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QUANTIFYING ABUNDANCE OF FRUITS FOR BIRDS IN TROPICAL HABITATS

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Abstract. Inherent biases in different sampling techniques influence our interpretations of fruit-frugivore interactions. We review three general methods for sampling fruits: phenological studies based on repeated sampling of individual plants, fruit fall traps, and area-based sampling techniques. Phenological studies provide the least amount of quantitative information on fruit abundance. Fruit fall traps sample an unknown area, do not adequately sample all types of fruits dispersed by birds, and measure a residual quantity (that which is not eaten). Area-based samples frequently will be the best approach for many bird studies. Unripe fruits are used by birds under certain circumstances and provide information on future availability of ripe fruit. Therefore, both ripe and unripe fruits should be included in samples of fruit abundance, but as separate categories.

Key Words: Fruits; frugivores; tropics; sampling.

INTRODUCTION

Approximately one-third of the resident bird species in many neotropical forests are frugivorous (Terborgh 1980a, Stiles 1985b, Blake et al. in press, Karr et al. in press); the percentage of species that at least occasionally eat fruit is much larger. An estimated 50–90% of trees in neotropical forests and up to 98% of neotropical understory shrubs produce fruits whose seeds are dispersed by animals (Howe and Smallwood 1982), including birds (Gentry 1982, Stiles 1985b).

The method by which fruit abundance is estimated is critical to assessment of fruit as a resource for birds. In this paper we critique three commonly used techniques of quantifying fruit abundance, reviewing those as they might be or have been applied to bird studies. First, we consider studies that determined phenological patterns of plant species, which provide a general description of the seasonal availability of fruit. Second, we review use of traps to collect fallen fruits; such data have been used to estimate fruit abundance, seasonality, and diversity. Third, we discuss use of actual or estimated counts of fruits, fruiting plants, and species over a predetermined area. These three general methods are not necessarily mutually exclusive. For example, a phenological study can be area-based, and fruit abundance can be assessed on the basis of actual numbers, biomass, energy content, or some other factor (e.g., nutrient content).

METHODS USED TO COUNT FRUITS

PHENOLOGICAL STUDIES

The classic method of documenting phenological patterns is to record flowering and fruiting activity of plants over time (e.g., Frankie et al. 1974). Phenological patterns may be determined from collections made for taxonomic studies (e.g., Croat 1969, 1975), but more detailed information is obtained when reproductive activities of a series of individually marked plants are recorded at some repeated interval (Table 1). (Use of marked plants reduces such observer errors as overlooking unfamiliar or cryptic fruits.) Presence or absence of fruits (and flowers) or a simple index or estimate of abundance (e.g., "none, few, many"; Frankie et al. 1974) is noted. When conducted over a number of years, a general understanding of seasonal phenological patterns emerges. Those results, however, provide little quantitative, comparative data and are of limited value in studies on influences of fruit abundance on bird populations.

Phenological studies also may be designed to determine fruit production of a selected, small set of species (Table 1). For example, Howe and Vande Kerckhove (1979) analyzed fecundity and seed dispersal in 65 *Casearia corymbosa* (Flacourtiaceae). Total fruit counts were made over a 2-day span to determine crop sizes; fruits on 17 trees were counted daily to determine rates of fruit removal. Intermediate between community- and species-oriented studies are those that follow fruit production in a group of plant species that are important to a particular bird species (Worthington 1982, Wheelwright 1983) or to the frugivore community (Wheelwright 1986a). For example, Worthington (1982) sampled plant species that were known to produce fruit eaten by two species of manakins (Golden-collared, *Manacus vitellinus*; Red-capped, *Pipra mentalis*). Crop sizes were counted at biweekly intervals and were used, in combination with data on relative abundance of plant species, to provide an estimate of total fruit production. Because she worked on a small (18 ha) island, Wor-

