Analysis of Diets of Plant-Visiting Bats

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1. INTRODUCTION

Approximately 250 species of bats in the paleotropical family Pteropodidae and the neotropical family Phyllostomidae regularly visit plants for either fruit or floral resources. Frugivorous bats feed on the fleshy arils, pericarps, or syconia of fruits, often ingesting seeds along with this material. No species, however, is known to actively seek seeds as dietary (nutritional) items. Flower-visiting bats seek nectar and/or pollen, the former being an important source of energy (carbohydrate) and the latter supplying necessary protein (Howell, 1974). Few species are likely to be totally specialized on either fruits or flowers; however, for the sake of simplicity I will refer to plant-visiting bats as either frugivores or nectarivores. In addition, some fruit bats may occasionally ingest leaves or buds (Cunningham von Someren, 1972; Wickler and Seibt, 1976; T. H. Fleming, pers. comm.), but the dietary significance of these items is uncertain.

Studies of the diets of frugivorous and nectarivorous bats can focus on four major questions. What kind of resource does a particular bat species eat (fruit or flowers)? What species of fruits or flowers does it seek? What sizes, stages of ripeness, or parts does it select? What nutrients does it extract during gut passage? In this chapter I will deal exclusively with the first three questions; nutritional approaches are covered in Chapter 15.

Few, if any, techniques for the study of the diets of plant-visiting bats are specialized or technically involved, so in treating this subject I will also consider the biases that may be introduced by sampling with different methods, at different localities, or at different times. Because few published data address

this aspect, I will draw on my own data collected during a two year study of the feeding ecology of a pteropodid community in Ivory Coast, West Africa (see Fenton and Thomas, 1984; Thomas, 1982, 1983, 1984a, 1984b; Thomas and Marshall, 1984).

2. DIET ANALYSIS FOR FRUGIVOROUS BATS

The foraging activities of frugivorous bats can be simply described as follows. At dusk a bat leaves its day roost and commutes to some feeding area where it locates a resource tree. From the available fruit crop it selects one fruit which it may eat in situ or which it may carry to a separate feeding roost. During feeding the bat may ingest all or only part of the fruit, leaving the remains as masticated rejecta pellets or uneaten parts below the feeding site. The bat then carries a gut load of fruit pulp and possibly seeds as it continues to forage or undertake other activities. It later voids this and subsequent gut loads during the night. The timing and hence location of defecation relative to feeding is determined by the transit time for material in the gut. At or before dawn the bat returns to its day roost with a final gut load of pulp and/or seeds which it voids beneath the roost during the day. These activities provide at least three convenient windows by which to view the diets of frugivorous bats: by means of feces collected from netted bats at night (net feces), by feces collected below day roosts, or by feces, rejecta pellets, or fruit parts left below feeding roosts.

2.1. Feces from Netted Bats

Bats captured in mist nets commonly defecate under the stress of handling, so feces can be readily collected from bats netted either at fruiting trees or at randomly selected netting sites. In savanna habitats in Ivory Coast, a mean of 23.3% of *Epomops buettikoferi* and *Micropteropus pusillus* (combined n=1224 captures) produced feces during the ca. five minute handling period. Heithaus et al. (1975) found a similar proportion (19%) in their study of a Costa Rican bat community. The exact proportion of bats that defecate during handling no doubt depends upon the time bats remain in nets and their pre-capture foraging success, so this may vary among habitats and seasons. This proportion (19%-23.3%) compares favorably with the 17.6% of frugivorous phyllostomids that had stomach contents when sacrificed (Fleming et al., 1972) and indicates that killing is unnecessary except when fresh stomach material may be required. The number of fecal samples collected may be increased by placing plastic sheets under nets to collect feces produced before handling. If minimizing the handling time is not a consideration, bats may also be held for about one hour in cloth bags to permit passage of gut loads.

