

Indices of Habitat-wide Fruit Abundance in Tropical Forests¹

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ABSTRACT

The assessment of fruit abundance is critical for studies of frugivore ecology. A variety of methods have been used to estimate habitat-wide fruit abundance. However, since the methods have not been calibrated with each other, it is difficult to compare results of different studies. Here we compare three methods used simultaneously to collect fruit abundance data in the Kibale Forest, Uganda. Estimates of fruit abundance derived from fruit traps were not correlated with estimates derived from either systematic transect sampling or estimates obtained from observing fruiting phenology of key species on a fruit trail. However, estimates based on fruit trail data and transect data were correlated. We review the advantages and disadvantages of methods that have been used to assess habitat-wide fruit abundance.

Key words: food abundance; frugivore; fruit; Kibale Forest; methodology; transects; Uganda.

MOST TROPICAL RAIN FOREST TREES produce fruit that are consumed by animals and rely on frugivores for their seed dispersal (Frankie *et al.* 1974, Howe 1986, Dowsett-Lemaire 1988). Concomitantly, a large proportion of the vertebrates in tropical forests are frugivorous (Terborgh 1980, 1986; Willis 1980; Fleming *et al.* 1987). The numerical strength of this guild of consumers highlights the importance of investigating their ecology, and the quantification of fruit abundance is an important component of such studies. Although a variety of methods have been employed to provide estimates of fruit abundance, calibration of the different methods has been neglected (Blake *et al.* 1990). Consequently, it is difficult to assess whether reported differences among studies are due to methodological differences or to other factors of biological significance, such as differences between seasons, habitats, or species.

In this paper, we first compare three different methods of assessing fruit abundance in the Kibale Forest, Uganda: fruit traps, a fruit trail system which monitored key species, and a systematic phenology transect system that determined the phenophase of all trees within a series of dispersed plots. We then review the literature for methods used to determine

habitat-wide fruit abundance and compare the potential biases of different methods and the effort they require.

METHODS

Kibale Forest consists of a mosaic of habitat types, including forest, swamp, grassland, and regenerating forest (Struhsaker 1975, Skorupa 1988). Fruit production was assessed in relatively pristine areas, and in areas which had been logged to varying intensities in the 1960s (Skorupa 1988).

FRUIT TRAPS.—Fruit traps consisted of a square frame (collecting area 0.08 m²) with a plastic bag suspended from its top, raised 0.4 m off the ground. Water drained out the bottom of the trap through small holes punctured through the plastic. The holes would have permitted small seeds, such as fig seeds, to be flushed through the trap, however small fruits (≥ 5 mm) would have remained. Following Terborgh (1983), the traps were set at 20 m intervals, 1 m off the side of existing trails (Fig. 1). Trails were selected so that they were dispersed throughout the existing system of trails. By setting the traps 20 m apart, we assume that the collections from sequential traps are independent (Terborgh 1983). Fruits, seeds, and leaves were collected from the traps every week (typically on Monday and Tuesday), and returned to camp where fruit type was assigned (fleshy fruit, wind dispersed, and husked).

¹ Received 20 November 1992; revision accepted 30 August 1993.

