

THE CONSEQUENCES OF TIMBER EXPLOITATION FOR BAT COMMUNITIES IN TROPICAL AMERICA

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The wealth of biological diversity in tropical forest ecosystems owes its existence to mutual relationships between species (Gilbert 1980). Some Neotropical forest bats (*Chiroptera*) are the mobile links in these interrelationships, benefiting plant species that depend on their ecological services for successful reproduction and seed dispersal. The loss of such links may have cascading effects on the health and productivity of tropical forest systems (Terborgh 1986b; Johns 1992a). In Venezuela, for example, approximately 1.3 million hectares of forest were cut in the western lowlands between 1950 and 1975, leading to the severe degradation of the three most important forest reserves north of the Orinoco River (Veillon 1976; Catalán 1993). The long-term ecological ramifications of these actions are virtually unknown, and the capacity of these reserves to recover to a state where they can once again provide a wide range of ecological and social services remains in doubt. Understanding this complex set of interrelationships is a major challenge confronting forest ecologists and resource managers, making management planning for the sustainable use of resources a difficult process (Whitmore 1980; WRI 1990; Thiollay 1992; Mason 1996; Ochoa 1998).

Planning and careful implementation of timber-harvesting practices, in an effort to minimize the impacts of logging on forest biodiversity and ecological processes, seldom occur in tropical forests. This failing is, in part, a function of our limited understanding of wildlife and their habitat requirements and the costs involved in obtaining such information (Mondolfi 1976; Ochoa 1992; see chapter 6). There are currently few examples of reasonably complete lists of vertebrates that inhabit these exploited areas (Voss and Emmons 1996), and even fewer studies of the effects of timber extraction on these animals (see other chapters in this section).

In this chapter, we explain the taxonomic and functional structure of bat communities in Neotropical lowland forests. We provide a synthesis of the available information regarding the effects of timber exploitation on these bat communities, and propose some management and research priorities that will help to safeguard the biological diversity of Neotropical forest bats in production forest landscapes.

Composition and Structure of the Bat Communities in Neotropical Rain Forests

Bat species represent approximately 50 percent of the mammal fauna associated with lowland Neotropical humid forest ecosystems, where between 35 and 65 species are commonly found per major forest type (i.e., Handley 1976; Ibáñez 1981; Mok et al. 1982; Webster and Jones 1984; Jones et al. 1988; Brosset and Charles-Dominique 1990; Ochoa et al. 1988, 1993; Ascorra et al. 1991, 1993; Medellín 1993, 1994, Pacheco et al. 1993; Voss and Emmons 1996). A recent survey carried out in Venezuelan Guayana found over 78 species coexisting in the Imataca Forest Reserve (Ochoa 1995; Ochoa 1997a). It is estimated that between 90 and 110 sympatric species exist in the lowland forests of the Amazon Basin (Voss and Emmons 1996). These communities show a similar taxonomic composition at supraspecific (families and genera) levels (see table 7-1). Inherent limitations in the survey methodologies, however, and a lack of taxonomic specialists mean that most surveys are incomplete and biased in their listing of the actual assemblages (Handley 1967; Voss and Emmons 1996). Only bat species occupying the lower strata of the forest are well represented in samples, while the majority of species in the Molossidae family—which are found above the canopy—are absent (see box 7-1).

Box 7-1 *Beyond mist-nets: what the rest of the bats can tell us about forests. (Bruce Miller)*

Determining which species are truly rare is a necessary first step before an assessment can be done of the impact of logging on Neotropical bat communities. Until recently, bat surveys in the Neotropics have been biased by traditional sampling methods—primarily mist-netting—towards the readily captured leaf-nosed bats (*Phyllostomidae*). Consequently, more is known of the phyllostomids than other families of bats in the Neotropics (Kalko 1997; see this chapter).

The important ecological role that leaf-nosed bats (*Phyllostomidae*) play in seed dispersal and pollination in the Neotropics is widely acknowledged (Findley 1993; see this chapter). The insectivorous bats—primarily the non-*phyllostomids*—play an equally important role by controlling leaf herbivores, stem and shoot borers, and seed predators. As this important component of Neotropical bat communities has not previously been adequately sampled, we are uncertain what species compositions or population levels exist in most forests.

