MOVEMENTS AND BEHAVIOR

M. Brock Fenton and Thomas H. Kunz

The published information on movements and behavior of phyllostomatids is limited and mainly anecdotal. However, owing to several technological developments, notably the availability of image intensifiers and microcircuits, new advances are anticipated in these areas. Both these tools have already been used to good advantage (see Schmidt and Greenhall, 1972; Williams and Williams, 1970) by providing means of studying, with minimal disturbance, the behavior and movements of bats under natural conditions. Concurrently, the successes of several workers (for example, Racey and Kleiman, 1970; Rasweiler and Ishiyama, 1973; Wimsatt et al., 1973) at maintaining various bats in captivity will encourage comparative studies of specific behavior patterns and responses under controlled conditions.

We expect that together these developments will produce a series of important studies of the movements and behavior of phyllostomatids in particular and bats in general. The results of such studies, when considered in the context of other work (such as the evolutionary and energetic implications of fruit and nectar feeding—Morton (1973) and Heinrich and Raven (1972), respectively—will permit observations on bats to be placed in a general biological context.

The availability of the aforementioned instruments and successes at maintaining bats in captivity would not be as significant as they are if it were not for the work that has been done on the systematics, distribution, and natural history of phyllostomatids. Only when such technological developments can be applied in areas where a good basic knowledge of the bats exists do they assume great importance. Specific areas that come to mind in this context include Trinidad (Goodwin and Greenhall, 1961; Williams and Williams, 1970), Costa Rica and Panamá (Brown, 1968; LaVal, 1970; Fleming et al., 1972), and various islands in the West Indies (Goodwin, 1970; Jones and Phillips, 1970).

Movements

Circadian

The roosting and feeding habits of bats govern the frequency and magnitude of daily movements between roosts and feeding grounds. Presently, little detailed information is available concerning foraging movements and territories of bats, but phyllostomatids provide one partial exception to this general situation.

Using radio tracking, Williams and Williams (1970) documented the feeding flights of Phyllostomus hastatus from three caves in Trinidad. Upon leaving the caves (the day roosts), bats flew directly to areas where they alternately roosted and made short flights in the feeding area. Feeding areas ranged from one to five kilometers in straight-line distances from the caves, and some individuals travelled four kilometers to reach a feeding area only three kilometers distant.
This study appears to be the only instance in which the movements of phyllostomatids between day roosts and feeding grounds have been documented.

Data obtained by banding (LaVal, 1970; Fleming et al., 1972) indicate that some phyllostomatids have regular feeding grounds. Further evidence of this is provided by the observations of Baker (1973) concerning the visits of some glossophagines and one stenodermine to flowers. Leptonycteris sanborni, Glossophaga sp., Glossophaga soricina, and Artibeus jamaicensis have been observed to make fleeting visits to flowers (Baker, 1973). Baker (1973) and others (Vogel, 1968-69; Baker et al., 1971) have remarked on the “trap lining” nature of these visits, which appears to indicate regular patterns of movements.

Phyllostomatids, including Macrotrus waterhouseii (Vaughan, 1959), Lonchiorina aurita (Nelson, 1965), and Leptonycteris sanborni (Hayward and Cockrum, 1971), but especially the Phyllonycterinae and the Desmodontinae, are active later in the evening than are many other bats (see Silva Taboada and Pine, 1969; Leen and Novick, 1969; Wimsatt, 1969; Crespo et al., 1972). In lowland rainforest in Guyana, one of us (Fenton) made similar observations. Using mist nets and ultrasonic detectors (Fenton et al., 1973), it was established that emballonurids, mormoopids, vespertilionids, and molossids were most active around dusk and dawn, whereas phyllostomatids (including Phyllostomus elongatus, Glossophaga soricina, Carollia perspicillata, Rhinophylla pumilio, Sturnira lilium, Uroderma bilobatum, Vampyrops helleri, Vampyressa bidens, Chiroderma villosum, C. trinitatum, Ectophylla macconnelli, Artibeus cinereus, A. concor, A. lituratus, Ameirida centurio, and Desmodus rotundus), based on captures in mist nets, were active later in the evening and throughout the night until about one hour before dawn. Further observations on phyllostomatid activity have recently appeared (Heithaus et al., 1974; Tuttle, 1974; Davis and Dixon, 1976).