Feces obtained from netted frugivorous bats either contain seeds or consist solely of pulp. Because seeds are relatively easily separated from the pulp, generally have recognizable and distinctive features, can be germinated, and can be kept for long periods if dry-stored, they constitute the primary means of fecal identification. In Ivory Coast, 90.5% of 1825 samples collected from nine species of pteropodids (*Epomops buettikoferi, Eidolon helvum, Hypsignathus monstrosus, Rousettus angolensis, Micropteropus pusillus, Megaloglossus woermanni, Myonycteris torquata, Nanonycteris veldkampi,* and *Scotonycteris zenkeri*) contained seeds. This proportion, however, may be expected to vary both geographically and locally among habitats depending on plant reproductive strategies. Van der Pijl (1957) listed large seed size as one of the characteristics of chiropterophilous (bat dispersed) fruits. His conclusions were based primarily upon studies in Amazonian and Malaysian primary forest where large seed size results from the large energy reserves necessary to maximize seedling survival under the low light levels of closed canopy forest. Ng (1978) indicated that 75% of Malaysian forest trees have seeds over one cm in length. Frugivorous bats forag-

ing in these areas and on these species would be expected to carry seed loads less frequently than bats foraging in successional communities where the mean seed size is smaller.

There are currently no "quick and dirty" means of identifying fecal seeds. I know of no comprehensive keys to the seeds of any tropical plant communities and such keys (if made) would be of only local value. Netolitzky (1926; cited in Corner, 1976) and Corner (1976) present data on seed characters and Corner includes a key to the seeds of dicotyledon families. However, these sources are of limited value since they rely on histological techniques and seeds can only be keyed to the family level. For this reason the identification of fecal seeds must usually be based upon a first hand knowledge of the plant communities where the bats forage. In my study in Ivory Coast, I relied upon weekly "fruit patrols" through samples of all the available habitats in order to gain some idea of which fruits were available and to collect seeds for a reference collection. Heithaus et al. (1975) relied on a similar inventory and reference collection in their study in Costa Rica. Such fruit patrols can be time consuming, and they rarely provide quantitative data on fruit abundance due to the extremely patchy nature of fruiting in space and time (methods of assessing resource availability are considered in Chapter 14). I spent approximately 15 h per week over 12 months on fruit searches before locating and identifying all the major fruits used by the local bat community. Seven species of fruits were never identified; however, none of these were found more than twice in feces and these seven were apparently rare species. The distribution of fruit patrols must necessarily be based upon some knowledge of the foraging movements of the bats in question. Some species may be relatively sedentary, such as *Micropteropus pusillus* in Ivory Coast where a mark-recapture study showed that it was confined to local patches of regenerating unburned savanna (Thomas, 1982), and fruit patrols may be similarly restricted. Other species may be more mobile. In Ivory Coast, *Myonycteris torquata*

relied primarily on *Solanum verbascifolium* (Solanaceae; 89.5% of fecal samples) and it was not until habitats 10 km distant from the netting sites were included that this fruit was identified. Central place foragers such as the colonial *Eidolon helvum* and *Pteropus poliocephalus* (Rosevear, 1965; Nelson, 1965) may commute much farther in a night, making fruit patrols even more difficult.

When fruit availability is assessed, a reference seed collection is made, and fecal seeds are "identified" by comparison with known species, the identification process is still not complete. The seeds of many large genera, such as *Ficus, Solanum,* or *Piper,* are sufficiently similar that final identification should be confirmed by germinating and growing a subsample.

Some feces do not contain seeds and these potentially pose a serious problem for identification. However, due to the relatively short transit time and "gentle" treatment of material in the guts of frugivorous bats, pulp is generally little modified in texture, color, or odor from the fruits themselves. Thus, fresh material can be compared with fresh pulp and so identified. By feeding suspected fruits to captive bats, palatability and fecal characteristics can be assessed. It is difficult to "prove" that a given fecal sample in fact represents a given fruit species; however, palatability to captive bats, similarity of fecal characteristics, and, if possible, observations of bats feeding in the wild should constitute adequate "proof."

