

THE EFFECTS OF LOGGING ON NONVOLANT SMALL MAMMAL COMMUNITIES IN NEOTROPICAL RAIN FORESTS

José Ochoa G. and Pascual J. Soriano

Recent literature on the study of mammal communities in Neotropical rain forests identifies the growing threat to many species (Patterson 1991; Terborgh 1992a, 1992b; Woodman et al. 1995, 1996; Voss and Emmons 1996) as a consequence of increased deforestation rates or degradation of primary forests by unsustainable resource exploitation (Uhl and Vieira 1989; Whitmore and Sayer 1992; Frumhoff 1995; Pinard and Putz 1996; Bryant et al. 1997; Miranda et al. 1998). Among the high levels of diversity that characterize the mammalian fauna in these ecosystems (Emmons and Feer 1990; Chesser and Hackett 1992; Voss and Emmons 1996), some taxonomic groups show a complex adaptive radiation and represent important regulatory elements in forest dynamics (Fleming et al. 1987; Smythe 1987; Emmons and Feer 1990; Terborgh 1992a). Marsupials and small rodents, after bats, represent the dominant fraction of mammals in Neotropical forested areas (Handley 1976; Emmons and Feer 1990; Ochoa et al. 1993; Voss and Emmons 1996), and constitute a major component of ecological processes and animal biomass (Emmons 1984; Robinson and Redford 1989; Janson and Emmons 1990). Very few projects, however, have assessed the ecological impacts of extractive activities on small tropical marsupials and rodents—in contrast to studies of other vertebrate groups (e.g., Wilson and Johns 1982; Johns 1986b, 1988, 1992a; Fenton et al. 1992; Thiollay 1992; Plumptre and Reynolds 1994; Mason 1996; Greiser Johns 1997; see chapters 4, 5, 7–14, and 24). Of those that have occurred on small mammals, most are from Old World localities (e.g., Kemper and Bell 1985; Isabirye-Basuta and Kasenene 1987; Pahl et al. 1988; Laurance and Laurance 1996).

In the Neotropics, there are a limited number of field inventories of small mammal communities (Patterson 1991; Voss and Emmons 1996), and few come from forests influenced by logging (Ochoa 2000). This condition is, in part, due to few researchers in Latin American countries having the taxonomic expertise to examine this topic, as well as few institutions considering this kind of work among their priorities. Even though knowledge of biological resources is fundamental to conservation strategies in this region (Blockhus et al. 1992; WRI et al. 1995), efforts to accomplish this goal lag far behind the wave of economically driven resource exploitation schemes impacting most forested areas (ITTO 1991a; Whitmore and Sayer 1992; Miranda et al. 1998).

This chapter reviews the response of Neotropical small mammals (excluding bats) to timber extraction, based on the available ecological information for this vertebrate group in forested areas and their importance in forest conservation (e.g., Julien-Laferrere and Atramentovitz 1990; Johns 1992a; González-M and Alberico 1993; Ochoa 1997a, 1997b, 2000). Research and management priorities are highlighted for addressing the negative impacts on small mammal communities that are associated with logging practices.

The Geographic, Taxonomic, and Ecological Context of This Chapter

In this chapter, Neotropical small mammals refer to marsupials and small rodents ubiquitously distributed across Central and South America, including their continental islands and the oceanic islands of the West Indies, Galapagos, and Falklands (Hershkovitz 1972). This review, however, is restricted to lowland rain forests (< 600 m) located in the following subregional categories (Voss and Emmons 1996): trans-Andean rain forests, coastal Venezuelan rain forests, Amazonian rain forests, and Atlantic rain forests (see figure 6-1). Included in this group of mammals are the Didelphimorphia (Didelphidae family) and Rodentia (Sciuridae, Geomyidae, Heteromyidae, Muridae, and Echimyidae families) orders (see table 6-1). These families comprise approximately 2.5 percent of the mammalian species recorded in Neotropical lowland rain forests (Handley 1976; Ochoa et al. 1993; Ochoa 1995; Voss and Emmons 1996). The taxonomic nomenclature follows Wilson and Reeder (1993), with several exceptions drawn from Voss and Emmons (1996).