In part, these temporal differences can be accounted for by the sequence of departures from the day roosts. At Mount Pleny Cave in Jamaica, Leen and Novick (1969) observed that Monophyllus redmani was the first species to depart in the evening, followed by Pieronotus psilotis, P. parnellii, Artibeus jamaicensis, and Phyllonycteris sp. Whether or not these departures represent differential sensitivity to light, roost locations, or differences in circadian periodicity remains to be determined.

Captures of bats at different locations during the night have been used to indicate activity patterns (Brown, 1968; LaVal, 1970). However, comparison of activity patterns from different areas or seasons is difficult because the basic patterns of activity reflect, among other things, the proximity of the study site to day and night roosts.

For example, when the activity patterns of Artibeus jamaicensis in Costa Rica (Fig. 1a and 1b) are compared with those we obtained in Puerto Rico for this species (Fig. 1c), marked differences are evident. Given that the values provided by Brown (1968) are absolute numbers and the other values are proportions, different levels of bat activity occur. Brown (1968) and LaVal (1970) obtained similar patterns of activity of A. jamaicensis in forests and banana groves, and we studied its activity at the entrance to a large cave system, parts of which were used
Fig. 1.—Nightly activity of *Artibeus jamaicensis*: A, Costa Rica, Banana Grove (after Brown, 1968; N = 30); B, Costa Rica, Dry Forest (after LaVal, 1970; N = 59); C, Puerto Rico, Cave entrance (This study, N = 124; a solid circle indicates per cent adult males).

as day roosts by this species. The three patterns indicate that some individuals of this species are active throughout the night. Adult male *A. jamaicensis* in Puerto Rico were more active one hour after dark and one hour before dawn, but did show sporadic activity throughout the night (Fig. 1c).

Williams and Williams (1970) found that much of the activity of *Phyllostomus hastatus* in Trinidad occurred in the first few hours after sunset, considering the times when most individuals returned to their daytime refuges. They also noted an additional period of activity just before sunrise, although LaVal (1969) failed to observe comparable predawn activity for other phyllostomatids in Costa Rica. The disparity of these two reports may reflect differences in behavior of bats as a function of proximity to the day roost, since predawn feeding may be restricted to the immediate vicinity of the day roost.

The effect of roost proximity and, of course, season and weather on activity patterns of bats makes detailed comparisons from different areas tenuous. Inasmuch as we lack detailed analyses of activity patterns of bats from any area
(with the possible exception of Nyholm's, 1965, data from some species of *Myotis*), a comprehensive understanding of the situation is presently unrealistic.

Similarly, other than anecdotal observations, there are few data on the effects of weather on the activity of Phyllostomatidae. Tamsitt and Valdivieso (1961) reported a strong inhibiting effect of moonlight on bat activity in Costa Rica, but this was not observed by LaVal (1970), who noted that his mist nets had been set in closed forest, whereas Tamsitt and Valdivieso (1961) had been working in more open situations. Crespo et al. (1972) found a strong inhibiting effect of moonlight on the activity of *Desmodus rotundus*. Other studies have documented the effects of moonlight on bat activity (Erkert, 1974; Turner, 1975), which may be related in some areas to the threat of predation (Fenton and Fleming, 1976; Fenton et al., n.d.). However, responses to possible predators is not a uniformly tenable explanation of the effects of moonlight on the activity of bats. Wimsatt (1969) suggested that heavy precipitation had a suppressing effect on foraging activity of *D. rotundus*, and pointed out the need for detailed work on the effects of local environmental conditions on the activity of bats.

Interpretation of nightly activity patterns and comparisons of activity between sympatric taxa also must consider competitive strategies of resource use. Horizontal and vertical patchiness of habitat (including food and roost sites) probably are important parameters selecting for a reduction in interspecific competition. Vertical stratification of Neotropical bat faunas has been noted by Handley (1967), McNab (1971), and Fenton (1972). For example, among phyllostomatids, *Vampyressa bidens* and *Artibeus lituratus* were more commonly taken in canopy sampling than at ground level, whereas the reverse was true of *Carollia subsulata* and *C. perspicillata* (Handley, 1967). Before reliable temporal comparisons of different species can be made, vertical sampling must be undertaken in a variety of habitats.