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KIBALE FOREST

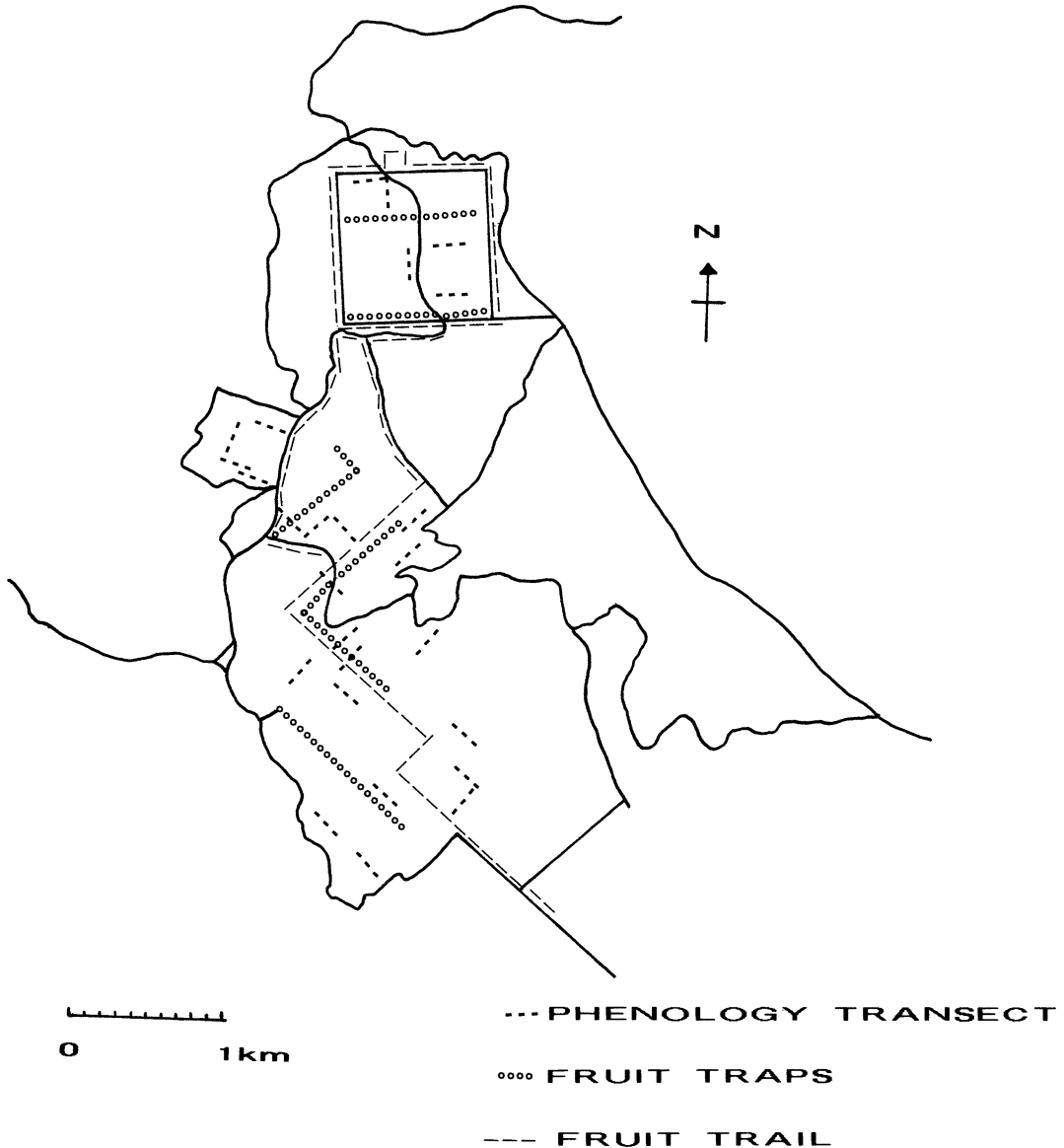


FIGURE 1. The location of the phenology transects (small dotted lines), the fruit trail (dashed lines), and the fruit traps (large dotted lines) used to estimate habitat-wide levels of fruit abundance in the Kibale Forest Reserve, Uganda. Solid lines represent major trails in the study area.

The total wet weight (± 0.05 g) of the fruits was determined that day, after which the fruits were dried for approximately one week, and weighed again. In July 1988 150 traps were set along 3 km of trails, and an additional 150 traps were set out in December 1988. During every sampling period,

estimates of the total area sampled were corrected for nonfunctioning traps (*e.g.*, those stepped on by an elephant).

FRUIT TRAIL.—A 12 km fruit trail was established in November of 1987 and sampled every second

TABLE 1. *The relationship between the different methods used to assess habitat-wide fruit abundance in Kibale Forest, Uganda (Pearson correlation values and probabilities are given).*

	Transect number	Transect DBH	Trail	Traps	
				Wet	Dry
Transect (# of fruiting trees)	—	—	—	—	—
Transect (sum of DBH)	0.970***	—	—	—	—
Trail	0.647**	0.608*	—	—	—
Fruit traps (wet weight)	0.259	0.228	-0.432	—	—
Fruit traps (dry weight)	-0.222	-0.157	-0.172	0.009	—

* $P < 0.10$; ** $P < 0.05$; *** $P < 0.001$.

week until June 1991. A total of 228 trees belonging to 17 species (9 fig and 8 nonfig) were tagged, the fruits of which were considered the most important arboreal food sources for chimpanzees (Wrangham *et al.* 1992). The nonfig fruiting trees on the fruit trail included 20 *Celtis durandii*, 20 *Tabernaemontana holstii*, 20 *Chaetacme aristata*, 9 *Cordia abyssinica*, 7 *Monodora myristica*, 11 *Mimusops bagshawei*, 12 *Pseudospondias microcarpa*, 20 *Teclea nobilis*, and 20 *Uvariopsis congensis*. The fig trees that we monitored included 14 *Ficus sarsibarica*, 4 *F. saussureana*, 1 *F. cyathistipula*, 20 *F. exasperata*, 9 *F. natalensis*, 5 *F. conraui*, and 15 *F. asperifolia* (fig nomenclature follows Berg & Hijman 1989). Trails were monitored every 2 weeks, the presence of fruit on all trees was noted, and their abundance ranked on a relative scale of zero to four. Monitoring this fruit trail required two days. Estimates of fruit abundance were based on the number of trees that were fruiting along the trail.

PHENOLOGY TRANSECTS.—In December 1989, 26 transects were built along the existing trail system (>155 km of trails) in randomly selected locations which were stratified by logging history. Each transect was 200 m × 10 m, providing a total area of 5.2 ha. Each tree greater than 10 cm diameter at breast height (DBH) within 5 m of each side of the trail was individually marked with a numbered aluminum tag and measured (DBH). A total of 2111 trees were marked on 26 transects. Transects were monitored during the first ten days of every month. The presence of fruit on all marked trees was determined, and their abundance was ranked on a relative scale of zero to four. We indexed habitat-wide levels of fruit abundance from the transects by two methods: by scoring the number of trees that contained ripe fruit and by summing the DBH of all trees producing fruit. The two estimates were highly correlated ($r = 0.970$, $P < 0.0001$; Table 1). In November and December of 1990,

the estimates were not available for the phenology transects and trail; these are treated as missing values in the analyses and expressed as means of the preceding and subsequent months in the plots.

LITERATURE REVIEW.—We reviewed studies that assess habitat-wide fruit availability in tropical habitats. The search was directed toward studies that attempted to relate the behavior of frugivores to the amount of fruit available across an area equivalent to the study animal's home range (habitat-wide). Thus, studies monitoring the phenology of a single plant species or botanical studies not linked (directly by the author or by subsequent publications) to the behavior of frugivores were not included. We consider studies of forest phenology that are commonly used by behavioral ecologists, but do not review studies concerned solely with measures of forest productivity. For a review of problems of data comparisons in such studies see Proctor (1983). We examined all articles published since 1980 in *Biotropica*, *American Journal of Primatology*, *Journal of Tropical Ecology*, *Folia Primatologica*, and the *International Journal of Primatology*. These journals are major sources of information on tropical forests, or more importantly for this review, sources of typical descriptions of the behavioral responses of frugivores to changes in fruit availability. In addition, we included any other study known to the authors. We used the best description of a method if it appeared in sequential papers from the same site. We recognize that the selection of journals leads to an overrepresentation of primate studies, however primatologists are frequently concerned with testing predictions relating frugivore behavior and fruit abundance.