TABLE 1. SELECTED STUDIES DESCRIBING PHENOLOGICAL PATTERNS OF TROPICAL PLANTS

Study length (months)	No. species	No. plants	Census interval	Count type[a]	Reference
			Community-oriented studies		
24	185	468	1 m	index	Frankie et al. 1974
14	113	1137	1 m	index	Frankie et al. 1974
36	154	?	6 wk	index	Opler et al. 1980
36	95	?	1 m	index	Opler et al. 1980
36	51±	145	1 m	index	Van Schaik 1986
108	44	61	2 wk	p/a	Medway 1972
13	?	?	?	p/a[b]	Charles-Dominique et al. 1981
21	?	?	2 wk	p/a[b]	Sabatier 1985
120	2	104	2 wk	p/a	Milton et al. 1982
24	13	109	?	p/a	Gautier-Hion et al. 1981
			Species-oriented studies		
12	21	210	2 wk	count	Worthington 1982
84	16	265	2 wk[c]	index	Wheelwright 1986
12	3	77	—[d]	count	Murray 1987
48	1	30–60	—[e]	count	Fleming 1981
4	1	5	—[e]	count	Bronstein & Hoffman 1987
2	1	65	—[f]	count	Howe & Vande Kerckhove 1979

[a] Count types: index = relative index of abundance, e.g., "many," "few"; p/a = presence/absence; count = direct count of fruits.
[b] Also weighed fruits fallen on trail.
[c] Counts conducted on biweekly intervals June 1980 to July 1981 and during 1–3 months in 1979, 1982–1985.
[d] Censused on 2 sequential days, 1–3 times/month.
[e] Censused once prior to fruit maturation.
[f] Censused on 2 sequential days; fruits counted daily on 17 trees.

thington was able to define community boundaries.

Wheelwright (1986a) investigated phenological patterns of 16 common Lauraceae species. He indexed fruit abundance by estimating percentage of canopy area in fruit, but did not obtain an actual count or estimate of fruit production. His research demonstrated the need for long-term studies; even 7 years were too few to represent adequately supra-annual cycles of fruit production displayed by those plants.

Finally, we include under phenological studies those that census fruiting and flowering trees along some set trail or series of trails. (When conducted systematically [i.e., with a set length and width of the sample area] such counts overlap with area-based sampling techniques described later.) Sabatier (1985) and Charles-Dominique et al. (1981), for example, collected and weighed all fallen fruits found along a series of trails. Such a technique is biased since many fruits likely were consumed and others rotted before they were tabulated. Information on general trends in fruit production may be achieved but information on total fruit production will be less reliable. Additional problems associated with sampling fallen fruits and sampling along trails are discussed in the following sections that deal with fruit fall traps and sample plots.

Phenological studies may be useful if the researcher can characterize the diet of the focal bird species (e.g., manakins, Worthington 1982; quetzals, Wheelwright 1983) and thus is able to identify the most important plant species. However, some fruits may be important to birds only in some seasons or years (Loiselle and Blake, this volume), and it may be difficult to determine *a priori* what fruit species should be sampled.

Considerations

Frankie et al. (1974) recommended a minimum of five individuals/species for tropical phenological studies while Wheelwright (1986a) suggested at least 10 individuals/species. However, the rarity of many species may make it difficult to obtain a representative sample, particularly since individuals of many species may show marked variation in phenology (e.g., Wheelwright 1986a). Similarly, unless the researcher knows the relative abundance of species, it will be difficult to estimate community-wide fruit abundance from phenological data.

Researchers should be cautious when using results of phenological studies to interpret results of bird studies conducted in different years. Although phenological patterns may be similar among years, marked annual variation in community-wide fruit production still may occur (Leighton and Leighton 1983, Wheelwright 1986a, Loiselle 1987).

FRUIT FALL TRAPS

Fruit fall traps have been used to estimate canopy fruit production in a variety of lowland trop-