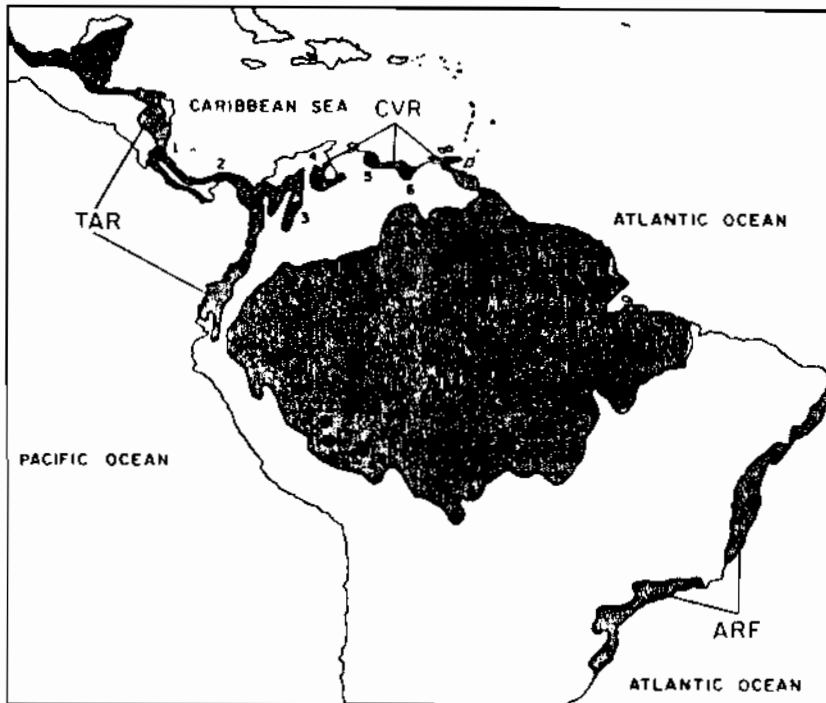


FIGURE 6-1 Geographic distribution of Neotropical lowland rain forests. Nomenclature for the subregions is presented in Table 6-1. Localities are: 1—La Selva and vicinity, Costa Rica; 2—Barro Colorado Island, Panama; 3—Foothills on Western Llanos of Venezuela; 4—Maracaibo Basin, Venezuela; 5—Foothill in the border of Falcon and Yaracuy States, Venezuela; 6—Guatopo National Park, Venezuela; 7—Imataca Forest Reserve, Venezuela; 8—Kartabo, Guyana; 9—Arataye, French Guiana; 10—Minimal Critical Size Ecosystems Reserves, Brazil; 11—Xingu, Brazil; 12—Balta, Peru; 13—Cocha Cashu, Peru; 14—Amazonian Cuzco, Peru.

To describe the structural patterns of small mammal communities in Neotropical rain forests and their responses to the ecological impacts of logging, each species was distinguished by its trophic strategy and principal foraging strata within a forest (Handley 1976; Charles-Dominique et al. 1981; Alho 1982; Robinson and Redford 1986; Ochoa et al. 1988; Emmons and Feer 1990; Janson and Emmons 1990; Nowak 1991; Maberley 1992; Ochoa, 2000). Eight guilds were identified (see table 6-1), including four based on diet (frugivores, herbivores, predators, and omnivores) and four based on forest strata use (arboreal, semiarboreal, terrestrial, semiaquatic). For some

TABLE 6-1 Genera of Nonvolant Small Mammals Recorded
in Neotropical Lowland Rain Forests (continued)

	Subregion										Ecological Guild	
	TAR			CVR			AMZ			ARF		
	a	b	c	d	e	f	g	h	i	j		
<i>Isthmomys</i> ^a												HO/Te
<i>Melanomys</i> ^b	1			1								FO/Te
<i>Neacomys</i> ^a					1	1	1	1	2			PO/Te
<i>Nectomys</i>			1	1			1	1	1	1		PO/Sa
<i>Neusticomys</i> ^c							1		1			P/Sa
<i>Nyctomys</i>	1											FO/Ar
<i>Oecomys</i>		2	2	1	2	3	6	5	3	1		FO/Sc
<i>Oligoryzomys</i>	1	1	1		1		1		1	2		HO/Te
<i>Oryzomys</i>	1	1	1	1	1	2	3	3	4	4		FO/Te
<i>Ototylomys</i> ^a												FO/Sc
<i>Oxymycterus</i>								1	1	4		PO/Te
<i>Peromyscus</i> ^a												FO/Te
<i>Phaenomys</i>										1		FO/Ar ^e
<i>Reithrodontomys</i> ^a												HO/Sc
<i>Rhagomys</i>										1		FO/Ar ^e
<i>Rheomys</i> ^a												P/Sa
<i>Rhipidomys</i>			2	1	1	1	3	2	1	1		FO/Ar
<i>Scolomys</i> ^d												PO/Te ^c
<i>Sigmodontomys</i>	1			1								FO/Te
<i>Tylomys</i>	1	1										HO/Sc
Echimyidae												
<i>Dactylomys</i>								1	1			H/Ar
<i>Diplomys</i>		1										FO/Ar
<i>Echimy</i>			1		1	1	2	2	1	5		FO/Ar
<i>Hoplomys</i>	1											FO/Te
<i>Isothrix</i>								1	1			FO/Ar ^c
<i>Kannabateomys</i>										1		H/Ar
<i>Lonchothrix</i>										1		FO/Ar ^e