The sensitivity of bats to disturbance is the main drawback to studies of bat activity that involve capture and marking of animals (either by banding or punch marking—Bonaccorso and Smythe, 1972). This is clearly reflected in the band recoveries reported by LaVal (1970) and Fleming et al. (1972), and further accentuated by our own experiences in Puerto Rico. Over four nights in May 1973, a total of 314 phyllostomatids was banded at Aguas Buenas Cave in Puerto Rico (168 *Artibeus jamaicensis*, 40 *Monophyllus redmani*, 80 *Brachyphylla cavernarum*, and 26 *Erophylla bombifrons*) and during this same period a total of 55 band recoveries was made (14.3 per cent of the total banded).

Remote sensing systems have been used to monitor the activity of some bats that use high intensity echolocating cries (Fenton et al., 1973). This approach avoids disturbance to the bats, but is not particularly useful for most phyllostomatids, which are low-intensity echolocators. Photocells, photographic apparatuses, and thermister sensors may provide means of remote monitoring of phyllostomatid activity and thus permit analysis of the effects of various environmental parameters on the activity of these bats without introducing biases resulting from disturbance.

The tendency of some bats to use alternate roosts—as reported for *Desmodus rotundus* by Wimsatt (1969) and *Erophylla sezekorni* by Goodwin (1970)
—further complicates the problem of the impact of disturbance on roost-oriented studies (Turner, 1975). Knowledge of the location of alternate roosts has definite survival value for bats, because it permits them to vacate roosts that are temporarily or permanently rendered unsuitable in favor of roosts that have not been jeopardized.

**Seasonal**

The seasonal movements (or migrations) of bats long have been of interest to biologists (see Allen, 1939), but most knowledge about them has been obtained in the temperate regions of the northern hemisphere and concerns rhinolophids, vespertilionids, and a few molossids. (Allen, 1939; Brosset, 1966; Leen and Novick, 1969; Griffin, 1970). Some Pteropodidae in various parts of their ranges, but particularly in eastern Africa and in Australia, have been shown to migrate, but the Phyllostomatidae are conspicuous by their absence from the roster of migratory bats.

Anderson (1969) suspected migration by *Macrotus waterhousii* (= *M. californicus*, part), and their seasonal absence from the American Southwest led Barbour and Davis (1969) to suggest migration for *Leptonycteris nivalis*, *L. sanborni*, and *Choeronycteris mexicana*. There is now evidence that some nectarivorous species (for example, *L. sanborni*) return year after year to the same summer colony (Hayward and Cockrum, 1971) and that seasonal movements in these species are probably in response to the flowering seasons (Leen and Novick, 1969). Davis (1945) reported declines in numbers of *Carollia perspicillata*, *Anoura geoffroyi*, and *Desmodus rotundus* from October through December in Brazil. Greenhall (1956) suggested that similar declines reflect shifts of populations in response to exhaustion of local food supplies. Local migration in response to reduced flower availability is characteristic of nectar-feeding birds throughout the world (Wolf, 1970; Keast, 1968) and similar movements can be expected to occur in nectar-feeding phyllostomatids. Why such movements may be more characteristic of flower feeders than frugivorous kinds is in the ephemeral nature of flowers as compared to fruits (Leck, 1972).

The use of multiple roosts also may account for local shifts in the distribution of bats. Wimsatt (1969) pointed out that use of alternate roosts presented an adaptive advantage to *Desmodus rotundus* because of the restricted water budget of vampires. Local population shifts by this species to areas near food resources would concurrently lower evaporative water loss related to movements to and from the roosts, and, for the same reason, reduce levels of food consumption. We suspect that strategies employed by other phyllostomatids throughout their ranges will involve local, latitudinal, and altitudinal displacements.

The absence of marked migrations by phyllostomatids stands in sharp contrast to the situation as it is known for some pteropodids, which is obviously a function of at least size and habitats. The pteropodids for which migration is known are large and tend to form conspicuous “camps,” which makes them easy to observe. The generally smaller and more secretive phyllostomatids are considerably less conspicuous.
(with the possible exception of Nyholm's, 1965, data from some species of *Myotis*), a comprehensive understanding of the situation is presently unrealistic.