RESULTS AND DISCUSSION

To date, the phenology transects have been sampled once a month for 17 months (February 1990 to

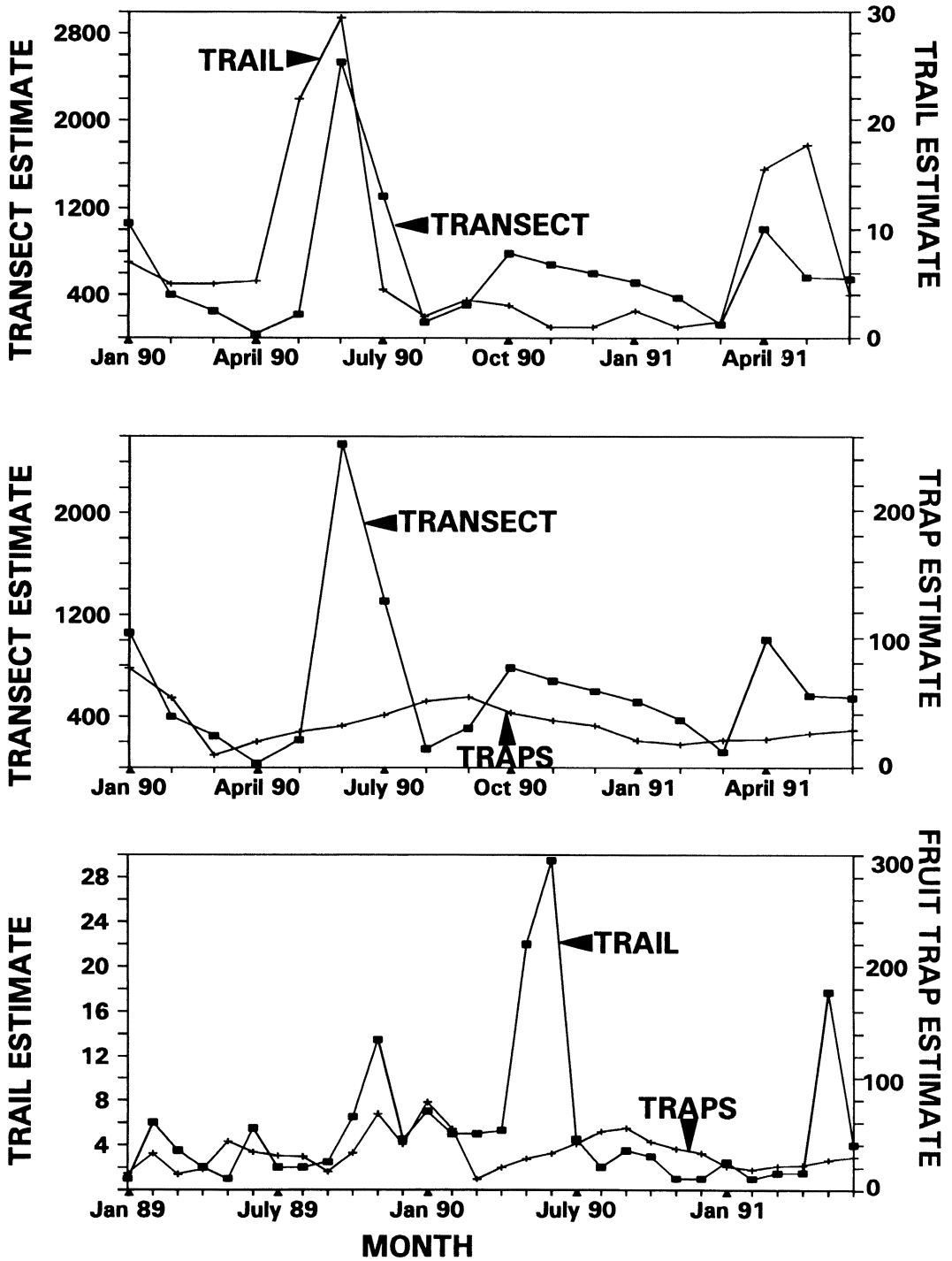


FIGURE 2. Comparisons of the monthly estimates of habitat-wide fruit production derived for an area of the Kibale Forest Reserve, Uganda, using three methods: phenological transect system (sum of the DBH of the trees with ripe fruit), fruit trail (number of trees with ripe fruit), and fruit traps (kg/ha).

June 1991) and the fruit trail every two weeks since December 1987 ($N = 84$ sampling periods; December 1987 to June 1991). Monthly estimates derived from the fruit trail were correlated with those derived from the transects during the period of overlap (Table 1; Fig. 2). The correlation may have been improved by accounting for the relative density of the trees on the phenology trail. For example, during the months when the trail produced an estimate that was much lower than that derived from the transects, *Uvariopsis congensis* was fruiting. This species occurs at a high density in Kibale (35.6 individuals/ha). Since we monitored only 20 *U. congensis* trees on the trail, their contribution to the total trail estimate underrepresents their abundance in the habitat.

The fruit trail was monitored twice a month. It is conceivable that once a month would have been adequate. With the available data we examined the effect of less intensive sampling. Of the 228 trees monitored each month, 6.85 were fruiting on average during any given month. The average difference between the two sampling periods within a month was 2.8 trees (SD 4.38; $N = 43$ mo). The average difference for the first sample of the month and the mean for the month was 1.28 trees (SD 2.38; $N = 43$ mo). Considering that an average of 6.85 trees were fruiting per month, such within month variability may represent a significant change to some frugivores.

To examine the effect of reducing the number of species sampled, we randomly removed different numbers of species from the total number sampled. This was performed ten times for each number of species removed and we report the average correlation between the new trail value and the transect estimate ($N = 16$ mo) and between the original and new trail estimates. When we reduced the number of species sampled by one, the new trail estimate was correlated with the original trail estimate 90 percent of the time (average $r = 0.454$), but only correlated with the transect estimate in 40 percent of the runs (average $r = 0.311$). When 4 species were randomly removed from the trail, the reduced trail estimate was correlated with the original estimate 50 percent of the time (average $r = 0.377$), and with the transect estimate 20 percent of the time (average $r = 0.197$). When we removed 8 species from the trail, the reduced estimate was correlated with the original estimate only 40 percent of the time (average $r = 0.269$), and was correlated with the transect estimates only 30 percent of the time (average $r = 0.160$).

Transects and trail estimates were not related to estimates derived from the fruit traps. The dif-

ference between the fruit traps and the other methods was particularly great during periods when the transect and trail methods indicated high fruit abundance (Table 1; Fig. 2).