TABLE 6-1 Genera of Nonvolant Small Mammals Recorded in Neotropical Lowland Rain Forests (continued)

	Subregion										Ecological Guild	
	TAR			CVR			AMZ			ARF		
	a	b	c	d	e	f	g	h	i	j		
Mesomys							1	1	1			FO/Ar
Nelomys											6	FO/Ar
Proechimys	1	1	1	1	1	1	3	4	4	5		FO/Te

The nomenclature for subregions (figure 6-1) is defined according to Voss and Emmons (1996):

TAR = Trans-Andean Rain forests; CVR = Coastal Venezuelan Rain forests; AMZ = Amazonian Rain forests; and ARF = Atlantic Rain Forests.

Numbers represent the species richness in the following localities (see figure 6-1): a—La Selva and vicinity, Costa Rica (Wilson 1990; Voss and Emmons 1996); b—Barro Colorado Island, Panama (Glanz 1990; Voss and Emmons 1996); c—Foothills on Western Llanos of Venezuela (Ochoa et al. 1988; Utrera 1996; Ochoa unpublished data); d—Maracaibo Basin, Venezuela (Handley 1976; Voss and Emmons 1996); e—Foothills on the border of Falcon and Yaracuy States, Venezuela (Handley 1976; Ochoa unpublished data); f—Guatopo National Park, Venezuela (Ochoa et al. 1995); g—Imataca-Venezuela, Kartabo-Guyana and Arataye-French Guiana (Ochoa 1995; Voss and Emmons 1996); h—Minimal Critical Size Ecosystems Reserves and Xingu, Brazil (Malcolm 1990; Voss and Emmons 1996); i—Balta, Cocha Cashu and Cuzco Amazónico, Peru (Emmons and Feer 1990; Janson and Emmons 1990; Woodman et al. 1997, 1996; Voss and Emmons 1996); j—Coastal forests of eastern Brazil (Emmons and Feer 1990; Wilson and Reeder 1993).

Ecological guilds include the following:

Frugivores whose diets are based on fruits or seeds (F); Herbivores (H); Predators, including insectivores (P); Omnivores (O); Terrestrials (Te); Arboreal (Ar); Semi-arboreal, corresponding to species using ground and tree strata (Sa); and Semi-aquatics, integrated by species using terrestrial and aquatic habitats (Sq).

^aRecorded in the trans-Andean region (Emmons and Feer 1990; Voss and Emmons 1996).

^bKnown from the Andean Piedmont (Amazonia) of eastern Ecuador (Voss and Emmons 1996).

^cRecorded in the Coastal Venezuelan Range from the type locality of *Neusticomys venezuelae* (Anthony 1929).

^dRecorded in the Amazonia (Emmons and Feer 1990; Voss and Emmons 1996).

^eDiet unknown; trophic strategy estimated by morphology and ecological habits (Alho 1982; Emmons and Feer 1990; Nowak 1991).

marsupial and rodents, however, the guild position can change according to the ecological gradients within their geographical range (Charles-Dominique et al. 1981), or as a result of adaptations to variations in the availability of certain resources following anthropogenic disturbances (e.g., decrease in fruit production caused by elimination or reduction of tree strata).

Small Mammal Communities in Neotropical Rain Forests

Species Richness and Taxonomic Composition

Voss and Emmons (1996) assessed the diversity of small mammal communities across Neotropical rain forest types (see figure 6-1). Their inventory includes fifty-two genera of nonvolant small mammals: twelve in the Didelphimorphia order and forty in the Rodentia order (see table 6-1), with the highest levels of richness occurring in the Amazon and the Atlantic forests of Brazil (see table 6-2). Among these taxa, nineteen (37 percent) are broadly distributed (present in more than two subregions), including ten marsupials and nine rodents (83 percent and 23 percent of the genera comprising these orders, respectively).

The trans-Andean forests have the greatest number of endemic or geographically restricted genera (see table 6-2), followed by the Atlantic and Amazon forests. Forest ecosystems located in the coastal range of Venezuela exhibit the lowest richness and are composed of communities whose members have been recorded in two or more subregions (see table 6-1). Among the twenty-seven genera whose known distributions are restricted to one sub-region (52 percent of those genera inhabiting Neotropical rain forests), only two are in the Didelphimorphia (*Caluromysiops* and *Glironia*) order, and both are confined to the Amazon Basin. The amount of diversification in these forests is determined by the evolutionary histories of each phylogenetic group, the colonization patterns that have influenced each biogeographical region, and the responses of small mammals to geographic variations in environmental characteristics such as soil quality and primary productivity (Hershkovitz 1972; Emmons 1984; Voss and Emmons 1996; Ochoa 1997b).

