1977a) and provides perhaps a third unique pattern of habitat dependence within the genus. *Colobus satanus* appears to depend heavily on exploiting the seeds of a few rare tree species to complement a folivorous diet fraught with deleterious secondary compounds (McKey, 1978). It is likely, although unproven, that the seed trees are *too* rare in disturbed forest to support the same densities of *C. satanus* found in undisturbed forest.

In most areas *Colobus* monkeys are heavily hunted for meat (e.g., Rodgers, 1981) or their pelts (e.g., Oates, 1977a). They are also very susceptible to being hunted to depletion, perhaps as a result of the generally sluggish metabolism and inattentive behavior associated with prolonged digestion of low-quality forage. While *Cercopithecus* monkeys can conceal themselves for hours (Kawai *et al.*, 1975), a *Colobus* monkey attempting to do so would often be revealed by audible emissions of gas resulting from digestive fermentation (Skorupa, personal observation). For those species normally found almost exclusively in the upper canopy of the forest, the lower stature of disturbed forest also leads to increased vulnerability to hunters.

In summary, it would be most useful to have at least one rigorous community-level study of primate response to habitat disturbance for each of the six major forest blocks distinguished by Oates *et al.* (1982). Already it may be too late to achieve optimal conjunction of protection and production forest in three blocks (Upper Guinea – West, Upper Guinea – East, and Cameroun). The remaining forest blocks (Gabon, Congo Basin, and Ituri) still offer opportunities for maximizing primate conservation within a protection/production forest mosaic. Consequently, studies in the latter three blocks are particularly needed. In addition, the present knowledge of primate persistence in forest/agriculture mosaics is deficient throughout tropical Africa, as is our knowledge of prosimian responses to selective logging (although the responses of callitrichids in the Neotropics may provide a reasonable basis for predicting African prosimian responses).

## CONCLUSIONS

A precise knowledge of local conditions can explain a good deal of the variation among primates following habitat disturbance. Clearly, most species are drastically reduced where disturbance is heavy (e.g., selective logging followed by forest management practices, agricultural encroachment, and/or heavy hunting). Only a few species are able to survive in large numbers in highly disturbed forest around human settlements or in agricultural areas [e.g., *Miopithecus* spp. (Gautier-Hion, 1971); *Callicebus moloch* (Johns, 1986a)], and in few cases are these species adapted primarily to rain-forest habitat.

Differences observed in the ability of primates to survive selective logging depend ultimately on the degree of damage caused, but also upon the extent to which important timber species are also important food sources for primates (Johns, 1983b). In western Amazonian and Malaysian sites, where logging had destroyed approximately 45–50% of the forest, but where the most frequently harvested trees are rarely used as food sources by primates, Johns (1986a, b) found that primates survive well. At a Ugandan site subject to the same level of logging damage, but where most trees provide foods for one or more species of primate, Skorupa (1986) found that five of the seven primate species exhibited significant population declines. In one plot damaged at an atypically low intensity, however, only one of the seven species showed a significant population decline. More specifically, the removal of food trees important to *Pongo pygmaeus* (Rijksen, 1978) and *Chiropotes s. satanas* (Johns, 1986a) resulted directly in the local demise of these species.

The response of a species to disturbance is, of course, dynamic. At Ponta da Castanha in Amazonia, Johns (1986a) indicated that many primates can use older logged forest because of the rapid regeneration of edible fruits, but there was no evidence to suggest that these same species could use large areas of recently logged forest (i.e., that they could maintain home ranges entirely within them). Evidence from elsewhere in Amazonia suggests that this would be unlikely. Some populations, particularly the adult segment, although persisting within disturbed areas, may respond only very slowly. For example, *Macaca sinica* showed little change in the density of adults following habitat disturbance, although the population as a whole declined by 15% due to food shortages (Dittus, 1977). Similarly, a *Cercopithecus aethiops* population showed little change in the density of adults 11 years after a massive mortality of food trees (Struhsaker, 1976). Some nonterritorial primates [e.g., *Pongo pygmaeus* (Davies, 1986)] have been shown to migrate away from disturbed areas, either returning at a later stage or concentrating in residual unlogged areas. Territorial species would be expected to move long distances only if facing a terminal food shortage (Johns, 1985c) and, where this happens, will suffer high mortality rates. Thus progressive changes in species density may occur for considerable lengths of time, even when the perturbation experienced is short and discrete, as with selective logging. Point samples (in time) of primate survival in disturbed habitats can be misleading.