It is typically assumed that traps catch fruit from the overhanging trees when they fruit, and thus this method should reflect fruit production in the trees above the traps. Data from this study demonstrate that this may not be the case. In our study, on average 1.66 species of fruits or seeds were collected from each trap, suggesting that we were monitoring the fruit production from ≥ 497 trees ($300 \text{ traps} \times 1.66 \text{ species/trap}$). Those species of trees that were directly over a trap or which had a trunk within 10 m of the trap were identified. Interestingly, only 19 percent of the species of seeds or fruits in the traps were of those species identified as being overhead. We did not collect data on the weight of each species per trap, so we cannot evaluate this in terms of biomass.

LITERATURE REVIEW.—The literature review had the following objectives: to review the methodology and potential biases of the different approaches, and to provide descriptive statistics of the effort required for each method (see Blake *et al.* 1990 for a similar review).

FRUIT TRAPS.—Fruit traps are usually placed at regular intervals, often just off existing trails. The distance between traps is set so that sequential traps do not collect the fruit falling from the same tree (Terborgh 1983—20 m; Goldizen *et al.* 1988—50 m). Fruit traps are typically placed at regular intervals along trails which can cause biases if environmental heterogeneity matches the spacing (*i.e.*, geological strata, stream beds). Further, the lines that are established are often along natural edges (*e.g.*, Terborgh 1983 along a lake edge) or along convenient trails (this study). Since such nonrandom placement can potentially lead to a biased estimate, a random placement would be desirable.

A potential criticism of fruit traps is that rodents or other frugivores or seed predators systematically remove fruit or seeds from the traps. Data collected by Goldizen *et al.* (1988) and from this study suggest that this is not the case. On seven occasions over 11 months Goldizen *et al.* (1988) placed five to eight fruits of a variety of species in 12 traps and checked them 1 week later. They found that less than 3 percent of the fruits disappeared. In Kibale, for six species we placed five fruits (range in size 3.1 cm to 0.66 cm) in each of ten traps ($N = 40$

fruits, some species monitored repeatedly) and checked them one week later. Less than 1 percent of the fruits disappeared.

Fruit traps measure fruit fall, not fruit production. Terborgh (1983) points out a number of related biases inherent in the fruit trap method. Fruit production is potentially underestimated during periods of fruit scarcity when frugivores consume a greater proportion of the available fruit than during periods of fruit abundance. Fruit traps are biased against more preferred fruits which are removed by frugivores and do not fall into the traps in the same proportion as less preferred fruits. Fruit traps may contain a high proportion of fruits that have been aborted by the parent trees, for example as a result of insect damage (Janzen 1983). Finally, fruit traps may be biased against plant species that produce fruits that ripen over a long period, since it is probable that a greater proportion of the fruits of slow ripening species are eaten and therefore do not fall into the traps. More generally, measures of fruit fall are insensitive to species with seasonal differences in the proportion of fruits that fall.

The construction, maintenance, and monitoring of a system of fruit traps is time-consuming. Consequently, sampling is often limited to a small proportion of the habitat used by the study animal. In previous studies the area directly sampled by the fruit traps has constituted an average of 0.004 percent of the area used by the study animal (range 0.00003–0.017%; $N = 6$ studies; Table 2). The average number of fruit traps used in the studies reviewed was 192 (range 75–312; $N = 6$ studies; Table 2), and they were generally sampled once a week.

The fact that fruit traps cover only a small proportion of the total area of interest can lead to biases. Depending on fruit trap placement, traps may be less likely to detect the fruiting of species with clumped distributions than methods that sample a greater area. Similarly, if traps are placed under a rare tree species, which produces many fruits and/or large fruits, fruit traps may overestimate habitat-wide fruit abundance when this tree species fruits. Such biases are likely exaggerated by nonrandom placement of fruit traps. Given this type of bias, fruit traps may be more suitable for studies that are comparing habitats, study areas, home ranges, seasons, or individual plant species. In such studies, fruit collected from the traps can be averaged over entire annual cycles or seasons.

PHENOLOGY TRANSECT OR QUADRATS.—Generally, monitoring phenology transects involves the establishment of areas in which trees are routinely mon-

itored for the presence of fruit (Table 3). Typically, a subset of all trees within the sampling areas is selected for phenological monitoring (*e.g.*, >3 m high; >10 cm DBH). Since a number of transects or quadrats can be established in different areas, sample stratification by habitat is feasible, with transects placed randomly within the habitat. Ideally each quadrat or transect includes only one type of habitat.

A variety of methods have been used to assess the size of the fruit crop on individual trees (Chapman *et al.* 1992; Table 3) along the transects. The most common method was to visually assess fruit crop size and assign a relative rank, typically on a scale of zero to four. The very simple approach of noting the presence or absence of fruit on a tree has also been frequently used. Alternatively, researchers have visually estimated the total number of fruits on a tree through counts of small subsections of the canopy that are multiplied by the proportion of the total canopy area the subsections are estimated to represent (Chapman *et al.* 1992). In some studies measurements are made of tree size (DBH or crown volume) and it is assumed that the size of the tree reflects the tree's ability to produce fruit. If an index of fruit crop size is to be used to weight the density estimate of fruiting trees, the period between successive monitorings of the transects must be on a short enough temporal scale that a realistic assessment of the crop size of all individuals of all species can be made. In areas or for species where fruits ripen quickly or stay on the tree for a relatively short period of time, this may necessitate a short inter-sample period.

In forests in which lianas are producing a large component of the fruit productivity, phenology transects may underrepresent fruit productivity. Individual lianas often span the crowns of many trees and send stems to the ground in many places. In such forests, the use of DBH to scale fruit production may be inappropriate. In Kibale, lianas are not common, and were unlikely to have biased the previous analyses. For methodologies to assess lianas, see Castellanos *et al.* (1992).

Transect studies require a large time commitment. In tropical forests, the upper canopy is often obscured. It may take an observer ten minutes to assess whether a tree has fruit and to estimate crop size. Investigations using this approach are usually of a long duration (mean of 26 studies in Table 3 = 15 mo; range 1 to 72 mo).

TOTAL AREA OF INTEREST AND PHENOLOGICAL STUDIES.—Some frugivores have a home range sufficiently small to allow all trees in the range to be

TABLE 2. A description of the methods used by studies which quantified habitat-wide fruit availability using a fruit trap method. The proportion of the study area represents the percent of the study site sampled in the habitat wide assessments, and the percentage of the crown area in the studies of individual tree species.