TABLE 2. SELECTED STUDIES USING FRUIT FALL TRAPS TO ESTIMATE FRUIT PRODUCTION

Study length (months)	Study area	Count interval	No. traps	Trap size (m^2)	Total sample (m^2)	% of study area	Reference
			Community-oriented studies				
12	±100 ha	2 wk	150	0.08	12	0.0012	Terborgh 1983
18	±100 ha	2 wk	100	0.07	7	0.0007	Janson et al. 1986
12	83 ha	1 wk	312	0.08	26.0	0.0031	Foster 1982a
12	83 ha	2 wk	120	0.08	10.0	0.0012	Foster 1982a
12	10 ha	1 wk	100	0.08	8.3	0.008	Leigh & Windsor 1982
12	10 ha	1 wk	150	0.08	12.5	0.012	Leigh & Windsor 1982
72	10 ha	1 wk	200	0.08	16.7	0.017	Leigh & Windsor 1982
16	10 ha	1 wk	75	2.31	173	0.17	Smythe et al. 1982
			Species-oriented studies				
6	19 trees	1 wk	9 ± 4	1.0	9 ± 4	≥10	Howe 1980
4	17 trees	1 wk	5–18	1.0	5–18	6–23	Howe & Vande Kerckhove 1981
2	7 trees	1–3 d	4[a]	1.0	4	?	Howe 1977
3	0.135 ha[b]	2 d	135	0.20	26.5	1.96	Coates-Estrada & Estrada 1986

[a] Traps were supplemented with belt transects in litter.
[b] Crown area of one tree.

ical areas (Table 2). In general, 75 to 200 traps of from 0.08 m^2 to 2 m^2 collecting capacity each are placed throughout the habitats or under specific trees being studied (Table 2). All collected fruits are separated by species and usually weighed to obtain biomass estimates (Smythe et al. 1982, Terborgh 1983). Alternatively, seeds may be counted and then converted to estimates of fruit number and biomass (Foster 1982a, Janson et al. 1986).

Studies using fruit traps vary in focus from a single tree to entire communities. Most studies directed at birds have used fruit traps to estimate production by, or fruit removal from, a single tree or species (Table 2). Some have used traps to examine seasonal and annual patterns of fruit production over considerably larger areas (Table 2), often for studies on mammalian frugivores (e.g., Smythe et al. 1982, Terborgh 1983).

Considerations

Once traps are in place, collection of fruits requires little time and fruits are easily counted. Further, if traps are checked frequently, biomass estimates of fresh material can be calculated (Terborgh 1983). Problems associated with sampling different forest strata in tall lowland rain forest make fruit traps useful in some instances. For example, although the canopy is an area of high fruit production in tropical forests (e.g., Foster 1982a), the great height of lowland forest trees makes estimation of canopy fruit production time consuming and difficult. Direct counts of fruit from the ground are frequently impossible; even if one ascends into the canopy only a few trees can be surveyed effectively (Loiselle, pers. obs.). Highland forests often have comparatively lower canopies than lowland forests, but even here direct enumeration of canopy fruits is difficult. Trees often are shrouded in clouds and the lush growth of epiphytes obscures much of the canopy.

As Terborgh and others have pointed out, fruit fall traps measure "a residual quantity: total fruit production minus amount eaten by arboreal frugivores, including insects" (Terborgh 1983). Further, not all fruiting plants are equally well sampled by fruit fall traps, as we discuss below. Thus, fruit fall data are, at best, an indirect measure of fruit abundance, not an estimate of what is directly available to arboreal frugivores. How patterns of fruit fall reflect patterns of absolute fruit abundance remain undetermined. If, for example, ripe fruits remain on the plant for a long time, they may all be eaten and never recorded in traps, even though they might be an important resource. Similarly, if trees ripen few fruits every day, all fruits may be removed quickly (Howe 1984, Catterall 1985), again preventing collection of fruits in traps. Further, fruit traps can overestimate seasonal variation in fruit production because a larger proportion of ripe fruit is eaten when fruits are scarce than when fruit is abundant (see Terborgh 1983).

A major problem with fruit fall traps is that the area being sampled is usually unknown. Contributions may come from plants not located directly over a particular trap (e.g., Foster 1982a), whose input is difficult or impossible to assess. Similarly, total area of the traps usually is a small fraction of the study area (Table 2). Unless the number of traps is large, estimates of community fruit production can be heavily biased by fruiting of a few individuals. If one uses the data (e.g., biomass or number of fruits/trap or total trap area) to extrapolate fruit production to a much larger total area (e.g., fruit production in kg/ha), substantial errors may occur. Moreover, extrapolated estimates of fruit production will be inaccurate if changes in sampling area occur and are not accounted for. For example, Van Schaik (1986) found that trap area decreased by about 10% in 2 years (about 8% in 1 year) as traps sagged under the weight of water and litter.