Despite the complexities outlined above, several general conclusions can be reasonably drawn. All else equal, large frugivores appear to be the first species endangered by habitat disturbance. There is, however, abundant evidence that moderately disturbed habitats are capable of supporting many primate species at viable densities. Consequently, moderate *sustainable* forms of forest exploitation may often be compatible with the conservation of rain-forest primates *when increased hunting pressure does not accompany exploitation.* Since disturbed rain forests will cover much larger areas than protected rain forests as the expansion of human activities in the tropics continues, high priorities should be given to determining which forms and intensities of forest exploitation are sustainable (e.g., Skorupa and Kasenene, 1984) and to studying more cases of primate response to moderate habitat disturbance in sufficient detail to guide conservation planning.

Although sustainably exploited rain forest can potentially serve an important role in assuring primate conservation, it is nonetheless essential to maintain a core of conservation areas which are fully protected from exploitation. Even moderately degraded habitat may profoundly alter long-term evolutionary processes (Conner, 1979). In addition, fully protected conservation areas provide insurance against the effects of unforeseeable catastrophic events. For example, during the El Nino-induced drought of 1982–1983 in East Kalimantan, Borneo, fires burned an estimated 36,000 km$^2$ of rain forest (New Scientist, 1984). However, damage caused by the fire was much more severe in selectively logged forest than in unexploited forest (Leighton and Wirawan, 1986; Asiaweek, 1984). Since such catastrophic droughts are believed to be long-term cyclic events (Leighton and Wirawan, 1986), it is obvious that the potential for primate conservation in moderately exploited forests should be developed only in addition to, and not in the place of, fully protected conservation areas.

## ACKNOWLEDGMENTS

Original information in this paper was collected during three field studies conducted by the authors. A. D. J. was supported in Malaysia by Contract N01-CO-85409, U.S. National Institutes of Health, with the University of Cambridge, and in Brazil by WWF-US, Project US-302. A. D. J. thanks these institutions, the Dean and Faculty of Veterinary Medicine and Animal Sciences, Universiti Pertanian Malaysia, and the Director and F. C. Novaes of Museu Paraense Emilio Goeldi, Belém, for their support. J. P. S. was supported by WWF-US Project 1969, by the New York Zoological Society (both of the above through Dr. Thomas T. Struhsaker), and by the California Primate Research Center (through Dr. Peter S. Rodman). J. P. S. also wishes to thank the Ugandan National Research Council, the Uganda Forests Department, and the Department of Zoology of Makerere University for their support. We are also grateful to the following for comments on various drafts of the manuscript: L. Berenstain, D. J. Chivers, A. G. Davies, D. R. Leighton, M. Kavanagh, J. M. Y. Robertson, P. S. Rodman, and three anonymous reviewers.

## REFERENCES

Adams, D. M. (1985). A spatial equilibrium model of African-European trade in tropical logs and sawnwood. *For. Ecol. Manag.* 13: 265-287.

Albrecht, H. (1976). Chimpanzees in Uganda. *Oryx* 13: 357-361.

Asiaweek (1984). Wound in the world. *Asiaweek* 10: 32-55.

Asibey, E. O. A. (1978). Primate conservation in Ghana. In Chivers, D. J., and Lane-Petter, W. (eds.), *Recent Advances in Primatology, Vol. 2, Conservation,* Academic Press, New York and London, pp. 55-74.