No. of traps	Proportion of study area	Trap size (m ²)	Freq. of sampling	Measure	# of Sp	Duration (months)	Source
150	0.0046-0.0008	0.08	1/2 weeks	Weight	187	12	Terborgh 1983
100 to 200	0.0008-0.017	0.08	1/week	Weight	—	8.3 years	Leigh and Windsor 1982
75	—	2.31	1/week	Weight	72 G ^a	18	Smythe 1970
312	0.00003	0.08	1/week	Count	259 ^b	12	Foster 1982a
120	0.006	0.78	7 d/month ^c	Count	—	12	Chapman, pers. obs.
240	0.0003	0.04	1/2 weeks	Weight	—	13	Goldizen <i>et al.</i> 1988
300	0.00016	0.08	1/week	Weight	—	31	This study
Under one tree species							
16-200/tree	5-10	0.50	1/2 days	Count	6	12	Estrada <i>et al.</i> 1984
135/tree	10	0.50	1/2 days	Weight	1	3	Coates-Estrada and Estrada 1986
5-18/tree	6-23	1	1/week	Count	1	4	Howe and Vande Kerckhove 1981
4/tree	—	1	1/week	Count	1	2	Howe 1977
7-8/tree	—	1	1/5 days	Count	1	20 d	Leighton and Leighton 1982

^a In this study, 72 genera were distinguished, the number of species was not available.

^b 245 identified species and 14 unidentified species.

^c In this study, traps were sampled over 7 consecutive days per month

^d In this study, traps were monitored over the fruiting cycle, but we have presented the total duration for the study period during which 6 tree species were sampled.

TABLE 3. Characteristics of the methods used by studies employing transects or quadrats. The methods of transect or quadrat placement are coded as: 1 = unreported, 2 = random, 3 = stratified random, 4 = ad hoc (e.g., using existing trails), 5 = by habitat, 6 = total area, 7 = systematic. P/A = Fruit abundance recorded as presence or absence. Rank = Rank of phenological characteristics.

Size	Number	Prop of area	Freq of sample	Measure	# Individual or species	Placement	Duration months	Source
2 x 50 m	60	0.4	Once	DBH	3846 ind	2	12	Strier 1987, 1989
5 x 580 m	5	—	1/month	Basal Area	—	4	11	McKey <i>et al.</i> 1981
12 x 1 m	100	—	1/month	Count/rank	—	4	12	Levey 1988a, b
500 x 20 m	3	—	1/2 weeks	P/A	—	1	12	Estrada <i>et al.</i> 1984
3 x 1000 m	1	—	1/2 weeks	Count/rank	164 sp/621 ind	1	14	Hilty 1980
14,400 x 5 m	1	—	1/month	Count/rank	21 sp/84 ind	7	13	Robinson 1986
1021/750 m	2	0.77-0.56	1/month	P/A	—	1	16	Davis 1945
50 m ²	20-54	3.1%	1/5-6 weeks	Count	—	1	4-15	Loiselle and Blake 1990
10 x 200 m	50	—	1/month	DBH/rank	4733	3	16+	Chapman <i>et al.</i> , pers. obs.
5 x 5 m	10	0.014%	1/month	P/A	—	2	10	Boinski 1987
20 x 20 m	6	—	1/week	P/A	—	1	4	Gautier-Hion <i>et al.</i> 1981 ^a
72 m ²	43	—	Once	Crown Vol	22 sp	3	9	Oates <i>et al.</i> 1980
40,000 m ²	3	7.1%	1/3 weeks	DBH	~5000	1	26	Chapman 1990a, b, 1987a, 1988
1 ha/0.25	2/7	6%	1/month	Crown Size	—	1	12	Reamaekers 1980
20 x 63 m	90	<6%	Once	—	2459 ind/162 type	4	—	Whitten 1982
25 m ²	2854	~4%	1/month	Crown Area	23 sp/50 ind	2	13	Harrison 1983, 1984
20 x 500 m	3	5%	Once	—	—	1	—	Estrada and Coates-Estrada 1984
3 ha	2	—	1/2 weeks	—	—	1	8	Milton 1978
1 ha	3	0.7%	1/10 days	P/A	36 sp/125 ind	5	4	Milton 1984, 1985
1 m ² herb	716	0.008%	Once	Weight	22 sp	3	2	Vedder 1984 ^b
10 m ² shrub	716	0.08%	Once	Weight	22 sp	3	2	Vedder 1984 ^b
100 m ² trees	716	0.8%	Once	Weight	22 sp	3	2	Vedder 1984 ^b
1 m ² herb	150	—	Once	Weight	—	3	1	Watts 1984 ^c
5 m ² shrub	150	—	Once	Weight	—	3	1	Watts 1984 ^c
10 m ² trees	150	—	Once	Weight	—	3	1	Watts 1984 ^c
30 x 30 m	15	—	1/month	Visual	—	4	24	Riper 1980
3.3 km	2	—	1/month	P/A	117 sp/265 ind	4 & 5	17	Wong 1986
5 x 50 m	272	18.6	Once	—	1818 ind	4	72	Burynski 1990
5 x 50 m	157	1.5	Once	—	1587 ind	4	72	Burynski 1990

^a Every week 6 out 52 quadrats were sampled, and the selection of the six changed weekly.
^b Each of 30 250 x 250 m quadrats was divided into 5 x 5 x 250 rectangles.
^c Biomass estimates by harvesting & weighing representative plants.