Fruit fall traps do not provide comparable estimates of fruit abundance for all types of fruiting plants; understory plants, especially small-seeded shrubs and herbs, are under-represented. In neotropical sites, where up to 98% of understory plants produce animal-dispersed fruits, fruit abundance in the understory may be an important component of community-wide fruit production, particularly for birds that rarely ascend into the canopy. Fruit traps are more likely to sample large-seeded, capsulate, and dry arillate fruits. Small, juicy berries decay rapidly and may become unrecognizable between visits to traps. In such cases, fruits must be identified from seeds remaining in traps and number of fruits must then be estimated from seed counts. Frequent checking also may be necessary if fruits or seeds are removed from the traps by understory frugivores and granivores.

Some fruits, particularly those produced by epiphytes, may not fall to the ground and thus will not be sampled in traps. In highland wet forests, fruit fall traps will provide poor estimates of community-wide fruit production because many fruits of both trees and epiphytes will become lodged in thick vegetation. Underestimation of epiphytic fruits may be a particular problem because epiphytes are important in highland forests (Loiselle 1987; F. G. Stiles, pers. comm.).

If the objective is to estimate community-wide fruit production, placement of traps is important. Most tropical forests support a large variety of fruiting trees, but each trap will sample fruit from only one or two. Consequently, a commensurately large number of randomly placed traps is needed to adequately sample a majority of species. Alternatively, one may place traps on the basis of some stratified design (e.g., based on habitat or tree distribution patterns). If placed in sufficient density, however, use of traps may become time consuming, costly, and unsightly.

Habitats differ in fruit abundance and phenology (Frankie et al. 1974, Opler et al. 1980, Loiselle 1987); thus, extrapolation to a community level may not be warranted unless all habitats are sampled. Unfortunately, habitats such as treefall gaps and early second-growth, which often are rich in fruits (Martin 1985a, Loiselle 1987, Levey 1988), are difficult to sample with traps because of the low, dense vegetation.

Most studies using fruit fall data disregard aborted fruits (which generally are not a resource to frugivores, but are common in traps [Foster 1982a]). Fruit abortion can be high in tropical trees (Stephenson 1981) and the contribution of aborted fruits to fruit abundance measures derived from traps should be discounted.

Studies directed at fruit production by a single tree (Coates-Estrada and Estrada 1986) or species (Howe 1977, 1980; Howe and Vande Kerckhove 1981) suffer from fewer of the sampling problems mentioned above (e.g., area being sampled, input from other species). Placement of traps, number of traps, area sampled, and sampling frequency all can be more specifically tailored to the question being addressed, resulting in less sampling error. However, fruit fall data still represent what is not eaten (except perhaps for capsulate fruits). Without information on rates of fruit removal by frugivores, the total of, temporal variation in, and spatial variation among trees in fruit production may be harder to estimate.

Area-based Samples

Area-based surveys of tropical fruit production have been employed by a number of researchers, primarily to sample understory fruits. Methods include those that sample fruits along long transects, often following trails through a study area (e.g., Wong 1986); and those that rely on circular plots or quadrats situated throughout the area (e.g., Denslow et al. 1986, Loiselle 1987).

Several researchers have sampled fruits along linear transects. In one of the earliest studies that simultaneously monitored fruit production and bird abundance, Davis (1945) made observations at monthly intervals on the presence of fruit growing on trees located within 3 m of a set trail (Table 3), but did not count fruits. Hilty (1980) indexed fruiting activity (0, 10, 50 or 100% of crown area in fruit) of all plants (>3 m tall) within 3 m of a 1000 m trail. He combined this index with an estimate of total crown surface to provide an index of total fruit production. Similarly, Wong (1986) counted all ripe and unripe fruits (or estimated if $\gg$ 1000 fruits) produced by understory fruits along narrow paths that provided access to mist nets (Table 3).