Ayres, J. M. (1981). *Observacoes Sobre a Ecologia e o Comportamento dos Cuxius* (Chiropotes albinasus *e* Chiropotes satanas, *Cebidae: Primates*), Grafisa, Belem.

Ayres, J. M. (1983). Conservation of primates in Brazilian Amazonia: problems and strategies. In Harper, D. (ed.), *Conservation of Primates and Their Habitats,* Vaughan Paper No. 31, University of Leicester, Leicester, pp. 2-33.

Ayres, J. M., and Milton, K. (1981). Levantamento de primatas e habitat no Rio Tapajos. *Bol. Mus. Pa. Emilio Goeldi N. Ser. Zool.* 111: 1-11.

Baldwin, P. J., McGrew, W. C., and Tutin, C. E. G. (1982). Wide-ranging chimpanzees at Mt. Assirik, Senegal. *Int. J. Primatol.* 3: 367-385.

Berenstain, L. (1986). Responses of long-tailed macaques to drought and fire in eastern Borneo: A preliminary report. *Biotropica* 18: 257-262.

Branch, L. C. (1983). Seasonal and habitat differences in the abundance of primates in the Amazon (Tapajos) National Park, Brazil. *Primates* 24: 424-431.

Butynski, T. M. (1985). Primates and their conservation in the Impenetrable (Bwindi) Forest, Uganda. *Primate Conservat.* 6: 68-72.

Chivers, D. J., and Hladik, C. M. (1984). Diet and gut morphology in primates. In Chivers, D. J., Wood, B. A., and Bilsborough, A. (eds.), *Food Acquisition and Processing in Primates,* Plenum Press, New York, pp. 213-230.

Clutton-Brock, T. H., and Harvey, P. H. (1977). Species differences in feeding and ranging behaviour in primates. In Clutton-Brock, T. H. (ed.), *Primate Ecology,* Academic Press, New York and London, pp. 557-584.

Clutton-Brock, T. H., and Harvey, P. H. (1984). Comparative approaches to investigating adaptation. In Krebs, J. R., and Davies, N. B. (eds.), *Behavioural Ecology: An Evolutionary Approach,* Sinauer Associates, Sunderland, Mass., pp. 7-29.

Coimbra-Filho, A. F. (1977). Natural shelters of *Leontopithecus rosalia* and some ecological implications (Callitrichidae: Primates). In Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae,* Smithsonian Institution Press, Washington, D.C., pp. 79-89.

Conner, R. N. (1979). Minimum standards and forest wildlife management. *Wildl. Soc. Bull.* 7: 293-296.

Davies, G. (1986). The orang-utan in Sabah. *Oryx* 20: 40-45.

Davies, G. (1986). Conservation of primates in the Gola Forest Reserves, Sierra Leone. *Primate Conservat.* (in press).

Defler, T. R. (1979). On the ecology and behaviour of *Cebus albifrons* in Eastern Colombia. 1. Ecology. *Primates* 20: 475-490.

Dietz, L. A. (1985). Captive-born golden lion tamarins released into the wild: A report from the field. *Primate Conservat.* 6: 21-27.

Dittus, W. P. J. (1977). The social regulation of population density and age-sex distribution in the toque monkey. *Behaviour* 63: 281-322.

Eggeling, W. J., and Dale, I. R. (1952). *The Indigenous Trees of the Uganda Protectorate,* Government Printer, Entebbe, Uganda.

Fonseca, G. A. B. (1985). Observations on the ecology of the muriqui (*Brachyteles arachnoides* E. Geoffroy 1806): implications for its conservation. *Primate Conservat.* 5: 48-52.

Freese, C. H., and Oppenheimer, J. R. (1981). The capuchin monkeys, genus *Cebus.* In Coimbra-Filho, A. F., and Mittermeier, R. A. (eds.), *Ecology and Behavior of Neotropical Primates,* Academia Brasileira de Ciencias, Rio de Janeiro, pp. 331-390.