Similarly, other than anecdotal observations, there are few data on the effects of weather on the activity of Phyllostomatidae. Tamsitt and Valdivieso (1961) reported a strong inhibiting effect of moonlight on bat activity in Costa Rica, but this was not observed by LaVal (1970), who noted that his mist nets had been set in closed forest, whereas Tamsitt and Valdivieso (1961) had been working in more open situations. Crespo et al. (1972) found a strong inhibiting effect of moonlight on the activity of *Desmodus rotundus*. Other studies have documented the effects of moonlight on bat activity (Erkert, 1974; Turner, 1975), which may be related in some areas to the threat of predation (Fenton and Fleming, 1976; Fenton et al., n.d.). However, responses to possible predators is not a uniformly tenable explanation of the effects of moonlight on the activity of bats. Wimsatt (1969) suggested that heavy precipitation had a supressing effect on foraging activity of *D. rotundus*, and pointed out the need for detailed work on the effects of local environmental conditions on the activity of bats.

Interpretation of nightly activity patterns and comparisons of activity between sympatric taxa also must consider competitive strategies of resource use. Horizontal and vertical patchiness of habitat (including food and roost sites) probably are important parameters selecting for a reduction in interspecific competition. Vertical stratification of Neotropical bat faunas has been noted by Handley (1967), McNab (1971), and Fenton (1972). For example, among phyllostomatids, *Vampsyressa bidens* and *Artibeus lituratus* were more commonly taken in canopy sampling than at ground level, whereas the reverse was true of *Carollia subrufa* and *C. perspicillata* (Handley, 1967). Before reliable temporal comparisons of different species can be made, vertical sampling must be undertaken in a variety of habitats.

The sensitivity of bats to disturbance is the main drawback to studies of bat activity that involve capture and marking of animals (either by banding or punch marking—Bonaccorso and Smythe, 1972). This is clearly reflected in the band recoveries reported by LaVal (1970) and Fleming et al. (1972), and further accentuated by our own experiences in Puerto Rico. Over four nights in May 1973, a total of 314 phyllostomatids was banded at Aguas Buenas Cave in Puerto Rico (168 *Artibeus jamaicensis*, 40 *Monophyllus redmani*, 80 *Brachyphylla cavernarum*, and 26 *Erophylla bombifrons*) and during this same period a total of 55 band recoveries was made (14.3 per cent of the total banded).

Remote sensing systems have been used to monitor the activity of some bats that use high intensity echolocating cries (Fenton et al., 1973). This approach avoids disturbance to the bats, but is not particularly useful for most phyllostomatids, which are low-intensity echolocators. Photocell, photographic apparatus, and thermister sensors may provide means of remote monitoring of phyllostomatid activity and thus permit analysis of the effects of various environmental parameters on the activity of these bats without introducing biases resulting from disturbance.

The tendency of some bats to use alternate roosts—as reported for *Desmodus rotundus* by Wimsatt (1969) and *Erophylla sezekorni* by Goodwin (1970)
Perhaps more significant, however, than size and roosting habits, are the differences in climate between South and Central America and Africa and Australia. Keast (1969) provided a convenient comparison of these three areas: whereas 32 percent of South and Central America is rainforest, this habitat accounts for 10 per cent and 5 per cent, respectively, of the area of Africa and Australia. Habitats in which marked seasonal fluctuations occur (with resultant seasonally available food sources) are more conducive to the evolution of migratory patterns than are habitats with less drastic fluctuations.

Climatic fluctuations also may account for the higher diversity of fruit and nectar-feeding bats in the Neotropics (relative to the Old World tropics). The larger size of the Pteropodidae (relative to the Phyllostomatidae) may reflect migratory habits because movement over long distances is proportionally less costly (energetically) for larger as opposed to smaller organisms (Schmidt-Nielsen, 1972; Thomas and Suthers, 1972; Thomas, 1975).