In light of the above patterns, small mammal communities from the rain forests of the Amazon, the Atlantic coast of southwestern Brazil, and the trans-Andean lowlands should be considered a high priority for protection. This recommendation gains particular relevance when the increasing rates of deforestation and primary forest degradation in these subregions are considered (Voss and Emmons 1996; WRI et al. 1996; Bryant et al 1997; Miranda et al. 1998).

TABLE 6-2 *Some Characteristics of Nonvolant Small Mammal Communities in Selected Lowland Rain Forests of the Neotropical Region*

	Subregions			
	TAR	CVR	AMZ	ARF
Species Richness (range)	16-18	15-20	22-33	60
Didelphimorphia	5-7	6-10	7-12	19
Rodentia	10-13	9-12	15-21	41
Total Number of Genera	34	24	30	28
Didelphimorphia	10	10	12	10
Rodentia	24	14	18	18
Endemic or Restricted Genera ^a	11	--	7	8
Didelphimorphia	--	--	2	--
Rodentia	11	--	5	8

^aIncludes endemic genera or those whose geographical distributions in the Neotropical Region embrace only one subregion (e. g., *Glironia* and *Peromyscus*).

NOTE: Bibliographic references and geographical context of subregions are described in table 6-1

Community Structure and Its Importance in Regulating Adaptability to Forest Disturbance

The guild structure of small mammal communities in several forested areas of the Neotropics is presented in figure 6-2. The following trends can be observed:

- Most species are semiarboreal or terrestrial. In all subregions, arboreal or semiaquatic species constitute the minority
- Most species, excluding those in aquatic habitats, have omnivore diets. Tropically specialized guilds, including strict predators and herbivores, contain the lowest number of species

In tropical forests, many nonvolant small mammals appear to be resilient to disturbances (Wilson and Johns 1982; Ochoa et al. 1988; Johns 1992a; Ochoa 1993, 2000; Laurance and Laurance 1996). This may be a function of their generalist habits and their adaptability to the ecological conditions found in secondary environments (e.g., scar-

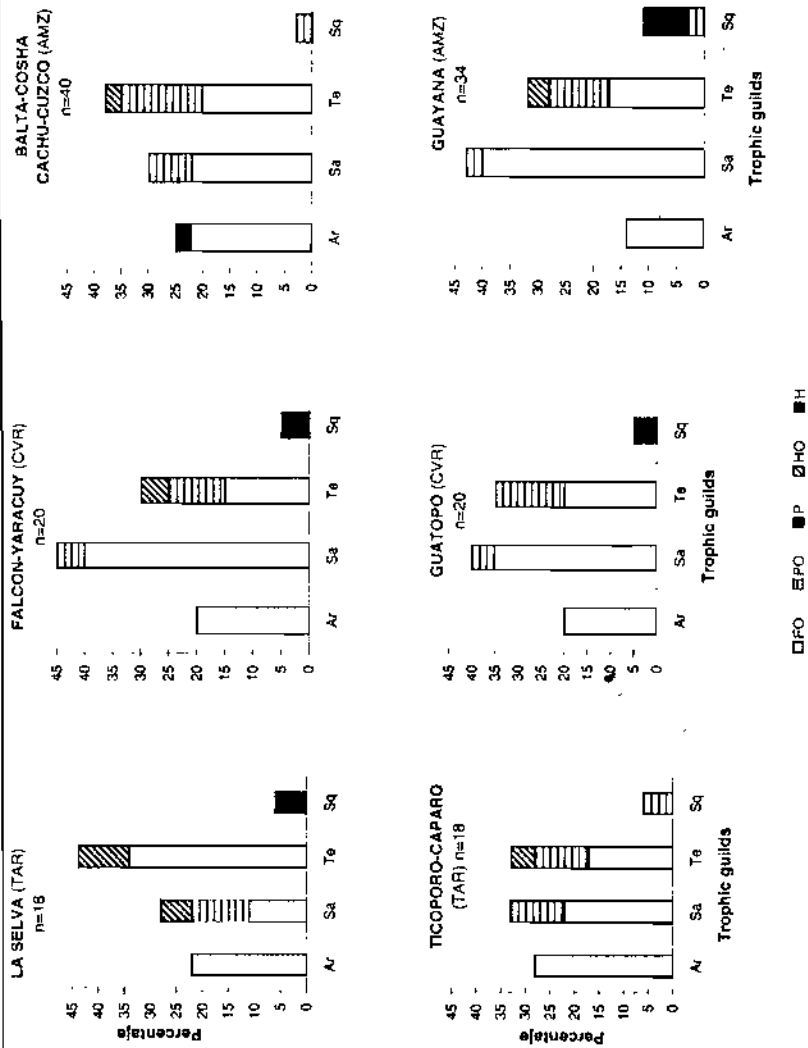


FIGURE 6-2 Estimated structures of small mammal communities in forested localities of the Neotropical Region. Nomenclature for the subregions and ecological guilds are described in table 6-1. The Atlantic rain forest subregion was excluded due to a lack of detailed inventories from specific localities.