Freese, C. H., Freese, M. A., and Castro, R. N. (1977). The status of callitrichids in Peru. In Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae,* Smithsonian Institution Press, Washington, D. C., pp. 121-130.

Freese, C. H., Heltne, P. G., Castro, R., N., and Whitesides, G. (1982). Patterns and determinants of monkey densities in Peru and Bolivia, with notes on distributions. *Int. J. Primatol.* 3: 53-90.

Gartlan, J. S., and Struhsaker, T. T. (1972). Polyspecific associations and niche separation of rain-forest anthropoids in Cameroon, West Africa. *J. Zool.* 168: 221-266.

Gaulin, S. J. C., and Gaulin, C. K. (1982). Behavioral ecology of *Alouatta seniculus* in Andean cloud forest. *Int. J. Primatol.* 3: 1-32.

Gaulin, S. J. C., and Konner, M. J. (1977). On the natural diet of primates, including humans. In Wurtman, R., and Wurtman, J. (eds.), *Nutrition and the Brain,* Raven Press, New York, Vol. 1, pp. 1-86.

Gautier-Hion, A. (1971). L'écologie du talapoin du Gabon. *Terre Vie* 25: 427-490.

Gittins, S. P. (1979). *Behavioural Ecology of the Agile Gibbon,* Hylobates agilis, Ph.D. thesis, University of Cambridge, Cambridge.

Hall, J. B., and Swaine, M. D. (1981). *Distribution and Ecology of Vascular Plants in a Tropical Rain Forest,* Dr. W. Junk, The Hague, Boston, and London.

Harcourt, A. H. (1981). Can Uganda's gorillas survive? A survey of the Bwindi Forest Reserve. *Biol. Conservat.* 19: 269-282.

Harding, R. S. O. (1984). Primates of the Kilimi Area, Sierra Leone. *IUCN/SSC Primate Special. Group Newslett.* 4: 32-34.

Hladik, A., and Hladik, C. M. (1969). Rapports trophiques entre vegetation et primates dans la forêt de Barro Colorado (Panama). *Terre Vie* 23: 25-117.

Howard, P. C. (1986). Conservation of tropical forest wildlife in Western Uganda. Unpublished annual report, WWF Project 3235.

Isbell, L. A. (1983). Daily ranging behavior of red colobus *(Colobus badius tephrosceles)* in Kibale Forest, Uganda. *Folia primatol.* 41: 34-48.

Jeffrey, S. M. (1978). The effects of logging on rainforest fauna of West Africa and East Kalimantan. In *Proceedings of the Eighth World Forestry Congress, Vol. VII,* Jakarta, Indonesia, pp. 393-400.

Johns, A. D. (1981). The effects of selective logging on the social structure of resident primates. *Malays. appl. Biol.* 10: 221-226.

Johns, A. D. (1983a). *Ecological Effects of Selective Logging in a West Malaysian Rain-forest,* Ph.D. thesis, University of Cambridge, Cambridge.

Johns, A. D. (1983b). Primates and selective logging: An overview. In Harper, D. (ed.), *Conservation of Primates and their Habitats,* Vaughan Paper No. 31, University of Leicester, Leicester, pp. 86-100.

Johns, A. D. (1983c). Wildlife can live with logging. *New Sci.* 99: 206-211.

Johns, A. D. (1983d). Tropical forest primates and logging: Can they co-exist? *Oryx* 17: 114-118.

Johns, A. D. (1985a). Current status of the southern bearded saki *(Chiropotes satanas satanas). Primate Conservat.* 5: 28.

Johns, A. D. (1985b). Primates and forest exploitation at Tefe, Brazilian Amazonia. *Primate Conservat.* 6: 27-29.

Johns, A. D. (1985c). Behavioral responses of two Malaysian primates *(Hylobates lar* and *Presbytis melalophos)* to selective logging: Vocal behavior, territoriality, and nonemigration. *Int. J. Primatol.* 6: 423-433.