TABLE 4. *The characteristics of studies that sampled the total area of interest or conducted strictly phenological studies, the results of which were not related specifically to frugivore behavior (P/A = presence/absence).*

Size	Num- ber	Prop of area	Freq of sampling	Measure	# Indiv. or species	Dura- tion	Source
100 × 100 m	51	100%	Once	—	—	8	Chapman 1985, 1987b, <i>et al.</i> 1988
250 m ²	36	100%	1/month	Crown Index	26 sp/430 ind	25	Marsh 1981 ^a
—	—	100%	1/week	—	96 sp/1699 ind	12	Glander 1978
—	—	100%	1/month	P/A	107 sp	27	Koptur <i>et al.</i> 1988
—	—	—	1/month	Rank	185 sp/468 ind	24	Frankie <i>et al.</i> 1974
—	—	—	1/6 weeks	Rank	154 sp	36	Opler <i>et al.</i> 1976, 1980a
—	—	100%	1/month	Rank	95 sp	36	Opler <i>et al.</i> 1980b
—	—	100%	1/10 days	P/A	79 sp	29	Lieberman 1982
20 × 20 m	360	100%	Once	—	135 sp	—	Hubbell 1979 ^b
—	—	100%	1/week	P/A	13 sp	12	Daubenmire 1972
—	—	—	1/2 weeks	P/A	44 sp/61 ind	108	Medway 1972

^a Phenology was recorded on all trees over 10 m in height.

^b All trees >2 cm DBH.

monitored (Table 4). This method removes many sources of sampling bias and error and is therefore useful for a variety of studies (*e.g.*, range use analysis, or quantifying dietary selection). However, for many animals that range widely, this method is not feasible.

The results of phenological studies initially intended as botanical investigations have been applied in some studies to understand frugivore behavior. Although such studies may provide information on when the greatest number of species are fruiting, actual densities are not usually determined. Relating phenological data to frugivore behavior without

knowing tree densities is difficult, since it will appear that more food is available during periods when many rare species fruit, than during periods when a single species, occurring at high density, fruits.

OTHER MEASURES OF FRUIT ABUNDANCE.—A variety of other methods have been used to provide relative measures of habitat-wide fruit abundance that can be compared between periods at one locality (Table 5). Such methods usually involve a sampling design that does not necessitate the estimation of fruiting tree density. For example, all the fruits falling to the ground along a set system of trails can be rou-

TABLE 5. *Characteristics of the methods used by studies employing nonsystematic methods, subsampling species of interest, and including fruit counts along trails.*

Spe- cies	Individ- uals per species	Freq of sampling	Measure	Length trail	Prop of area sampled	Dura- tion	Source
52	10–30	1/month	Visual × WT	200 m	—	18	Dinerstein 1986 ^{a,c}
20	25	1/month	Visual/rank (0–5)	—	—	11	Lawes <i>et al.</i> 1990 ^b
21	10	1/2 weeks	Visual/actual #	—	—	12	Worthington 1982 ^{a,b,c}
21	~6	1/monthly	Visual/rank (0–4)	—	—	14	Robinson 1986 ^{b,c}
—	145	1/monthly	Visual/rank (0–4)	—	—	37	van Schaik 1986 ^{c,b}
—	—	1/monthly	Count	4610	—	34	van Schaik 1986 ^d
—	—	1/monthly	Count	4.7–17.4 km	variable	28	Butynksi 1990 ^d
122	—	1/2 weeks	Collect/weight	6 km × 70 cm	0.21%	12	Gautier-Hion <i>et al.</i> 1985 ^d
17	$\bar{x} = 13$	1/2 weeks	Visual/rank (0–4)	12 km	—	36+	Wrangham <i>et al.</i> 1991a, b ^{c,b}

^a No standard placement of trails or transects reported.

^b Criteria for selection of individual trees not reported.

^c Collected phenology data of marked individuals along trails or viewpoints.

^d Fruit on trail count.

^e Select species samples, but density of those species determined quantitatively.

tinely censused (biased by frugivores that feed on the ground; Butynski 1990).

CONCLUSIONS

A researcher's decision concerning the type of method to use in estimating habitat-wide fruit abundance will depend on the accuracy of the method and the amount of time available to determine fruit abundance. We have no "true" measure of habitat-wide fruit abundance, thus we cannot assess accuracy. However, it seems probable that accuracy will increase when a greater proportion of the study animal's home range is sampled. This will be particularly true when fruiting resources occur in a clumped distribution pattern. Fruit trap construction and monitoring is time-consuming, and in our study, produced results that show little concordance on a monthly scale with those derived from phenology transects or from a fruit trail. In our study, the sampling of the fruit traps took two 7-hr days for two people every week. In addition, because of their small size and the difficulty of constructing a large number of fruit traps, only a small proportion of the area used by most frugivores is sampled.

Selecting between a systematic regime, such as transects, or a nonsystematic regime, such as a fruit

trail, will depend upon the amount of time the investigator has available for sampling. However, it is valuable for investigators to calibrate the estimates derived from methods such as fruit trails, by determining the actual density of the trees. Thus, the nonsystematic regime could be done repeatedly to determine phenology and the proportion of the population of each species fruiting, while a systematic sampling regime could be conducted once during the study to determine the actual density of each tree species.

ACKNOWLEDGMENTS

Permission for this research was given by the Office of the President, Uganda, National Research Council, and the Ugandan Forest Department. We express our gratitude to the Department of Zoology at Makerere University, and to the New York Zoological Society for providing logistical support, without which this research would not have been possible. Funding for this research was provided by NSF, National Geographic Society, USAID, and the MacArthur Foundation. We would like to thank D. Gebo, L. Gardner, D. Levey, R. Malenky, J. Moore, C. Tutin, and N. Wheelwright for helpful comments on this project. We are grateful to A. Clark for all the help he provided with setting up the fruit trap sampling.