Double-frame harp traps can augment mist-netting surveys by capturing bats that use echolocation to avoid nets (LaVal and Fitch 1977; Voss and Emmons 1996). These traps are double-framed arrays of vertical monofilament lines spaced approximately 2.5 cm apart (with the lines offset). The echolocating bats do detect these lines, but because they are adept at flying through clutter, they simply tilt and fly between the lines of the first panel where they strike the second set of offset lines and fall unharmed into a collection bag under the trap. Although harp traps provide a better means of sampling non-*phyllostomid* bats than mist-nets, they still collect too few samples of many species (Miller 1998).

The identification of free-flying bats using their unique vocal signatures (Kalko 1995; O'Farrell 1997; O'Farrell and Gannon 1999; O'Farrell and Miller 1997, 1999; O'Farrell et al. 1999a, b) has allowed the greatest insight into the non-*phyllostomid* community (Kalko 1995, 1997; Kalko et al. 1996; Miller 1998; H. Schnitzler and E. Kalko, unpublished data). To obtain the highest quality, least-biased inventories, acoustic identification should be combined with other sampling methods such as harp traps and mist-nets (Kalko 1997; Miller 1998; O'Farrell and Gannon 1999).

From October 1995 through October 1997, new acoustic sampling techniques were developed during a study of the non-*phyllostomid* bat community in northwestern Belize. The tropical hardwood forests of the study site reflect more than 150 years of light, selective timber extraction. This extraction ended in the mid-1960s, and most trees in the canopy today are old-growth species with substantial regeneration in the undisturbed understory (Brokaw and Mallory 1993). Nine vegetation habitats (Wright et al. 1959) were surveyed using harp traps and new acoustic methods to evaluate habitat preferences of many species for which little ecological information previously existed. As a result, two species considered rare—Thomas's bat, or shaggy bat (*Centronycteris centralis*) (Gardener et al. 1970; Timm et al. 1989) and Van Gelder's bat (*Bauerus dubiaquercus*) (Engstrom et al. 1987)—were found to be among the most common species in many forest habitats. This implies that rarity, as defined from studies using mist-nets, may be an artifact of biased sampling and not of actual low population numbers (Gaston 1994; Kalko et al. 1996).

In the same study noted above, it was also discovered that *C. centralis*, *Natalus stramineus* (Mexican funnel-eared bat), *B. dubiaquercus*, and *Myotis elegans* (elegant myotis) appeared restricted to forested areas, suggesting these species may serve as indicators of mature, closed-canopy forests. At a finer level, *C. centralis* was abundant and *M. elegans* common in one forest type (Sapote-Silion-Mahogany). In another forest type (Sapote-Ramon-Spice), the reverse pattern was found. As both of these species are suspected tree roosters (Timm et al. 1989; LaVal and Fitch 1977), it may be that a yet unknown tree species association exists. This

suggests that these bats may serve as indicators of habitat at a much finer level of detail than previously known in two very similar forest types.

In most production forests, timber extraction has profound effects on forest structure and bat roost sites (Crampton and Barclay 1996; Grindal 1996; Perdue and Steventon 1996; see chapter 2). In Australia, logging was found to have its greatest impact at the microhabitat level for many bat species (Crome and Richards 1988; Crome et al. 1996). In northwestern Belize, bat species that prefer medium to dense understory disappeared from survey sites after brushing (<2 m width) was carried out along trails. Although these species returned to the sites after understory vegetation regenerated, the apparent sensitivity to very localized structural changes suggests that larger scale changes that result from logging may have management implications. Finally, the impact herbivorous insects can have on tropical forests is significant (Lowman 1984, 1991, 1992a,b; Aide and Zimmerman 1990; Gerhardt 1993; Dial and Roughgarden 1995). The extent of damage from herbivorous insects can be related to the presence or absence of insectivores (Marquis and Whelan 1994). It follows then, that if habitat modification decreases the aerial insectivore component of the bat community, the resulting increase in deleterious insects could have adverse effects on forest resources for years or even decades.