Johns, A. D. (1986a). *Effects of Habitat Disturbance on Rainforest Wildlife in Brazilian Amazonia,* Unpublished report to WWF-US, Washington, D.C.

Johns, A. D. (1986b). The effects of commercial logging on a West Malaysian primate community. In King, F. A., and Taub, D. (eds.), *Proceedings of the IXth IPS Congress,* Van Nostrand Reinhold, New York, 206-211.

Johns, A. D. (1986c). Effects of selective logging on the behavioral ecology of West Malaysian primates. *Ecology* 67: 684-694.

Johnson, D. H. (1981). How to measure habitat: A statistical perspective. In Capen, D. E. (ed.), *The Use of Multivariate Statistics in Studies of Wildlife Habitat,* USDA Forest Service General Technical Report RM-87, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo., pp. 53-58.

Kano, T. (1984). Distribution of pygmy chimpanzees *(Pan paniscus)* in the central Zaire basin. *Folia primatol.* 43: 36-52.

Karr, J. R. (1982). Population variability and extinction in the avifauna of a tropical land bridge island. *Ecology* 63: 1975-1978.

Kawai, M., Ando, S., and Mizuno, A. (1975). A quantitative study on the activities of the forest-living monkeys in the Kibale Forest of Uganda by using a telemetric method. *Kyoto Univ. Afr. Stud.* 9: 1-20.

Kay, R. F. (1984). On the use of anatomical features to infer foraging behavior in extinct primates. In Rodman, P. S., and Cant, J. G. H. (eds.), *Adaptations for Foraging in Nonhuman Primates,* Columbia University Press, New York, pp. 21-53.

Kingdon, J. (1971). *East African Mammals, Vol. I,* Academic Press, New York.

Kinzey, W. G. (1977). Diet and feeding behaviour of *Callicebus torquatus.* Clutton-Brock, T. H. (ed.), *Primate Ecology,* Academic Press, New York and London, pp. 127-151.

Kinzey, W. G. (1981). The titi monkeys, genus *Callicebus.* In Coimbra-Filho, A. F., and Mittermeier, R. A. (eds.), *Ecology and Behavior of Neotropical Primates, Vol. 1,* Acad. Bras. Cien., Rio de Janeiro, pp. 241-276.

Kortlandt, A. (1983). Marginal habitats of chimpanzees. *J. hum. Evol.* 12: 231-278.

Lanly, J. P. (1982). Tropical forest resources, Forestry Paper No. 30, FAO, Rome.

Leighton, M., and Leighton, D. R. (1983). Vertebrate responses to fruiting seasonality within a Bornean rainforest. In Sutton, S. L., Whitmore, T. C., and Chadwick, A. C. (eds.), *Tropical Rain Forest: Ecology and Management,* Blackwell Scientific, Oxford, pp. 181-196.

Leighton, M., and Wirawan, N. (1986). Catastrophic drought and fire in Bornean tropical rain forest associated with the 1982-83 ENSO event. In Prance, G. T. (ed.), *Tropical Rainforest and World Atmosphere,* Am. Assoc. Adv. Sci., Sel. Symp. 101, Westview Press, Boulder, Colo., pp. 75-102.

Lovejoy, T. E., Rankin, J. M., Bierregaard, R. O., Jr., Brown, K. S., Jr., Emmons, L. H., and van der Voort, M. E. (1984). Ecosystem decay of Amazon forest remnants. In Nitecki, M. H. (ed.), *Extinctions,* University of Chicago Press, Chicago, pp. 295-325.

Lovejoy, T. E., Bierregaard, R. O., Jr., Rylands, A. B., Malcolm, J. R., Quintela, C. E., Harper, L. H., Brown, K. S., Jr., Powell, A. H., Powell, G. V. N., Schubart, H. O. R., and Hays, M. B. (1986). Edge and other effects of isolation on Amazon forest fragments. In Soule, M. E. (ed.), *Conservation Biology (II),* Sinauer Associates, Sunderland, Mass., pp. 257-285.