- Species-specific affinity to primary forest environments
- Dependence on arboreal (mainly canopy) resources
- Geographic distribution pattern and population densities
- Estimated ecophysiological requirements
- Vulnerability to the hunting activities of both local people and loggers (Arita et al. 1990; Emmons and Feer 1990; Ochoa et al. 1993; Wilson and Reeder 1993; Ochoa 1995; Voss and Emmons 1996)

In logged forests, members of the Sciuridae and Echimyidae families exhibited the greatest extirpation probabilities among nonvolant small mammals. A high proportion of the species in these families depend on resources in the canopy (e.g., arboreal/frugivore-granivores like *Sciurus* spp., *Echymys* spp., and *Isotryx bistrata*; and terrestrial/frugivore-granivores of the genus *Proechimys*). Some species in these families also occur at low densities or have restricted geographic distributions (e.g., *Isotryx bistrata*, *Dactylopsax dactylinus*, and *Proechimys cuvieri*). In contrast, members of the Didelphidae and Muridae families appear less sensitive to logging. Most species in this group have widespread distributions, or they use resources found within the understory strata of secondary forests. Predictions of this type facilitate efforts to conserve small forest-dwelling mammals within areas to be logged, especially when rapid assessments are needed to identify those species at risk (Ochoa et al. 1993, 1995).

Forest Fragmentation

In logged areas it is common to find fragments of primary forests surrounded by secondary vegetation (sometimes highly degraded), plantations, or areas deforested for agriculture and infrastructure development (Johns 1988; Uhl and Vieira 1989; Ochoa 1993). Even though specific studies on small mammal communities in these kinds of fragments have not been published, the theoretical and experimental work on forest fragments (e.g., Bennett 1987; Friend 1987; Johns 1988; Terborgh 1992a; Andren 1994; see box 6-1) allows general predictions of the effect of fragmentation on such communities.

Box 6-1 *Unifying the study of fragmentation: external vs. internal forest fragmentation. (Jay R. Malcolm)*

The extent of deforestation in the tropics varies greatly from one region and development activity to another. Perhaps equally important, the spatial grain of deforestation also exhibits variability. At one extreme, large-scale industrial agriculture can result in coarse-grained, externally fragmented landscapes, wherein large forest fragments are interspersed with large clearings. At the other extreme, in what is termed *internal fragmentation* or *forest perforation* (Forman 1995), selective logging results in a fine-grained mosaic of small clearings, treefall gaps, and roads. Although both configurations are known to have important implications for the flora and fauna of the remaining forest, possible parallels between the two have only recently begun to be investigated. The identification of these links has great potential for conservation. In the light of accelerating loss and disturbance of tropical forests, and urgent needs for effective conservation guidelines and management techniques, the ability to apply knowledge and understanding from one type of landscape transformation to another is needed.

Recent research suggests that the ability to link and apply results from one type of forest fragmentation to another can be made through a common feature of human disturbances—the creation of canopy openings. Small gaps resulting from treefalls have long been known to play an important role in tropical forests because of the change in the physical environment that they bring and the resultant implications for plant growth and regeneration (Richards 1996). The importance of the large and/or abundant gaps created during human activities, however, has only recently been appreciated. In coarse-grained landscapes, where forest fragments abut large clearings, enormous changes occur in the forest close to clearings (Laurance and Bierregaard 1997). A suite of pervasive ecological changes quickly follows the creation of edges. Understorey vegetation growth accelerates in response to increased light levels. Trees along the edge are exposed to the ravages of wind turbulence, and as they blow over, further possibilities for the growth of understorey plants are provided. As a result of these changes, obvious edge-induced changes extend 50–100 m into fragments within a few years after edge creation (Malcolm 1994) and subtle effects may extend much further (Laurance and Bierregaard 1997). Several vertebrate communities, including both small mammals and birds (see chapters 8–10), respond quickly to the changes (Bierregaard and Lovejoy 1989, Malcolm 1997). Pronounced changes in species diversity and community composition are observed, especially in small fragments where perimeter-to-area ratios are high and edge impacts are strong.