In addition to fruit, a variety of other items may be included in the diets of frugivorous bats and so show up in fecal samples. For this reason fecal samples should also be examined at low and high magnification to search for insect parts, moth scales, pollen, and possibly leaf or bud fragments. Insect remains may be from three possible sources: 1) insects that were actively hunted, captured, and ingested, 2) insects that were accidentally ingested along with fruit pulp, and 3) parts rather than whole insects that were incidentally ingested. To date there has been little consideration of these three sources of insect

remains in feces of plant-visiting bats, although from a nutritional perspective they may be dramatically different. Phyllostomids may regularly include whole, captured insects in the diet and these may represent a significant nutrient source. Fleming et al. (1972) showed that insects composed up to 25% of the stomach volume of the frugivorous phyllostomids *Artibeus jamaicensis* and *A. lituratus,* and Gardner (1977) provides a comprehensive review of other similar reports. Howell and Burch (1974) reported that insect remains were common in Costa Rican frugivorous bats and that "lepidopteran" parts (probably scales but not specified; see Thomas, 1984a) accounted for 79.7% of those samples with insects. The presence of moth scales does not necessarily indicate the active pursuit and capture of Lepidoptera by frugivorous bats. I found that although moth scales were common in the feces of *Epomops buettikoferi* in Ivory Coast, these could be accounted for statistically by the bats' feeding on fruits that had scales as a surface contaminant (Thomas, 1984a). Thus, scales are not evidence that *E. buettikoferi* (and 79.7% of phyllostomids?) pursues and captures moths so they may not be important dietary and nutritional items.

Similarly, insect exoskeleton fragments may be found in some bats' fig (*Ficus;* Moraceae) feces, but these do not necessarily represent active hunting. The insect parts most commonly found are of agaonid wasps and their hymenopteran parasites which may be ingested incidentally along with fig syconia. These have been proposed as a potentially important source of protein to frugivorous bats (Morrison, 1980); however, this does not appear to be justified. Ripe figs are generally wasp-free (by consuming fruits, frugivores must exert a strong selection against those wasps that remain in ripe syconia). In Ivory Coast I found that only 16% of ripe (orange or red) *Ficus capensis* fruits that I sampled (n=50) had any wasps and those that did had only a mean of 6.4 mg. At a protein level of 18% by fresh mass (Morton, 1973) these wasps could represent a maxi-

mum contribution of only 1.2 mg protein/infested fig and an entire night's foraging would supply only approximately 3% of a frugivorous bat's estimated daily protein requirement (Thomas, 1982, 1984b).

Feces that contain *Ficus* may also include pollen. Due to the unique retention of flower parts inside ripe syconia, pollen may remain and so be ingested incidentally. Such pollen occurs at low density in feces (unquantified pers. obs.) and is unlikely to make an important nutritional contribution.

While the presence of insect parts, moth scales, and *Ficus* pollen in feces does not necessarily indicate active search on the part of fruit bats for these items, neither does the absence of insect parts necessarily indicate a lack of insect hunting. Ayala and d'Alessandro (1973) reported that *Carollia perspicillata* and *Glossophaga soricina* rejected the hard exoskeleton when feeding on some insects and so had no recognizable hard parts in stomach (and presumably fecal) samples. Unfortunately, there appears to be no simple means of resolving these two confounding problems (the possible presence of insect parts without any nutritional input and the possible absence of insect parts despite active hunting and ingestion), and the inclusion of non-fruit or flower items in the diets must continually be questioned before being accepted or rejected.