Location or placement of sample plots varies with study objectives. We have used quadrats placed parallel to mist nets to estimate local fruit production in connection with bird studies (Loiselle 1987, Levey 1988) and circular plots (Denslow et al. 1986) to sample fruits over a wider area (Table 3). Our studies have focused on understory shrubs, treelets, lianas, and epiphytes (<10–20 m above ground) and have not included estimates of canopy fruit production. Leighton

TABLE 3. SELECTED STUDIES USING AREA-BASED SAMPLES TO ESTIMATE FRUIT ABUNDANCE

Study length (months)	Study area (ha)	Count interval	Sample no.	Sample area (m²)	Total sample (ha)	% of study area	Count type[a]	Reference
12	?	1 m	100	12	0.12	?	index	Levey 1988
12	2.5	1 m	50	12	0.06	2.4	index	Levey 1988
5	46	1 wk	6	1 ha	6	13	p/a	Gautier-Hion et al. 1981
5	43	1 wk	6	1 ha	6	14	p/a	Gautier-Hion et al. 1981
24	300	1 m	30	5000	15	5	count	Leighton & Leighton 1983
12	300	1 m	25	2500	6.25	2.1	count	Leighton & Leighton 1983
17	?	1 m	50	100	0.5	?	index	Denslow et al. 1986
14	16	1 m	—	—	1.32[b]	4.1	count	Wong 1986
15	4.8	5–6 wk	60	25	0.15	3.1	count	Loiselle 1987
15	4.8	5–6 wk	60	25	0.15	3.1	count	Loiselle 1987
11	4.8	5–6 wk	60	25	0.15	3.1	count	Loiselle 1987
4	8.6	5–6 wk	108	25	0.27	3.1	count	Loiselle 1987
15	?	2 wk	1[c]	3000	0.3	?	index	Hilty 1980
16	40	1 m	1[d]	3100	0.31	0.77	p/a	Davis 1945
16	40	1 m	1[e]	2200	0.22	0.56	p/a	Davis 1945

[a] Count type; see Table 1.
[b] 6.6 km of transects, 2 m wide.
[c] 1 km of transect, 3 m wide.
[d] 1021 m transect, 3 m wide.
[e] 750 m transect, 3 m wide.

and Leighton (1983) used much larger quadrats to sample fruits produced by lianas, epiphytes, and trees (>4 cm diameter) in Borneo (Table 3), where fruiting plants are less abundant than in the neotropics. Gautier-Hion et al. (1981) divided their area into subplots that were sampled on the basis of use by monkey troops (see also Estrada and Coates-Estrada [1986]); unused plots were not sampled while frequently used plots could be sampled every week. A similar, focal animal approach, could be adapted for bird studies.

Considerations

Once quadrats are delineated, it is easy to count fruiting individuals and fruit crops on a regular basis. Quadrat samples (and fruit traps) have the advantage that both spatial and temporal variation in fruit production can be analyzed statistically. Direct comparisons among studies are facilitated as well, although such comparisons necessarily assume that similar foliage strata and life forms were sampled. As with fruit traps, care must be taken in placement of quadrats or transects. Trailside studies are convenient, but understory fruit production is likely to be overestimated if transects are placed along well established trails because of the greater light availability along such trails. Since trails are not randomly distributed, sampling along trails may not produce an accurate assessment of community-wide fruit abundance.

Quadrat size and number will depend on the objectives and scale of study. Estimation of canopy fruits will require larger sample areas than those needed to estimate fruit production of understory shrubs and treelets. For accurate estimates of both canopy and understory fruits, the best area-based method will probably include some combination of large and small quadrats.

DISCUSSION

Quantifying fruits as a resource is not simply a matter of sampling technique, because various attributes influence whether a particular type of fruit is suitable for a particular species or type of bird (Denslow and Moermond 1985, Martin 1985b, Moermond and Denslow 1985). Ideally, a fruit that is never used by a particular bird species should not be included in estimates of fruit available for that bird. From a practical standpoint, this frequently is impossible to achieve, as diets of many neotropical birds are poorly known.

WHAT TO COUNT

Fruit quality

One of the first decisions is whether or not to count unripe as well as ripe fruit. Birds prefer ripe fruits (Moermond et al. 1986), but do feed on unripe fruits, especially during times of fruit scarcity (Foster 1977, pers. obs.). Counts of ripe fruits alone may underestimate fruit production if fruits are removed rapidly as they ripen (Howe 1984, Catterall 1985). Unripe fruits may provide an estimate of future availability of fruits, particularly for species that ripen fruits relatively synchronously (Bronstein and Hoffman 1987).

In addition to ripeness, other factors relating to fruit quality may influence fruit selection by frugivores, including flavor (Sorensen 1981), lipid content (Leighton and Leighton 1983), and sugar content of fruit (Levey 1987a).