LITERATURE CITED

- BERG, C. C., AND M. E. E. HIJMAN. 1989. Flora of tropical East Africa: Moraceae. A. A. Balkema, Rotterdam, Netherlands.
- BLAKE, J. G., B. A. LOISELLE, T. C. MOERMOND, D. J. LEVEY, AND J. S. DENSLOW. 1990. Quantifying abundance of fruits for birds in tropical habitats. *Studies in Avian Biology* 13: 71-77.
- BOINSKI, S. 1987. Habitat use by squirrel monkeys (*Saimiri oerstedii*) in Costa Rica. *Folia Primatol.* 49: 151-167.
- BUTYNSKI, T. M. 1990. Comparative ecology of blue monkeys (*Cercopithecus mitis*) in high- and low-density subpopulations. *Ecol. Monogr.* 60: 1-26.
- CASTELLANOS, A. E., R. DURAN, S. GUZMAN, O. BRIONES, AND M. FERIA. 1992. Three dimensional space utilization of lianas: a methodology. *Biotropica* 24: 396-401.
- CHAPMAN, C. A. 1985. The influence of habitat on behaviour in a group of St. Kitts green monkeys. *J. Zool. (Lond.)* 206: 311-320.
- . 1987a. Flexibility in the diets of three species of Costa Rican primates. *Folia Primatol.* 49: 90-105.
- . 1987b. Selection of secondary growth areas by vervet monkeys (*Cercopithecus aethiops*). *Am. J. Primatol.* 12: 217-221.
- . 1988. Patch use and depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour* 105: 99-116.
- . 1990a. Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behav. Ecol. Sociobiol.* 26: 409-414.
- . 1990b. Ecological constraints on group size in the three species of neotropical primates. *Folia Primatol.* 55: 1-9.
- , L. M. FEDIGAN, AND L. FEDIGAN. 1988. Ecological and demographic influences on the patterns of association in St. Kitts vervets. *Primates* 29: 417-421.
- , L. J. CHAPMAN, R. W. WRANGHAM, K. HUNT, D. GEBO, AND L. GARDNER. 1992. Estimators of fruit abundance of tropical trees. *Biotropica* 24: 527-531.
- COATES-ESTRADA, R., AND A. ESTRADA. 1986. Fruiting and frugivores at a strangler fig in the tropical rain forest of Los Tuxtlas, Mexico. *J. Trop. Ecol.* 2: 349-357.
- DAUBENMIRE, R. 1972. Phenology and other characteristics of tropical semi-deciduous forest in north-western Costa Rica. *J. Ecol.* 60: 147-170.

- DAVIS, D. E. 1945. The annual cycle of plants, mosquitos, birds and mammals in two Brazilian forests. *Ecol. Monogr.* 15: 243–295.
- DINERSTEIN, E. 1986. Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. *Biotropica* 18: 307–318.
- DOWSETT-LEMAIRE, F. 1988. Fruit choice and seed dissemination by birds and mammals in the evergreen forests of upland Malawi. *Rev. Ecol.* 43: 251–285.
- ESTRADA, A., AND R. COATES-ESTRADA. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *Am. J. Primatol.* 6: 77–91.
- , AND ———. 1986. Frugivory in howling monkeys (*Alouatta palliata*) at Los Tuxtlas, Mexico: dispersal and fate of seeds. In A. Estrada and T. Fleming (Eds.). *Frugivores and seed dispersal*, pp. 93–104. Dr. W. Junk, Dordrecht, Netherlands.
- , ———, C. VASQUES-YANES, AND A. OROZCO-SEGOVIA. 1984. Comparison of frugivory of howling monkeys (*Alouatta palliata*) and bats (*Artibeus jamaicensis*) in the tropical rain forest of Los Tuxtlas, Mexico. *Am. J. Primatol.* 7: 3–13.
- FLEMING, T. H., R. BREITWISCH, AND G. H. WHITESIDES. 1987. Patterns of tropical vertebrate frugivore diversity. *Annu. Rev. Ecol. Syst.* 18: 91–109.
- FOSTER, R. B. 1982a. The seasonal rhythm of fruitfall on Barro Colorado Island. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and longterm changes*, pp. 151–172. Smithsonian Institution Press, Washington, D.C.
- FRANKIE, G. W., H. G. BAKER, AND P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62: 881–919.
- GAUTIER-HION, A., J. P. GAUTIER, AND R. QURIS. 1981. Forest structure and fruit availability as complimentary factors influencing habitat use by a troop of monkeys (*Cercopithecus cepus*). *Rev. Ecol.* 35: 511–536.
- , J.-M. DUPLANTIER, R. QURIS, R. FEER, C. SOURD, J. DECOUX, G. DUBOST, L. EMMONS, C. ERARD, L. HECKETSWEILER, A. MOUNGAZI, C. ROUSSILHON, AND J.-M. THIOLLAY. 1985. Fruit characteristics as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324–337.
- GLANDER, K. E. 1978. Howling monkey feeding behaviour and plant secondary compounds: a study of strategies. In G. Montgomery (Ed.). *The ecology of arboreal folivores*, pp. 561–574. Smithsonian Institution Press, Washington, D.C.
- GOLDIZEN, A. W., J. TERBORGH, F. CORNEJO, D. T. PORRAS, AND R. EVANS. 1988. Seasonal food shortage, weight loss, and the time of births in saddle-back tamarins (*Saguinus fuscicollis*). *J. Anim. Ecol.* 57: 893–902.
- HARRISON, M. J. S. 1983. Patterns of range use by the green monkey, *Cercopithecus sabaenus*, at Mt. Assirik, Senegal. *Folia Primatol.* 41: 157–179.
- . 1984. Optimal foraging strategies in the diet of the green monkeys, *Cercopithecus sabaenus*, at Mt. Assirik, Senegal. *Int. J. Primatol.* 5: 435–471.
- HILTY, S. L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. *Biotropica* 12: 292–306.
- HOWE, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58: 539–550.
- . 1986. Seed dispersal by fruit-eating birds and mammals. In D. R. Murray (Ed.). *Seed dispersal*, pp. 123–190. Academic Press, New York, New York.
- , AND G. A. VANDE KERCKHOVE. 1981. Nutmeg dispersal by tropical birds. *Science* 210: 925–927.
- HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299–1309.
- JANZEN, D. H. 1983. Physiological ecology of fruits and their seeds. In O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler (Eds.). *Physiological plant ecology*, pp. 625–655. Springer-Verlag, Berlin, Germany.
- KOPTUR, S., W. A. HABER, G. W. FRANKIE, AND H. G. BAKER. 1988. Phenological studies of shrub and treelet species in tropical cloud forest of Costa Rica. *J. Trop. Ecol.* 4: 323–346.
- LAWES, M. J., S. P. HENZI, AND M. R. PERRIN. 1990. Diet and feeding behaviour of Samango Monkeys (*Cercopithecus mitis labiatus*) in Ngoye Forest, South Africa. *Folia Primatol.* 54: 57–69.
- LEIGH, E. G., AND D. M. WINDSOR. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest: seasonal rhythms and longterm changes*, pp. 111–122. Smithsonian Institution Press, Washington, D.C.
- LEIGHTON, M., AND D. R. LEIGHTON. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14: 81–90.
- LEVEY, D. J. 1988a. Tropical wet forest treefall gaps and distributions of understory birds and plants. *Ecology* 69: 1076–1089.
- . 1988b. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. *Ecol. Monogr.* 58: 251–269.
- LIEBERMAN, D. 1982. Seasonality and phenology in a dry tropical forest in Ghana. *J. Ecol.* 70: 791–806.
- LOISELLE, B. A., AND J. G. BLAKE. 1990. Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology* 13: 91–103.
- MARSH, C. W. 1981. Diet choice among red colobus (*Colobus badius rufomitratu*) on Tana River, Kenya. *Folia Primatol.* 35: 147–178.
- MCKEY, D. B., J. S. GARTLAN, P. G. WATERMAN, AND G. M. CHOO. 1981. Food selection by black colobus (*Colobus satanas*) in relation to plant chemistry. *Biol. J. Linn. Soc.* 16: 115–146.
- MEDWAY, L. 1972. Phenology of a tropical rain forest in Malaya. *Biol. J. Linn. Soc.* 4: 117–146.