2.2.   Feces Below Day Roosts

Bats may regularly return to day roosts with gut loads which they later void. This provides an alternate and sometimes more readily accessible source of feces. Feces may be collected from leaf surfaces or on screen, plastic, or paper sheets placed below the roost. How many samples are available, and when they should be collected depends on the roosting behavior of the bat species in question. Some foliage roosting species such as *E. buettikoferi* (a solitary species; Fenton and Thomas, 1984) and *Hypsignathus monstrosus* (roosting in small groups; Bradbury, 1977; Fenton and Thomas, 1984) may use the same roosts

for long periods if undisturbed, yet abandon these sites immediately if disturbed (Fenton and Thomas, 1984). In such cases, roosts should be approached and the feces collected at night while the bats are foraging. Colonial species appear to be less sensitive to disturbance. Both *Eidolon helvum* and *Carollia perspicillata* are disturbed by activity below the roost but usually will not abandon the site if approached during the day. In these cases feces can be collected at more convenient times.

Feces collected from below day roosts can be treated and identified in the same fashion as net feces.

2.3. Rejected Pellets and Fruit Parts Below Feeding Roosts

The use of feeding roosts provides yet another means of assessing the diets of frugivorous bats. Although not all species use feeding roosts, those that do leave ample evidence of feeding in the form of rejecta pellets and uneaten fruit parts. These parts are generally easily identified since they include seeds and uneaten parts that are more readily matched with fruits collected in the field than are feces. Feeding roosts potentially provide a large amount of data for a given individual. For example, in Ivory Coast some *Epomops buettikoferi* used the same feeding roosts for up to 79 consecutive days, although individuals often used more than one roost on a given night (Thomas, 1982, 1984b). Sampling from such long-term roosts can provide valuable information on dietary shifts between seasons and inter-individual foraging differences.

Data collected from feeding roosts, however, are not entirely compatible with and additive to data based on net or roost feces (see below). Because bats treat each fruit differently, rejecting more of one species than of another, the use of fruit species cannot be scored on a "percent of total mass" or "percent of rejecta pellets" basis. Unless some means of identifying how many fruits of a given species were consumed and their rela-

tive contribution to the diet on a mass basis is devised, fruits can only be scored on a "presence/absence" basis. This will underestimate the contribution of large or important fruit species and overestimate the contribution of small or rarely used species.

2.4. Sampling Biases

Feces collected from netted bats, feces from below day roosts, and rejecta pellets and/or uneaten fruit parts at feeding roosts all provide information on the diets of frugivorous bats, but it is important to question whether these three sources provide equivalent results. It is unlikely that they do. The most easily evaluated is the difference between data sets based on net feces and rejecta pellets and/or uneaten fruit parts collected from below feeding roosts. During the period of 1 July to 31 October 1979 and 1980, I collected 145 net feces from free-ranging *E. buettikoferi* and also scored the presence or absence of different fruit species below 32 *E. buettikoferi* feeding roosts over a total of 366 roost days. Figure 1 shows the relative abundance of different fruit species in the two samples. Despite the larger sample size from roosts, they had only 37% as many species as net feces. Fruit from *Ficus capensis* was the most common item in each data set, yet was almost twice as common at feeding roosts as in net feces (83.6% at roosts vs 44.8% in net feces). The number two and three ranking species in terms of frequency of use differed between the two data sets (net feces: *Adenia cissampeloides* and *A. miegei* = 15.9%, *Vitex doniana* = 8.2%; feeding roosts: *Psidium guajava* = 8.4%, *Nauclea latifolia* = 4.0%. Clearly the two data sets are not equivalent; apparent dietary breadth and evenness are reduced at feeding roosts. The reasons for this are not entirely clear but are in part related to fruit size. The major difference between the two data sets is the under-representation of small (<2 cm) fruits at feeding roosts, leaving the large fruits to dominate. Feeding roosts may well be used only for handling large fruits or ones that require relatively long handling
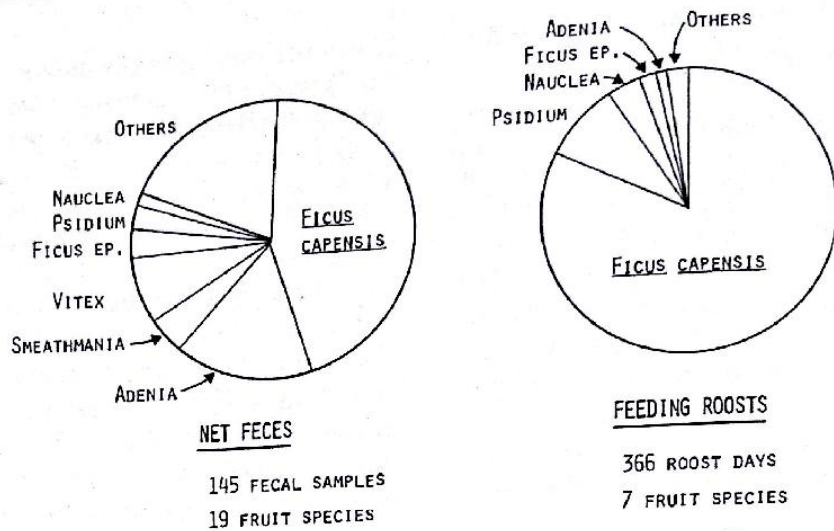
Figure 1. The proportion of *Ficus capensis*, *Adenia cissampeloides*, *A. miegei*, *Psidium guajava*, *Vitex doniana*, *Smeathmania pubescens*, *Nauclea latifolia*, and epiphytic *Ficus* species present in samples of net feces and fruit parts collected from below *Epomops buettikoferi* feeding roosts.