Homing

Griffin’s (1970) review of studies of homing by bats included one phyllostomatid. Williams et al. (1966) and Williams and Williams (1967, 1970) used radio tracking to examine homing by Phyllostomus hastatus and showed that bats displaced more than 30 kilometers from their homes were less effective at returning there than those displaced shorter distances. These studies also demonstrated the importance of visual cues to homing in P. hastatus. Banding studies have indicated homing by Macrotrus californicus (Bradshaw, 1961; Davis, 1966) and Leptonycteris sanborni (Hayward and Cockrum, 1971).

The whole question of homing in bats was succinctly addressed by Wilson and Findley (1972) who, after examining the available evidence, including the aforementioned studies of Williams and colleagues, concluded that no one had demonstrated other than random movements by displaced bats. We concur with this opinion and with the importance of having information concerning the familiarity of bats with the area involved (for P. hastatus, up to 20 kilometers from home—Williams and Williams, 1970).

The size of the familiar area is greatly influenced by the roosting habits of the bats involved and, as indicated by Fleming et al. (1972), by the size of the bat. Future studies involving displacements of bats from their home roosts probably will demonstrate that larger bats and bats that form large colonies will have proportionally larger spatial areas of familiarity than small or solitary bats. Migratory species such as Leptonycteris nivalis, L. sanborni, Choeronycteris mexicana, and Macrotus californicus will have a greater degree of spatial familiarity than sedentary species of the same size.

Using rates of recovery of marked individuals, LaVal (1970) suggested that Phyllostomus discolor, Carollia brevicauda, and C. castanea (for which he obtained high recovery rates) may have smaller home ranges than species for which he had low recovery rates, such as Artibius jamaicensis, Glossophaga commissaris, and Uroderma bilobatum. Because body size or colony size (or both) generally reflect resource requirements and distribution of resources, it is clear that
the local and geographic differences in areas of familiarity will in part be a function of resource distribution and density. Present agricultural practices and high cattle densities in some areas of the Neotropics may select against a large familiar area for bats using such artificial concentrations of food resources (for example, *Desmodus rotundus*).

**Behavior**

**Sensory**

The eyes of phyllostomatids probably serve regular complex visual functions (Chase and Suthers, 1969), such as surveillance for predators (Suthers, 1970), distance orientation (Williams *et al.*, 1966), and the location of feeding areas (Williams and Williams, 1970). Suthers (1970) postulated that passive visual surveillance by a resting bat may function to permit it to select visually important events before making a more detailed acoustical investigation. The relative importance of visual as opposed to acoustical information in the responses of phyllostomatids is not well understood, but probably depends upon light conditions (as it does for *Rousettus sp.*) and the general circumstances (Manske and Schmidt, 1976). The importance of vision in surveillance for predators also is suggested by some anatomical features such as the transparent dactylopatagium minus of some phyllostomatids (Vaughan, 1970).

The hypothesis that vision is important in orientation and feeding is supported from experiments conducted by Williams and colleagues (Williams *et al.*, 1966; Williams and Williams, 1967, 1970) and from theoretical constraints relating to the relatively short effective range of echolocation (Griffin, 1958, 1971; Suthers, 1970; Fenton, 1974).

Well-developed vomeronasal organs and associated olfactory bulbs as reported by Schneider (1957), Mann (1961), and Suthers (1970) and anecdotal observations indicate well-developed olfactory senses in the Phyllostomidae. *Phyllostomus hastatus* can locate fruit hidden from view (Mann, 1961) and the sniffing behavior of *Desmodus rotundus* before licking and biting prey (Greenhall, 1972; Schmidt, 1973) points to the importance of olfaction. The acute odor discrimination shown by *D. rotundus* probably permits it to detect differences between breeds of cattle (Schmidt, 1973). Olfaction may be equally important for nectar and pollen-feeding bats; Baker (1973) noted that one of the characteristics of flowers visited by bats is a sour smell. Recent comparisons of the olfactory systems of some phyllostomatids with those of other bats (Bhatnagar, 1975; Bhatnagar and Kallen, 1974, 1975) further emphasizes the importance of odor in the lives of bats.