- MILTON, K. 1978. Behavioural adaptations to leaf-eating by the mantled howler monkey (*Alouatta palliata*). In G. Montgomery (Ed.). The ecology of arboreal folivores, pp. 535-550. Smithsonian Institution Press, Washington, D.C.
- . 1984. Habitat, diet, and activity patterns of free-ranging woolly spider monkeys (*Brachyteles arachnoides* E. Geoffroyi 1806). Int. J. Primatol. 5: 491-514.
- . 1985. Mating patterns of woolly spider monkeys, *Brachyteles arachnoidea*: implications for female choice. Behav. Ecol. Sociobiol. 17: 53-59.
- OATES, J. F., P. G. WATERMAN, AND G. M. CHOO. 1980. Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. Oecologia 45: 45-56.
- OPLER, P. A., H. G. BAKER, AND G. W. FRANKIE. 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. J. Biogeogr. 3: 231-236.
- , ———, AND ———. 1980a. Plant reproductive characteristics during secondary succession in neotropical lowland forest ecosystems. Biotropica 12: 40-46.
- , ———, AND ———. 1980b. Comparative phenological studies of treelets and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. J. Ecol. 68: 167-188.
- PROCTOR, J. 1983. Tropical forest litter fall. I. Problems of data comparisons. In S. L. Sutton, T. C. Whitmore, and A. C. Chadwick (Eds.). Tropical rain forest: ecology and management, pp. 267-273. Blackwell Scientific Publications, Ltd., Oxford, England.
- RAEMAEKERS, J. 1980. Causes of variation between months in the distance traveled daily by gibbons. Folia Primatol. 34: 46-60.
- RIPER VAN, C. 1980. The phenology of the dryland forest of Mauna Kea, Hawaii, and the impact of recent environmental perturbations. Biotropica 12: 282-291.
- ROBINSON, J. G. 1986. Seasonal variation in use of time and space by the wedge-capped capuchin monkeys *Cebus olivaceus*: implications for foraging theory. Smithson. Contrib. Zool. 431.
- SKORUPA, J. P. 1988. The effect of selective timber harvesting on rain-forest primates in Kibale Forest, Uganda. Ph.D. Dissertation, University of California, Davis.
- SMYTHE, N. 1970. Relationships between fruiting season and seed dispersal methods in a neotropical forest. Am. Nat. 104: 25-35.
- STRIER, K. B. 1987. Ranging behaviour of woolly spider monkeys. Int. J. Primatol. 8: 575-591.
- . 1989. Effects of patch size on feeding associations in muriquis (*Brachyteles arachnoides*). Folia Primatol. 52: 70-77.
- STRUHSAKER, T. H. 1975. The red colobus monkey. University of Chicago Press, Chicago, Illinois.
- TERBORGH, J. 1980. Causes of tropical species diversity. XVII International Ornithological Congress, pp. 955-961.
- . 1983. Five New World primates. Princeton University Press, Princeton, New Jersey.
- . 1986. Community aspects of frugivory in tropical forest. In A. Estrada and T. H. Fleming (Eds.). Frugivores and seed dispersal, pp. 371-384. Dr. W. Junk, Dordrecht, Netherlands.
- VAN SCHAİK, C. P. 1986. Phenological changes in a Sumatran rain forest. J. Trop. Ecol. 2: 327-347.
- VEDDER, A. L. 1984. Movement patterns of a group of free-ranging mountain gorillas (*Gorilla gorilla beringei*) and their relation to food availability. Am. J. Primatol. 7: 73-88.
- WATTS, D. P. 1984. Composition and variability of mountain gorilla diets in the central virungas. Am. J. Primatol. 7: 323-356.
- WHITTEN, A. J. 1982. A numerical analysis of tropical rain forest, using floristic and structural data, and its application to an analysis of gibbon ranging behaviour. J. Ecol. 70: 249-271.
- WILLIS, E. O. 1980. Ecological roles of migratory and resident birds on Barro Colorado Island, Panama. In A. Keast and E. Morton (Eds.). Migrant birds of the Neotropics, pp. 202-225. Smithsonian Institution Press, Washington, D.C.
- WONG, M. 1986. Trophic organization of understory birds in a Malaysian dipterocarp forest. Auk 103: 100-116.
- WORTHINGTON, A. 1982. Population sizes and breeding rhythms of two species of manikins in relation to food supply. In E. G. Leigh, A. S. Rand, and D. M. Windsor (Eds.). The ecology of a tropical forest: seasonal rhythms and longterm changes, pp. 213-225. Smithsonian Institution Press, Washington, D.C.
- WRANGHAM, R. W., A. P. CLARK, AND G. ISABIRYE-BASUTA. 1992. Female social relationships and social organization of Kibale Forest chimpanzees. In T. Nishida, W. C. McGrew, P. Marler, M. Pickford, and F. de Waal (Eds.). Human origins, pp. 81-98. University of Tokyo Press, Tokyo, Japan.