times. This means that feeding roosts will consistently sample only a subset of the total diet of frugivorous bats.

The relatively rapid transit time for food in the guts of fruit bats may also influence the accuracy of fecal samples relative to the true feeding performance of the bats. Both phyllostomid and pteropodid frugivores have transit times of 15-60 min (Fleming and Heithaus, 1981; Wolton et al., 1982), and fecal samples collected at either netting sites or day roosts may be representative of local foraging only. This bias would be most pronounced in samples collected at day roosts. Species such as *Eidolon helvum* may commute over 50 km from day roosts to feeding areas (Rosevear, 1965). If this represents approximately a one hour flight, then fecal samples collected below day roosts may be heavily biased towards the last meal of the night, possibly collected en route away from rather than at the primary feeding area. For other species which forage within minutes of the day roost (e.g., *Artibeus jamaicensis* and *Carollia perspicillata;* Morrison, 1978; Heithaus and Fleming, 1978) this bias may be insignificant.

Rapid food transit times may also affect the conclusions drawn from feces recovered from netted bats. Bats may preferentially forage in one habitat but for some reason (net position, visibility, etc.) they are captured most frequently in another. This would bias fecal samples towards fruit species only occasionally eaten in non-preferred habitats. This problem would be most pronounced in cases where capture and foraging habitats were separated by considerable distances and the bats did not "carry over" gut loads. Fleming and Heithaus (1981) showed that "foreign" feces were common around fruiting trees, creating a diverse seed rain in terms of species and suggesting high "carry over" during foraging. In Ivory Coast I caught *Hypsignathus monstrosus* almost exclusively in nets set at heights of one to four meters, yet fecal samples showed that fruit species associated with the forest canopy 20 m above this level constituted over 47% of the diet (Thomas, 1982). In this case, it appears that foraging areas and capture sites were sufficiently close to minimize the effects of transit times. Similarly, *Solanum verbascifolium* constituted 89.5% of the *Myonycteris torquata* fecal samples despite the fact that no plants were located closer than 10 km from the netting sites. Bats probably move fast enough that "carry over" is high and net feces provide the most accu-

rate measure of the true diet of frugivorous bats.