Using multiple survey methods, a more complete picture emerges of bat species composition in tropical forests, and a better understanding is gained of the often subtle differences in species-habitat associations. As these new methods are implemented in previously surveyed areas, species considered rare or yet undocumented are likely to be found. Once we understand the *where* and *why* of species occurrence, we will be in a better position to evaluate the impacts of anthropogenic habitat change on bat communities and the ecological functions they perform. The richness of coexisting species may be partially explained by the *guild* or functional structure of bat communities. Bat communities are organized in large, independently functional categories (guilds) related to principal food sources (Bonaccorso 1979; Fleming and Heithaus 1981b): insectivores, frugivores, nectarivores, carnivores, piscivores, and sanguivores (vampires) (McNab 1971; Wilson 1973; LaVal and Fitch 1977; Bonaccorso 1979). Variations also exist between species found in the same guild, in terms of methods of obtaining food, size differences of certain anatomical features, and the use of flying space. These characteristics allow greater resolution—or niche partitioning—of each assemblage (e.g., Handley 1967; Smith and Genoways 1974; Carranza et al. 1982; Humphrey and Bonaccorso 1979; Humphrey et al. 1983; Soriano 1983, 1985; Ascorra and Wilson 1992).

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TABLE 7-1 Taxonomic Composition of Several Neotropical Rain Forest Bat Communities

Locality	Bat Families and Subfamilies													Total Species
	Emb	Noc	Mor	Phyllostomidae					Nat	Fur	Thy	Ves	Mol	
				Phy	Glo	Car	Ste	Des						
La Selva (Costa Rica) ^a	8	2	2	19	6	3	13	1	0	1	1	7	2	65
BCI (Panama) ^a	7	2	2	16	3	3	16	1	0	0	2	6	6	64
Primary forest (French Guiana) ^b	7	0	3	27	6	3	18	1	0	1	2	4	6	78
Sn. Juan Manapiare (Vzla) ^c	10	1	1	19	6	2	16	2	0	0	0	5	6	68
Imataca (Venezuela) ^d	9	2	1	18	8	3	20	1	0	0	1	6	9	78

Abbreviations: Emb. = Emballonuridae, Noc. = Noctilionidae, Mor. = Mormoopidae, Phy. = Phyllostominae, Glo. = Glossophaginae, Car. = Carolliinae, Ste. = Stenodermatinae, Des. = Desmodontinae, Nat. = Natalidae, Fur. = Furipteridae, Thy. = Thyropteridae, Ves. = Vespertilionidae, Mol. = Molossidae

SOURCE: ^aVoss and Emmons 1996, ^bBrosset et al. 1996, ^cHandley 1976, ^dOchoa 1996.

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At least two general foraging strategies can be clearly differentiated in the most well represented trophic groups—the insectivores and frugivores. Insectivorous bats may be classified as either aerial insectivores, which capture their prey in the air while flying, or foliage gleaners, which pluck their prey from surfaces. Representatives of the former can be stratified vertically in the forest according to their preferred area of activity, including the area above the forest canopy. High-flying species may show a marked reduction in the width of the wings—a characteristic found in members of the Molossidae family (which show a flying behavior similar to that of swifts and swallows)—making them more efficient in the capture of prey from open spaces above the forest canopy (Fenton 1972, 1990; Norberg and Rayner 1987). In contrast, foliage gleaners detect and capture invertebrates that are sitting on the ground or on leaves. Bats using this strategy usually have elongated ear

pinnae, which allow more efficient detection of sounds made by prey (Norberg and Rayner 1987; Fenton 1990).