Structural attributes

Fruit selection may be limited by a variety of structural characteristics that interact with morphological capabilities of frugivores to determine the bounds of their diet (Janson 1983, Gautier-Hion et al. 1985). Some fruits, especially those enclosed in capsules, are available to few birds (e.g., Leighton and Leighton 1983, Pratt and Stiles 1985) and are unavailable to other species.

Size of fruit also may limit types of fruit that can be consumed (Moermond and Denslow 1985, Wheelwright 1985). This is particularly true for species that swallow fruits whole (e.g., Pipridae); birds that can bite off pieces of fruit (e.g., many Thraupinae) are less limited by fruit size (see also Leighton and Leighton 1983, Foster 1987).

Location of fruits on a plant (e.g., close to a perch, on the tip of a slender twig) can influence choice (Denslow and Moermond 1982, Moermond and Denslow 1983). Accessibility will influence the type of foraging maneuver needed to obtain it and morphological constraints may determine which fruits are accessible to a particular species of bird (Moermond et al. 1986).

The many factors that govern fruit selection will determine its perceived abundance. Ideally, fruit abundance should be weighted by its importance to frugivores. This may be possible if a specific species is being studied, but is difficult for community studies. Information is available on nutrient content of some tropical fruits, but we know too little about the diets of most frugivores, particularly temporal and spatial variation, to determine which fruits to sample. Similarly, too few tropical fruits have been analyzed for energy and nutrient content for complete community analyses. Particularly for community studies, it seems best to sample as thoroughly as possible all fruits that are likely to be eaten by birds. Over time, as more information on diets of specific species becomes available, analyses of bird-fruit interactions may be more precisely addressed.

Sampling Technique

When sampling fruits, one must decide whether to count all fruits or simply to use an index of relative abundance. We favor direct counts because they likely are more relevant to understanding bird populations. Relative indices of fruit abundance are less likely to be useful for comparative analyses. Quantitative samples of fruit abundance allow one to make direct, statistical comparisons among studies and to make direct correlations with bird populations, either in terms of fruit numbers, biomass, or nutrient content. Direct counts of fruits allow later conversion to a relative scale, but the reverse is not true.

Direct counting of large numbers (i.e., > 1000) of fruits can be time consuming and often difficult. When direct counts are not possible, one can count a subsample of fruits (e.g., on one infructescence or branch) and then use those data to estimate total fruit abundance (e.g., Worthington 1982). One must recognize, of course, that such estimates always will involve some level of error, often of unknown magnitude. However, the increase in sample size allowed by the time saved in counting may be substantial. "Knowing that a particular fig bore 32,489 fruits in 1987 is not as valuable as knowing that 10 of 100 trees produced about 20,000 fruits each and the rest produced none" (N. T. Wheelwright, pers. comm.).

Fruit abundance can either be represented in terms of numbers of fruits or in terms of biomass. The latter requires information on weights (including pulp and seed weights) of all species of fruits. Once such data are available, conversion to biomass is easy if quantitative estimates of fruit abundance (numbers) also are available. In her study on reproductive ecology and food selection by two species of manakins, Worthington (1982) measured fresh and dry weight of fruit pulp (minus seeds) and then converted counts of fruit to biomass. Studies that include seed predators (e.g., parrots, many finches and sparrows, pigeons, cracids) would need to modify biomass measures accordingly.

Problems may arise on how to count some fruits, particularly some unripe ones. For example, for arillate fruits enclosed in capsules (e.g., Guttiferae, Malvaceae, Monimiaceae), does one count the capsule as a single unripe fruit or as some number of unripe fruits, dependent on the average number of arillate fruits per capsule? We favor the latter as birds consume fruits separately once they are exposed. Aggregate, spike-like fruits such as *Piper* typically are eaten piecemeal and one could estimate the average number of "bites" available per fruit. Birds vary in amount taken at one time, however, and we favor counting each spike as a single fruit.

When to Sample

If parallels are to be drawn between fruit and frugivore cycles of abundance, it is necessary that populations be sampled simultaneously. Some studies of birds, for example, have relied on patterns of fruit abundance documented by other researchers at other sites in other years. Because site-to-site and year-to-year variation can be appreciable, this practice may lead to invalid conclusions.

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