2.5. Non-Random Fruit Selection

In the eyes of frugivores, not all fruits are equally attractive. Within and between fruit crops there is considerable variability in ripeness, hardness, size, composition, and other physical attributes, and frugivorous bats may select specific fruits on a non-random basis. For example, Bonaccorso (1978) showed that within the "canopy frugivore guild" at Barro Colorado Island, Panama Canal Zone, the mass of *Ficus insipida* fruits that *Artibeus jamaicensis, A. lituratus,* and *Vampyroides caraccioli* carried into nets was significantly correlated with body mass. August (1981) found that the number of bats captured at *Ficus* spp. trees in Venezuela was positively correlated with mean fruit size and negatively correlated with fruit hardness. Fleming et al. (1984) also showed that under captive conditions *Carollia perspicillata, C. subrufa,* and *Glossophaga soricina* selected the ripest fruits of *Muntingia calabura* from the range available. These studies indicate strong selectivity on the part of fruit bats for size (Bonaccorso, 1978; August, 1981), hardness (August, 1981), ripeness (Fleming et al., 1984), or nutritional quality (Fleming et al., 1984).

Non-random fruit selection may be tested by measuring the parameters of interest, marking fruits for individual identification, and monitoring the probabilities of removal in the field. This, however, leaves the identity of the frugivores unknown. Alternately, non-random selection can be tested, possibly in a more controllable fashion, either by presenting bats with fruit arrays in flight cage situations (e.g., Fleming et al., 1984) or by presenting arrays of fruits on display poles in the field (e.g., Fleming et al., 1977). These latter two experiments appear to be the only ones testing fruit selection to date; however, given the extreme importance of non-random selection to studies of fruit intake, nutrition, and foraging decisions, such studies should be stressed in the future.

Once selection of a given fruit has been made, a foraging bat handles the fruit, ingesting some parts and rejecting others. Rarely is the entire fruit consumed. Handling is an important consideration in detailed studies of feeding. The details of handling may be inferred by collecting fruit parts below feeding sites (fruiting trees or feeding roosts) and "reconstructing" fruits. This may be difficult to do if the size, ripeness, or other features of the original fruit are unknown. As with selection experiments, handling may readily be studied by presenting captive bats with known fruits and directly observing their feeding. I believe that such experimental approaches to feeding studies will yield useful results in the future.

3. DIET ANALYSIS FOR NECTARIVOROUS BATS

Foraging nectarivorous bats visit flowers for nectar and/or pollen. In feeding they may: 1) pierce the corolla to extract nectar without contacting the anthers, 2) extract nectar by entering the corolla and contacting the anthers, but without actually feeding on them, or 3) feed directly on pollen with or without ingesting nectar. During a night's foraging, nectarivorous bats may potentially exhibit all or some combination of these feeding modes at a number of different flower species before returning to the day roost. At the day roost bats may void pollen which they ingested directly from the anthers, and/or they may groom pollen from the fur and void this later.

Because nectar-feeding alone (e.g., case 1 above) is undetectable without killing the bats to examine the stomach contents (and nectar in the stomach has few features permitting species identification), pollen is generally used as a "tracer" indicating flower visitation. This limits the recognition of flower visits to cases where the bats contact the anthers (cases 2 and 3) and probably act as legitimate pollinators (e.g., Gould, 1978). Cases where the bats pierce the corolla (e.g.,

Micropteropus pusillus at *Spathodea campanulata;* Ayensu, 1974) would remain undetected.

Pollen used to indicate flower visits may be present either in the feces or on the fur and so may be sampled by collecting feces from netted bats, feces from below day roosts, or by collecting pollen from the fur of netted bats. Fecal samples, whether collected from netted bats or at day roosts, can be moistened, mounted directly on glass slides, dried, and covered for later microscopic examination. Samples of pollen can be collected from the body surfaces by snipping samples of fur from the desired body region, saving this in contamination-free pouches (stamp collectors' glassine envelopes work well), and later mounting the hair on slides for examination. Alternately, pollen can be removed from the hair by swabbing with an adhesive substance. Beattie (1971) published the recipe for a basic fuschin-stained gelatin useful in collecting and mounting pollen. This consists of 175 ml of distilled water, 150 ml of glycerine, 50 g of gelatin, and 5 g of crystalline phenol mixed together and warmed. Crystalline basic fuschin is then added until the desired density of stain is achieved (usually the color of claret, but it is advisable to experiment for the optimal stain density). The gelatin can be cut into small cubes which can be pressed to the bat's fur with forceps, placed on a slide under a coverslip, warmed over an alcohol lamp or cigarette lighter, and stored for later examination. This technique is particularly useful since it both stains and preserves the pollen in a permanent mount. Because small amounts of pollen may contaminate the samples, it is advisable to use some minimum number of pollen grains to indicate a flower visit. Heithaus et al. (1975) used three or more grains as this criterion.