Amongst fruit eaters, nomadic frugivores consume fruits from plant species with relatively wide-spaced individuals and fairly high fruit production during short periods of time. Variations in fruit patterns may cause the movement of nomadic frugivore populations to new areas of the forest when resources become scarce (Soriano 1983). Morrison (1979) showed that the common large fruit-eating bat (*Artibeus jamaicensis*) can fly up to ten kilometers in one night between its refuge and its foraging area. This temporal variation often requires the near-daily identification of new roost sites, which are usually found in the foliage of large trees. In contrast to these nomads, sedentary frugivorous bats have fairly fixed search itineraries every night, and prefer fruits of plant species that produce continuously but offer only a few ripe fruits per plant each night. Species with more sedentary strategies inhabit proportionally smaller fixed areas and their refuges are more stable, such as hollow tree trunks and caverns (see photo 7-1). Members of the Carollinae and Phyllostominae subfamilies, and the genus *Sturnira* (Stenodermatinae) represent this group (Soriano 1983, 1985). These different feeding habits and strategies make each group sensitive to the environmental changes related to its particular requirements. The consequences of the effect of timber exploitation on each functional component of the bat community may be very different..

Effects of Timber Exploitation on Bat Communities

The activities involved in selective exploitation of timber species, such as the use of heavy machinery to construct roads, affect the structure and climate within forests (Uhl and Guimaraes 1989; Johns 1992a; Thiollay 1992; Mason 1996; Ochoa 1998). These environmental changes include:

- Complete deforestation of certain areas
- Fragmentation and isolation of intact forest
- Breaks in the continuity of the forest canopy
- Changes in the microclimate beneath the canopy (i.e., luminosity, temperature, humidity)

In extreme cases, the decrease in relative humidity may facilitate forest fires, which in turn causes severe modifications in the composition and structure of the understory and availability of prey populations.



PHOTO 7-1 *Small cavern that serves as refugia for bat species with sedentary strategies. (WCS)*

The wide range of differences between bat guilds, resulting from the different kinds of resources used by each group, makes Chiropterans ideal indicators of environmental disturbance (Fenton et al. 1992). The available information on the effects of timber exploitation on bat communities in Neotropical localities is very scarce, however, with two general trends recognized to date: 1) some species show a negative response to changes in the structure and composition of the forest, and 2) other species in the community show population increases due to a reduction in competition or an increase in preferred resources.

Species Whose Populations Are Adversely Affected by Timber Exploitation

Studies by Brosset et al. (1996) in French Guiana and Ochoa (2000) in the Imataca Forest Reserve (Venezuelan Guayana Region) have demonstrated the local extinction of certain species—and the reduction in guild complexity of bat communities—where trees larger than 40 cm dbh were logged (approximate 5.8 m³/ha harvested). Guild reduction was greater where silvicultural treatments such as *enrichment strips* were established after logging (see table 7-2). The most affected species were the specialized insectivorous and vertebrate pred-

ator species (Kikkawa and Dwyer 1992; Gardner 1977) found in the Phyllostominae subfamily, which seems to have the highest sensitivity to timber exploitation (Fenton et al. 1992; Brosset et al. 1996; Utrera 1996; Ochoa 2000). The abundance of some species appreciably decreases (e.g., the black large fruit-eating bat [*Artibeus obscurus*], small yellow-eared bat [*Vampyressa bidens*], spear-nosed bat [*Phyllostomus elongatus*], and the round-eared bat [*Tonatia saurophila*],) or even disappears (e.g., the false vampire bat [*Vampyrum spectrum*], round-eared bat [*Tonatia sylvicola*], and the woolly false vampire bat [*Chrotopterus auritus*]) in disturbed forests (see photo 7-2). Some Emballonuridae such as the common doglike sac-winged bat (*Peropterix kappleri*) also show similar patterns (Ochoa 2000). These data are in agreement with those of Brosset et al. (1996), who reported the loss of rare species in disturbed areas of French Guiana.

Trees of greatest size are preferentially selected during timber exploitation, which may cause drastic reductions in roost availability for Chiropteran species (i.e., round-eared bats [*Tonatia* spp.], the woolly false vampire bat, the false vampire bat, and the free-tailed bat family Molossidae). This effect may be especially pronounced in regions where the geomorphology does not favor the formation of caverns that offer alternative roost sites. Causes for the reductions of carnivorous and insectivorous Phyllostomid bats have not been completely established. We postulate the joint action of several factors:

- Reduction in the food supply resulting from a numeric decrease or disappearance of prey (mainly invertebrates), which may be affected in their various larval stages by microclimatic changes related to the loss of canopy continuity (Fenton et al. 1992)
- Breaks in the canopy that cause a reduction in specialized fruit and flower availability (Charles-Dominique 1986; Johns et al. 1985; Johns 1988; Uhl and Guimaraes 1989). In some instances these conditions sever interdependent plant-animal links, negatively impacting keystone species of commercial value (i.e., *Inga* spp., *Spondias mombin* and *Ceiba pentandra*) and bat communities in the season of lowest fruit productivity (Fleming et al. 1987; Johns et al. 1985; Johns 1988; Terborgh 1986b; see chapter 6)
- Reduction or elimination of refuges such as holes in trunks or branches due to the felling of trees with diameters greater than 40 cm
- Loss of termite nests (usually constructed in large trees) which are consumed by certain species of Phyllostominae bats

Finally, some very specialized frugivores such as the visored bat (*Sphaeronycteris toxophyllum*), and the wrinkle-faced bat (*Centurio*

TABLE 7-2 Differences in Taxonomic Composition Between Primary and Exploited Forests at Unit V of Imataca Forest Reserve, Venezuela

Imataca Forest Reserve	Bat Families and Subfamilies										Total Species
	Emb	Noc	Mor	Phyllostomidae					Ves	Mol	
				Phy	Glo	Car	Ste	Des			
Primary forest	6	0	1	13	3	3	13	1	3	2	45
Exploited forest	6	2	1	10	3	3	13	1	6	5	50
Enrichment stripes	2	0	1	5	2	3	13	0	0	1	27

Abbreviations: Emb. = Emaballonuridae, Noc. = Noctilionidae, Mor. = Mormoopidae, Phy. = Phyllostominae, Glo. = Glossophaginae, Car. = Carollinae, Ste. = Stenodermatinae, Des. = Desmodontinae, Ves. = Vespertilionidae, Mol. = Molossidae. (Source: Ochoa 2000).

cenex)—as well as some small-sized species of Honduran white bats (*Ectophylla* spp.), and small yellow-eared bats (*Vampyressa* spp.)—are probably affected by disturbances associated with forest management practices such as elimination of understory palms required for tent roosts and/or loss of certain critical foods. Limited information about the natural histories of these species does not allow us to make any definitive conclusions.

Species Whose Populations Are Favored by Timber Exploitation

Bats that appear to be favored by logging include many of the seed-dispersing frugivorous genera (i.e., short-tailed fruit bats [*Carollia*], fruit-eating bats [*Artibeus*], and the yellow-shouldered bats [*Sturnira*] (see photo 7-3a) that are mutualistically associated with pioneer plants (i.e., *Piper*, *Cecropia*, *Solanum*, and *Vismia* genera). This relationship generates a positive feedback effect: the more these plants prosper in an area, the greater the carrying capacity for their associated Chiropteran species (Charles-Dominique 1986; Fleming 1988; Fenton et al. 1992; Kikkawa and Dwyer 1992; Brosset et al. 1996; Utrera 1996; Ochoa 2000). These bats may quadruple their population densities in disturbed sites, as reported by Brosset et al. (1996) in French Guiana. Some of the large species of fruit-eating bats (*Artibeus* spp.) in clearings seem to have a greater influence on seed dispersal of *Cecropia* spp. than most frugivorous birds. These bats typically fly long distances, favoring the colonization of pioneer plant species (Charles-Dominique 1986), and thereby creating a positive feedback mechanism that favors the



PHOTO 7-2 Photographs of select insectivores or predator bat species whose populations are adversely affected by timber exploitation: (top) *Tonatia saurophila*; (bottom) *Phyllostomus elongatus*. (P. J. Soriano)

population growth of these bat species. Similarly, the introduction of cattle to areas of exploited forests that are converted into pastures may serve to supply large additional feeding sources for the vampire bats (see photo 7-3b), leading to increases in their population levels (Johns et al. 1985; Wilkinson 1985; Johns 1988, 1992a; Fenton et al. 1992).