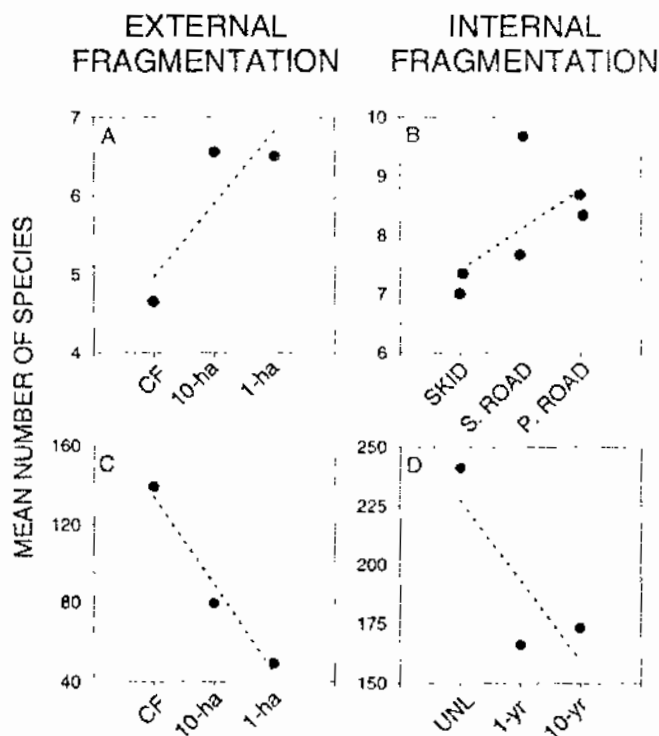
Although canopy openings created during selective logging are much smaller than those arising from modern agricultural development, the density of clearings may be high—especially in areas where many trees are being harvested. Under such conditions, the relatively weak edge effects of individual clearings may begin to overlap and interact and result in edge effects that are strong in an overall sense (see chapter 2). Computer simulations that incorporate this overlap highlight the potential for widespread and powerful edge effects (Malcolm 1998, 2001). Perhaps most seriously, they suggest that even slight increases in harvest rates can lead to disproportionate edge-induced habitat change.

Edge effects may thus provide a common currency for understanding some of the changes that diverse types of development activities bring. In some cases, because of pervasive edge-induced habitat change, it appears that very different patterns of forest clearing can result in similar wildlife responses. As increasingly strong edge effects in forest fragments led to increased small mammal abundance and diversity in the central Amazon (see box figure 6-1A), increasingly strong edge effects along 12- and 19-year-old log extraction routes in the Central African Republic also led to increased small mammal abundance and diversity (Malcolm and Ray 2000) (box figure 6-1B). The increases in abundance, which were true of nearly all rodent species found in undisturbed forest, suggest that the forest changes that accompany edge formation may be positive for at least some rain forest taxa.

For many other rain forest groups (including birds), however, edge effects led to a strong decline in diversity—both in coarse-grained fragmented landscapes in the central Amazon (box figure 6-1C; Bierregaard and Lovejoy 1989) and in fine-grained selectively logged landscapes in French Guiana (box figure 6-1D; Thiollay 1992). In these last two studies, individual bird species responded in similar ways despite the differences in the grain of the forest clearing. Of the twenty-four species affected by the landscape transformation in both studies (a species was judged to be affected by the landscape transformation if its abundance was consistently highly or lower in disturbed forests than in undisturbed forest), the sign of the impact (either positive or negative) was the same for 17 of them ($P = 0.06$, two-tailed Binomial Test). Evidently, many of the bird species that are adapted to the conditions of undisturbed forest are intolerant of edge-induced habitat change, both in the coarse- and fine-grained landscapes. Even the increase in small mammal abundance and diversity along edges may, unfortunately, have negative implications for the rest of the ecosystem. Small mammals are important predators of seeds and seedlings, and a superabundant small mammal fauna may alter patterns of plant regeneration. Struhsaker (1997) suggested that seed and seedling predation by small mammals was a key causative agent in suppressing tree regeneration in heavily logged forests in Africa—resulting in transformation of the original rain forest to a more-or-less stable herbaceous and semi-woody plant community. From the standpoint of conserving intact rain forest ecosystems, therefore, edge creation appears to have strong negative impacts.

These results provide a clear message for forest managers in the tropics: reduce canopy openings (and hence edge effects) wherever and whenever possible. This can be accomplished in fragmented landscapes by setting aside large reserves and wide corridors that provide the interior forest conditions required by so many tropical forest organisms (see chapter 23). In logged landscapes, the frequency and size of openings should be minimized through low harvest rates and careful logging techniques (see chapter 21, 24). An important task of future research will be to measure the responses (and tolerance thresholds) of tropical species to these edge effects, and to determine the exact manner in which forest openings interact in determining overall levels of edge-induced habitat change.