MacKinnon, J. R. (1979). A glimmer of hope for Sulawesi. *Oryx* 15: 55-59.

MacKinnon, J. R., and MacKinnon, K. S. (1980a). Niche differentiation in a primate community. In Chivers, D. J. (ed.), *Malayan Forest Primates,* Plenum Press, London, pp. 167-190.

Marsh, C. W., and Wilson, W. L. (1981). *A Survey of Primates in Peninsular Malaysian Forests. Final Report,* Universiti Kebangsaan Malaysia.

Marsh, C. W., Johns, A. D., and Ayres, J. M. (1986). Effects of habitat disturbance on rainforest primates. In Gartlan, J. S., Marsh, C. W., and Mittermeier, R. A. (eds.), *Primate Conservation in Tropical Rain Forest,* Alan Liss, New York, pp. 83-107.

Martin, C., and Asibey, E. O. A. (1979). Effect of timber exploitation on primate populations and distribution in the Bia rain forest area of Ghana. Paper presented to VIIth IPS Congress, Bangalore, India.

Martin, R. D. (1981). Field studies of primate behaviour. *Symp. zool. Soc. London* 46: 287-336.

McKey, D. (1978). Soils, vegetation, and seed-eating by black colobus monkeys. In Montgomery, G. G. (ed.), *Arboreal Folivores,* Smithsonian Institution Press, Washington, D.C.', pp. 423-437.

Melillo, J. M., Palm, C. A., Houghton, R. A., Woodwell, G. M., and Myers, N. (1985). A comparison of two recent estimates of disturbance in tropical forests. *Environ. Conservat.* 12: 37-40.

Mergen, F. (ed.) (1981). *Tropical Forests,* School of Forestry and Environmental Studies, Yale University, New Haven, Conn.

Mittermeier, R. A., and Coimbra-Filho, A. F. (1977). Primate conservation in Brazilian Amazonia. In H. S. H. Rainier III and Bourne, G. H. (eds.), *Primate Conservation,* Academic Press, New York and London, pp. 117-166.

Mittermeier, R. A., Bailey, R. C., and Coimbra-Filho, A. F. (1977b). Conservation status of the Callitrichidae in Brazilian Amazonia, Surinam, and French Guiana. In Kleiman, D. G. (ed.), *The Biology and Conservation of the Callitrichidae,* Smithsonian Institution Press, Washington, D.C., pp. 137-146.

Mohamed Khan bin Momin Khan (1978). Man's impact on the primates of peninsular Malaysia. In Chivers, D. J., and Lane-Petter, W. (eds.), *Recent Advances in Primatology. Vol. 2: Conservation,* Academic Press, New York and London, pp. 41-46.

Murnyak, D. F. (1981). Censusing the gorillas in Kahuzi-Biega National Park. *Biol. Conservat.* 21: 163-176.

Myers, N. (1984). *The Primary Source,* W. W. Norton, New York and London.

Myers, N. (1986). Tropical deforestation and a mega-extinction spasm. In Soule, M. E. (ed.), *Conservation Biology (11),* Sinauer Associates, Sunderland, Mass.

New Scientist (1984). The world's worst fire: Counting the cost. *New Sci.* 104 (1431): 9.

Nie, N. H., Bent, D. H., and Hull, C. H. (1970). *Statistical Programs for the Social Sciences,* McGraw-Hill, New York.

Oates, J. F. (1977a). The guereza and man. In H. S. H. Rainier III and Bourne, G. H. (eds.), *Primate Conservation,* Academic Press, New York, pp. 419-467.

Oates, J. F. (1977b). The guereza and its food. In Clutton-Brock, T. H. (ed.), *Primate Ecology,* Academic Press, New York, pp. 275-321.