As with seeds, there is no simple means of identifying the pollen of tropical plants from a given area. Although palynologists have developed keys permitting the identification of fossil and subfossil pollen to family and occasionally genus, these keys require considerable familiarity and are unlikely to be of much use to biologists requiring rapid field identification. Generalized searches for flowers in the habitats available to the bats, the construction of a reference collection, and the comparison of unknown samples with this collection will usually form the basis of the identification procedure.

Collecting samples of pollen and assessing the use of different flower species must be subject to several important considerations. Flowers with different morphologies and anther positions may deposit pollen on different body regions of bats. Howell (1977) described how the phyllostomid *Anoura geoffroyi* carried pure *Mucuna* pollen ventrally, *Crescentia* pollen dorsally, and *Inga* and an unidentified Bombacaceae pollen on the face and neck. There may be little or no carry over of pollen between body regions, so surface samples (swabs or hair samples) must be taken from all these sites and either pooled or treated separately.

Because different plant species may invest more or less in pollen production, the relative amounts of different pollen types (i.e., percent species *A* pollen in a sample) in surface samples or feces cannot be used to indicate relative use. Pollen must be scored on a "presence/absence" basis only. Data on the presence of pollen in fecal samples can be grouped with data on the frequency of different fruit types in fecal samples for a given bat species to indicate the relative importance of floral of fruit resources in its diet. However, data based on surface samples is not comparable with data on fecal samples. Pulp, seeds, and pollen will remain in bat guts for only 15-60 min (the transit time), while it is currently unknown how long pollen will remain on the fur. The latter duration is probably at least until the first post-feeding grooming which may be 12 h after feeding. The duration could be even longer if grooming is not 100% effective. Thus, surface pollen may be detectable for longer than gut loads of pollen or fruit, and this would result in a consistent overestimate of flower use if surface samples were compared with feces.

The timing of nectar secretion and hence

flower visitation may also affect sampling. Bat pollinated flowers open and commence nectar secretion at night, but not all species behave in similar ways. In Central America, *Inga marginata* secretes nectar and attracts bats approximately six to eight hours earlier in the night than *Bauhinia ungulata* (Howell, 1977). Fecal samples collected from bats late at night or at the day roosts would be unlikely to contain *Inga* pollen and these samples would be strongly biased toward *Bauhinia*. In general, data sets based on roost feces (e.g., Start and Marshall, 1976) may be strongly biased towards flower species with late night peaks in nectar secretion and so they may show lower diet breadth than surface samples. Due to the longer retention time of pollen on the fur, surface samples would not be expected to be as subject to this bias. Howell (1977), however, showed that the abundance of *Inga* pollen on the fur of *Glossophaga soricina* declined rapidly after peak nectar production, which suggests that the bats groom repeatedly during the night and thus reduce the pollen retention time.

4. SUMMARY AND CONCLUSIONS

In this chapter I have tried to present a general overview of methods used to examine the diets of plant-visiting bats. For frugivores and nectarivores, feces collected from netted bats, feces collected from day roosts, fruit parts found below feeding roosts, and swabs taken from facial, ventral, or dorsal fur may all yield information on fruit or flower species included in the bats' diets. I have stressed, however, that not all data sets provide equivalent and accurate views of the diets and that not all data sets can be combined or compared directly. In any given study a researcher must be clearly aware of the biases that may be introduced by using different sampling methods and so must design the data collection and experiments so as to strive towards the most accurate portrayal of the bats' "real" diets.

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