Preliminary results of field inventories in the Western Llanos of Venezuela and the Guayana region immediately after logging (Ochoa unpublished data), where small forest fragments (< 50 ha) surrounded



BOX FIGURE 6-1 Small mammal (part A) and avian (part C) species richness in continuous forest (CF) and 10- and 1-ha forest fragments in the central Amazon (Bierregaard and Lovejoy 1989; Malcolm 1997) compared with small mammal richness in unlogged forest and along timber extraction routes in the Central African Republic (part B; UNL = unlogged forest, SKID = skidder trails, S. ROAD = secondary access roads; P. ROAD = primary access roads; Malcolm and Ray unpublished data) and avian richness in French Guiana (part D; UNL = unlogged, 1-yr = 1 year postlogging, 10-yr = 10 years postlogging; Thiollay 1992). In each plot, edge-modified sites are to the right of undisturbed forest sites.

by selectively logged areas (8–10 m³/ha) and deforested sectors were examined, showed these fragments to contain a high proportion of small mammal species found in undisturbed forest communities. Some species even increased in their relative abundance. Three years later, population densities of the most specialized taxa declined (e.g., arboreal/frugivore-granivores), and in some areas, forest-dwelling species were found inter-mixed with some typical small mammals of non-forest environments (e.g., *Zygodontomys brevicauda* and *Sigmodon alstoni*;

Soriano and C. Lulow 1988). The latter penetrated into newly logged areas using forest openings as colonization routes. Survival of typical, forest-dwelling small mammal communities in these fragments depends on the range of available resources (partially influenced by habitat complexity and heterogeneity in the isolated patch of forest), and the likelihood of gaining access to complementary food sources within the habitat matrix found in surrounding areas (Uhl and Vieira 1989; Johns 1992a; Terborgh 1992a; Frumhoff 1995; Malcolm 1995: see box 6-1). These trends, however, suggest that some species remaining in fragmented forests after logging could be a risk, at least in the medium or long term—which, in turn, may influence certain ecological processes within the forest (Terborgh 1992a; Ochoa 1997a, 2000).

Studies by Fonseca (1989) and Fonseca and Robinson (1990) in the Brazilian Atlantic coast provide a preliminary evaluation of the combined effect of fragmentation processes and the level of perturbation on the isolated forest patch as a consequence of tree extraction. Their results suggest a *fragment size/small mammal diversity* relationship that is partially explained by habitat structure and specific interactive mechanisms, such as predation. These authors found that in large secondary forest fragments (35,973 ha), mammal communities included the top predators (e.g., *Leopardus* spp.), which regulate population levels of generalist species with high trophic plasticity and competitive abilities (e.g., *Didelphis marsupialis*). When unregulated, these generalists have the potential to exclude other ecologically related faunistic elements (*Metachirus nudicaudatus*, *Marmosa* spp., and *Oryzomys trinitatis*) (see photo 6-1), such as found in small secondary fragments (60 ha). Some of these excluded mammals play a crucial role in forest dynamics and regeneration, mainly through the dispersal of seeds and the pollination of many tree species (Charles-Dominique et al. 1981; Emmons and Feer 1990).

Changes in Availability of Food and Denning Resources After Logging

The composition of vertebrate communities reflects the ecological conditions at a given locality (Smythe 1986; Terborgh 1986; Fleming et al. 1987; Johns 1988; Kikkawa and Dwyer 1992). These conditions influence a species' access to often scarce and highly dispersed resources such as roosts in hollows of mature trees, fruits, and nectar produced by some trees. These scarce resources are expected to decline in exploited areas (Johns 1986b, 1988, 1992a, 1992b; Uhl and Vieira