Oates, J. F., Gartlan, J. S., and Struhsaker, T. T. (1982). A framework for planning African rain-forest primate conservation. *Int. Primatol. Soc. News* 1: 4-9.

Oliveira, J. M. S., Lima, M. G., Bonvincino, C., Fleagle, J. G., and Ayres, J. M. (1986). Preliminary notes on the ecology and behaviour of the Guianan saki (*Pithecia pithecia,* Linnaeus, 1766; Cebidae, Primates). *Acta Amazon.* (in press).

Payne, J. B. and Davies, A. G. (1982). *A Faunal Survey of Sabah,* World Wildlife Fund Malaysia, Kuala Lumpur.

Primack, R. B., and Chai, P. (1984). Growth rates of Moraceae trees in Sarawak rain-forest. In Chadwick, A. C., and Sutton, S. L. (eds.), *Tropical Rain-Forest,* Spec. Publ. Leeds Phil. Lit. Soc., Leeds, U.K., pp. 316-317.

Ricklefs, R. E. (1979). *Ecology,* Chiron Press, New York and Concord.

Rijksen, H. D. (1978). *A Field Study of Sumatran Orang-utans (*Pongo pygmaeus abelii, *Lesson 1827): Ecology, Behaviour, and Conservation,* H. Veenman and Zonen, B. V. Wageningen.

Robinson, J. G., and Ramirez, C. J. (1982). Conservation biology of neotropical primates. In Mares, M. A., and Genoways, H. M. (Genoways, (eds.), *Mammalian Biology,* Spec. Publ. No. 6, Pymatuning Laboratory of Ecology, University of Pittsburgh, Linesville, Pa., pp. 329-344.

Rodgers, W. A. (1981). The distribution and conservation status of colobus monkeys in Tanzania. *Primates* 22: 33-45.

Rodman, P. S. (1973). Synecology of Bornean primates: A test for interspecific interactions in spatial distribution of five species. *Am. J. phys. Anthrop.* 38: 655-660.

Rucks, M. G. (1976). Notes on the problems of primate conservation in Bia National Park. Unpublished report to Department of Game and Wildlife, Accra, Ghana.

Ryan, T. A., Jr., Joiner, B. L., and Ryan, B. F. (1981). *Minitab Reference Manual,* Duxbury Press, Boston.

Rylands, A. B. (1981). Preliminary field observations on the *Callithrix humeralifer intermedius* (Hershkovitz, 1977) at Dardanelos, Rio Aripuana, Matto Grosso. *Primates* 22: 46-59.

Salter, R. E., and MacKenzie, N. A. (1981). Habitat-use behaviour of the proboscis monkey *(Nasalis larvatus)* in Sarawak. National Parks and Wildlife Office, Forest Department, Sarawak.

Skorupa, J. P. (1986). Responses of rainforest primates to selective logging in Kibale Forest, Uganda: A summary report. In Benirschke, K. (ed.), *Primates: The Road to Self-Sustaining Populations,* Springer Verlag, New York, pp. 57-70.

Skorupa, J. P. (1987). *Effects of Selective Timber Harvesting on Rain-Forest Primates in Kibale Forest, Uganda,* Ph.D. thesis, University of California, Davis (in preparation).

Skorupa, J. P., and Kasenene, J. M. (1984). Tropical forest management: Can rates of natural treefalls help guide us? *Oryx* 18: 96-101.

Struhsaker, T. T. (1975). *The Red Colobus Monkey,* University of Chicago Press, Chicago.

Struhsaker, T. T. (1976). A further decline in numbers of Amboseli vervet monkeys. *Biotropica* 8: 211-214.

Struhsaker, T. T. (1978). Food habits of five monkey species in the Kibale Forest, Uganda. In Chivers, D. J., and Herbert, J. (eds.), *Recent Advances in Primatology. Vol. 1: Behaviour,* Academic Press, New York and London, pp. 225-248.