**Intraspecific**

Phyllostomatids show a variety of roosting habits with respect to numbers of individuals occupying a roost. Estimates of colony size vary considerably and have usually been based on visual counts during emergence or directly in roosts under low light levels (usually after the bats have been disturbed). Some phyllosto-
matids appear to roost alone or in small groups (for example, *Micronycteris megalotis*, *M. minuta*, *M. hirsuta*, *M. brachyotis*, *Lonchorina aurita*, *Tonatia sylvicola*, *Tonatia bidens*, *Phyllostomus elongatus*, and *Artibeus phaeotis*—Goodwin and Greenhall, 1961; Leen and Novick, 1969; Tuttle, 1970; Goodwin, 1970). Others are sometimes found in small aggregations or on other occasions in large colonies (for example, *Carollia perspicillata*—Pine, 1972; *Phyllostomus hastatus*—Williams and Williams, 1970; *Artibeus jamaicensis*—Leen and Novick, 1969), whereas still others appear to occur only in large aggregations (such as *Brachyphylla cavernarum* in Puerto Rico). The size of the roost may exert an important limiting factor on the size of the colony, as is indicated by the occurrence of larger aggregations of individuals of some species in artificial structures than are known from natural roosts (*Desmodus rotundus*, for example). Species that regularly roost in large rooms in caves probably are more commonly encountered in large aggregations than are those that roost in cavities of trees.

Aside from observations on colony or cluster size, little has been published on intraspecific behavior of bats in colonies. Some evidence is available indicating that there are social units of groups within colonies and that these may play important roles in reproduction, food gathering, and orientation. It seems logical to expect more elaborate social interactions in gregarious than in solitary species (as in some Canidae—Kleiman, 1972).

Williams and Williams (1970) reported “coherent social groups” for *Phyllostomus hastatus* ranging from five to 20 individuals and consisting of groups of both sexes with one or more dominant males. Bradbury (n.d.) has provided more information on the social groups of *Phyllostomus hastatus* and *P. discolor*.

*Phyllostomus hastatus* forms large colonies in caves and the population in any roost site consists of harems (25 to 30 females per male) and nonharem juveniles and males. Harem males protect their females and perform elaborate displays when another male approaches. To feed, females leave the harem singly and in twos, whereas the male departs when the number of remaining females is at its lowest, and remains away for only a short time. Removal of a harem male results in his replacement by another male with little or no turnover among the harem females.

*Phyllostomus discolor* establishes colonies in hollow trees and again the populations include harem (one to 12 females per male) and nonharem bats. However, harem composition in this species is more variable than in *P. hastatus*, with some females being regularly present in the harem and others somewhat nomadic. Female *P. discolor* are more aggressive than female *P. hastatus* and are actively involved in maintaining the integrity of the harem. A bat returning to a harem group performs elaborate displays, which include tactile, olfactory, and vocal cues, to gain admission to the group. Allogrooming by members of harems is common.

In both species, the nonharem groups may be quite stable in their composition and tend to be more nomadic than the harems. F. Potter (personal communication) has observed harem structures in *Carollia perspicillata* and it seems likely that this situation may be common in phyllostomatids that aggregate in large numbers.
Departures of groups of bats from roosts (for example, *Leponycteris sanborni*—Hayward and Cockrum, 1971; *Desmodus rotundus*—Wimsatt, 1969, and Greenhall et al., 1971) also suggest the presence of social groupings. Similar observations have been reported for other bats (Rhinolophidae—Mohres, 1967; Vespertilionidae—Hall and Brenner, 1968, and Dwyer, 1970) and indicate that this behavior may be widespread in the Chiroptera.

Segregation of females into discrete groups prior to parturition and until the young are weaned has been reported for *Artibeus jamaicensis* (Leen and Novick, 1969) and implied by the observations of Jones et al. (1973) for *Desmodus rotundus*. The observations of Leen and Novick (1969) for *A. jamaicensis* and those of Schmidt (1973) for *D. rotundus* indicate that olfactory cues may be important in social organization and mother-young relationships. However, other information, some of it from phyllostomatids, suggests that vocalizations are important in interactions between females and their young (Brown, 1976; Gould, 1975a, 1975b; Gould et al., 1973; Schmidt and Manske, 1973) and in a variety of other intraspecific contexts (for example, Bradbury and Emmons, 1974; Wickler and Siebt, 1976).