Finally, the loss of continuity in the forest canopy caused by clearing large areas for logging roads gives certain species of flying insectivores—which restrict their activity to the upper layer of the canopy in natural conditions—access to lower forest strata. An increase in prey availability, combined with access to additional water sources, partially explains the positive response exhibited by this group. Some structures, such as logging camps, may also provide alternative refuges for species with more flexible requirements. This is the case for some Emballonuridae and Molossidae, which may roost in or on man-made structures and forage in camp clearings (Brosset et al. 1996; Ochoa 2000).

Protection of Chiropteran Communities in Logged Landscapes

Timber exploitation affects Chiropteran communities by altering the composition and structure of vegetation, availability of food resources, number of refuges, and microclimate (Johns 1992a; Macedo and Anderson 1993; Frumhoff 1995; Ochoa 1997a; see chapter 6). Measures taken to protect bat communities, therefore, should focus on mitigating these disturbance factors.

Of the possible measures for protecting bats in timber production forests, the most important is protecting old-growth areas in forest landscapes destined for timber exploitation (Thiollay 1992; Ochoa 1993; see chapter 23). When selecting these sites, the natural composition and structure of the forest should be considered in an effort to maintain representative areas of preharvest habitat across the managed forest (Lovejoy and Bierregaard 1990; Frumhoff 1995). Corridors of uncut vegetation, such as gallery forests, should connect these *within* landscape refugia, thereby allowing movement between the different protected areas (Johns 1992a; Thiollay 1992; Mason 1996; Ochoa 1993, 1997a; see chapters 21 and 23).

Within areas slated for exploitation, measures must be taken to reduce the impacts of harvesting practices. Selective logging is often very *unselective*, impacting more than 50 percent of the trees in



PHOTO 7-3 Photographs of select bat species whose populations are favored by timber exploitation: (top) the short-tailed fruit bat, *Carollia perspicillata*; and (bottom) the vampire bat, *Desmodus rotundus*. (P. J. Soriano)

exploited stands (Johns et al. 1985; Johns 1992a; Frumhoff 1995; Ochoa 1998). It is, therefore, very important to implement reduced impact-logging procedures (see chapter 21), and to strengthen forest planning that favors a mix of exploited and reserve sites (Frumhoff 1995; see chapter 20), to preserve the integrity of production forest habitat. Such measures should be accompanied by sufficient financial support to guarantee the implementation of basic and applied scientific research programs, designed to:

- Assess the ecological roles (pollination and dispersal) and requirements of individual bat species
- Monitor their activities in recovering stands
- Train technical personnel to translate research findings into improved forest management practices (Johns et al. 1985; Ochoa 1992; see chapters 18 and 19)

Research Priorities for Conserving Forest Bat Communities

Baseline information of bat communities is lacking for most forests. The most complete inventories possible need to be compiled, combining the use of different capture and detection methodologies for sympatric species. With sufficient information, geographical distribution of the Chiropteran species could be generated. These inventories should begin in the regions under greatest forestry use, so that rare, threatened, and sensitive species may be detected and conservation strategies developed.

Surveys of bat communities cannot be made adequately and reliably without resolving the inherent taxonomic problems associated with certain genera (i.e., *Choeromiscus*, *Platyrrhynchus*, and *Molossus*), which are urgently in need of revision (Voss and Emmons 1996). This task cannot be guaranteed without an adequate series of specimens and the support of collections where the voucher specimens are housed. It is of strategic importance to put an aggressive program into practice to stimulate the development of already existing zoological collections and museums in different countries within the region, to create new collections where they are lacking, and to employ appropriate personnel to oversee their administration and conservation.

Although important progress has been made in the knowledge of the diet and habitat requirements of many Chiropteran species found in Neotropical forests, the available information is far from complete (Gardner 1977). Obtaining this information remains a priority—particularly for Phyllostominae species that are sensitive to logging practices, and Glossophaginae and Stenoderminae species that are likely to be potential pollinators or seed dispersers of commercially important timber and non-timber plants. Research based on radio telemetry will allow better knowledge of the movement patterns and home ranges of sensitive species, and the establishment of minimum area requirements for protected areas (Frumhoff 1995). The goal of such an effort is to better understand the links between bats and forest tree species, thereby helping to design restoration plans for degraded areas and sustainable forest management plans for natural forests managed for timber resources.

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