Struhsaker, T. T. (1981). Polyspecific associations among tropical rain-forest primates. *Z. Tierpsychol.* 57: 268-304.

Struhsaker, T. T., and Oates, J. F. (1975). Comparison of the behavior and ecology of red colobus and black-and-white colobus monkeys in Uganda: A summary. In Tuttle, R. H. (ed.), *Socio-ecology and Psychology of Primates,* Mouton, The Hague and Paris, pp. 103-123.

Suzuki, A. (1971). On the problems of conservation of the chimpanzees in East Africa and the preservation of their environment. *Primates* 12: 415-418.

Teleki, G., and Baldwin, L. (1979). Known and estimated distributions of extant chimpanzee populations *(Pan troglodytes* and *Pan paniscus)* in Equatorial Africa. Unpublished Special Report to IUCN/SSC Primate Specialist Group.

Terborgh, J. (1983). *Five New World Primates,* Princeton University Press, Princeton, N.J.

Terborgh, J. (1986). Keystone plant resources in the tropical forest. In Soule, M. E. (ed.), *Conservation Biology (II),* Sinauer Associates, Sunderland, Mass., pp. 330-344.

Terborgh, J., and Winter, B. (1980). Some causes of extinction. In Soule, M. E., and Wilcox, B. A. (eds.), *Conservation Biology,* Sinauer Associates, Sunderland, Mass., pp. 119-133.

Tilson, R. L. (1977). Social behaviour of Simakobu monkeys and its relationship to human predation. *J. Mammal.* 58: 202-212.

Tutin, C. E. G., and Fernandez, M. (1984). Nationwide census of gorilla *(Gorilla g. gorilla)* and chimpanzee *(Pan t. troglodytes)* populations in Gabon. *Am. J. Primatol.* 6: 313-336.

UNESCO (1978). *Tropical Forest Ecosystems,* UNESCO-UNEP, Paris.

van Roosmalen, M. G. M. (1980). Habitat preferences, diet, feeding strategy and social organisation of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. Rijksintituut voor Natuurbeheer, Rapport 80/13, Leersum.

van Roosmalen, M. G. M., Mittermeier, R. A., and Milton, K. (1981). The bearded sakis, genus *Chiropotes.* In Coimbra-Filho, A. F. and Mittermeier, R. A. (eds.), *Ecology and Behavior of Neotropical Primates, Vol. 1,* Acad. Bras. Cien., Rio de Janeiro, pp. 419-441.

Watanabe, K. (1981). Variations in group composition and population density of the two sympatric Mentawaian leaf-monkeys. *Primates* 22: 145-160.

Watkins, B. E., Ullrey, D. E., and Whetter, P. A. (1985). Digestibility of a high-fibre biscuit-based diet by black and white colobus *(Colobus guereza). Am. J. Primatol.* 9: 137-144.

Willis, E. O. (1974). Populations and local extinctions of birds on Barro Colorado Island, Panama. *Ecol. Monogr.* 44: 153-169.

Wilson, C. C., and Wilson, W. L. (1975). The influence of selective logging on primates and some other animals in East Kalimantan. *Folia primatol.* 23: 245-274.

Wilson, C. C., and Wilson, W. L. (1976). Behavioral and morphological variation among primate populations in Sumatra. *Yb. phys. Anthrop.* 20: 207-233.

Wilson, W. L. and Johns, A. D. (1982). Diversity and abundance of selected animal species in undisturbed forest, selectively logged forest, and plantations in East Kalimantan, Indonesia. *Biol. Conservat.* 24: 205-218.

Wolfheim, J. H. (1983). *Primates of the World,* University of Washington Press, Seattle and London.

Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In Clutton-Brock, T. H. (ed.), *Primate Ecology,* Academic Press, New York, and London, pp. 503-538.

Young, O. P. (1982). Aggressive interaction between howler monkeys and turkey vultures: The need to thermoregulate behaviorally. *Biotropica* 14: 228-231.