Evidence from other mammals strongly suggests that bats will be shown to exhibit various patterns of social dominance within groups. Places where these interactions may be expected are roosts and common feeding sites. Laboratory observations of Schmidt and Greenhall (1972) on the interactions of feeding vampires support this suggestion; they suggested that certain “dominant” animals in a group feed first and that, while they are feeding, they chase off other individuals as in some carnivores (Ewer, 1973). Similar interactions will certainly be reported from situations where food resources are localized (for example, concentrations of ripe fruit). However, species that are nectarivorous or carnivorous (including insectivorous) where food resources are diffuse are more apt to demonstrate territorial interactions than dominance hierarchies at feeding sites (see, for example, Baker’s, 1973, observations of trap-lining in some nectar-feeding bats).

The whole subject of sexual behavior and the details of mother-young interactions are poorly known, and we were unable to find any published information on this subject for phyllostomatids.

**Interspecific**

Various species of bats are known to share the same roosts, but in some cases, use of a roost by one species will result in its being abandoned by another species (for example, *Artibeus jamaicensis* and *Molossus* sp.—Leen and Novick, 1969). Often several species of bats may roost in one structure (tree, cave, building, and so forth) and not come into physical contact with one another except possibly at times of arrival or departure. There is little information on interspecific behavior of bats, although biting is presumed to occur and possibly be involved with the epidemiology of rabies virus (Constantine, 1970). As with intraspecific interactions, it is likely that interspecific altercations will occur where food resources or roosts are localized or limited. The work of Colwell (1973) on the interactions of some hummingbirds suggests that similar interspecific behavior patterns may
be described for nectar-feeding bats, especially in the light of the trap-lining nature of the visits of some of these bats to flowers.

Miscellaneous

Several species of bats are known to carry their young with them away from their roosts. Tamsitt and Valdivieso (1965) observed this for Artibeus lituratus in Colombia, but Fenton (1969) found no evidence of it for A. jamaicensis in Puerto Rico. In a review of the literature on this subject, Davis (1970) reported that some phyllostomatids had been found to transport their young after disturbances in their roosts (Macrotus californicus, Choeronycteris mexicana, Leptonycteris sborni), whereas others would do this even in the absence of disturbance (Glossophaga soricina and Leptonycteris sborni). It is likely that species that use alternate roosts will be found to transport their young more regularly than those that do not, but certainly the presence of disturbance is an important consideration in this regard.

Tuttle (1970) reported that the vocalizations of a captured Mimon crenulatum attracted other individuals of the same species to the site of capture, and similar effects were elicited by the “distress calls” of several species of bats. At present we have no definite information as to which frequencies of bat cries are important in “distress” or other calls that evoke responses from other individuals. Recent work has indicated that some bats respond preferentially to “distress” calls of conspecifics (Fenton et al., 1976).

Further Research

From the preceding discussion, it should be obvious that almost any aspect of the movements and behavior of phyllostomatids will provide productive topics for research. Documentation of the daily and seasonal patterns of the activity of these bats with respect to various environmental parameters such as meteorological conditions, lunar cycles, and seasonal changes in the abundances of food (from insects to fruit) should be a primary goal. At the same time, the whole spectrum of intra and interspecific behavior patterns (territoriality, partitioning of food and roost resources, reproductive, and mother-young behavior) requires close attention.

As we have pointed out, many of these subjects may now be addressed with the aid of electronic equipment (notably for telemetry and observation at low light levels) and a reasonable knowledge of the phyllostomatids that occur in different areas. This situation is reflected by a variety of recent studies ranging from roosting behavior (Timm and Mortimer, 1976), through feeding and orientation behavior (Howell 1974a, 1974b; Fleming et al., n.d.), to detailed studies of specific bats (Turner, 1975).

The programs of recent North American Symposia on Bat Research indicate that work on some of these subjects is in progress for some species. We expect that the next few years will see the publication of results that will greatly advance our knowledge of the movements and behavior of bats in general and the Phyllostomatidae in particular.
LITERATURE CITED


KLEAST, A. 1968. Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. Emu, 67:159-209.


KLEIMAN, D. G. 1972. Social behavior of the maned wolf (Chrysocyon brachyurus) and bush dog (Speothos venaticus): a study in contrast. J. Mamm., 53:791-806.