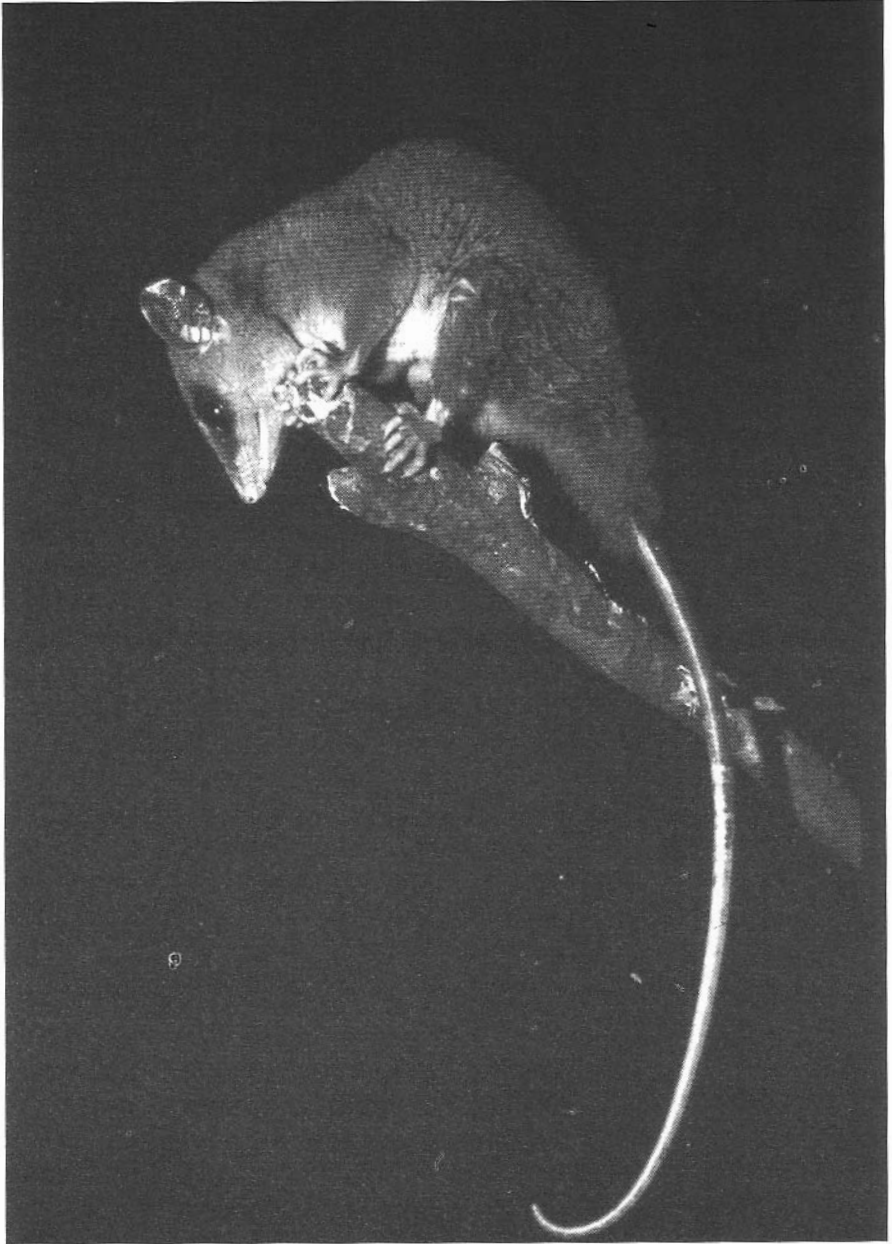


PHOTO 6-1 The marsupial *Metachirus nudicaudatus* is one of the most common terrestrial small mammals in some logged forests of the New World. It is an omnivore species which prefers invertebrate preys (e.g., worms and beetles). (J. Ochoa G., Imataca Forest Reserve, Venezuelan Guayana Region)

1989; Kikkawa and Dwyer 1992; Frumhoff 1995) where logging and other related activities lead to:

- A reduction in the absolute availability of canopy-linked resources (e.g., large den trees and canopy epiphytes, nectar and large-seeded fruits)
- A reduction in the density of keystone plants (e.g., some species of Chrysobalanaceae, Lecythidaceae, and Hippocrateaceae)
- Modifications to phenological patterns of trees, with a predominance of vegetative growth phases over reproductive ones
- An alteration in microclimatic conditions in the understory, with consequences for some species with ecophysiological restrictions (e.g., *Erismia uncinatum* and *Anacardium rhinocarpus*)

In spite of these predictions, several studies have shown increases in small mammal species' richness and density in secondary forests (Isabirye-Basuta and Kasenene 1987; Fonseca 1989; Julien-Laferrere and Atramentowitz 1990; Frumhoff 1995; Malcolm 1995). This is sometimes the result of the arrival of savanna/forest ecotone species in disturbed areas (e.g., *Zygodontomys brevicauda* and *Sigmodon alstoni*), and an increase in densities of some interior-forest mammals, which can use the resources present in exploited areas (e.g., *Didelphis* spp. and *Proechimys* spp.). The greater vegetative cover at the understory level of secondary forests (as a result of the high density of heliophitic plants and fallen trunks), and the higher structural complexity of the midlevel forest strata, also increase feeding and shelter opportunities for many terrestrial or semiarboreal species (Fonseca 1989; Ochoa 1997a).

Studies in the lowland rain forests of southern Venezuela (locality 7 in the Amazon rain forests subregion of figure 6-1) indicate that after four years of selective timber extraction (trees > 40 cm dbh, with an average volume removal of 5.8 m³/ha), small mammal communities undergo significant changes in their original structure and composition (Ochoa 1997b, 2000). These changes lead to a predominance of semiarboreal/omnivore-predators in secondary habitats (e.g., *Didelphis* spp. and *Philander opossum*). Terrestrial/frugivore-omnivores (e.g., *Proechimys* spp.), the most common foraging guild in undisturbed forests, also continue to be important in logged forests. Both guilds are able to use the abundant resources after logging disturbances: e.g., fruits of colonizer plants, invertebrates from the soil, and denning sites under fallen trunks (Charles-Dominique 1986; Fonseca 1989; Emmons and Feer 1990) (see photo 6-2). In contrast, the more arboreal frugivores and granivores (e.g., *Rhipidomys* spp. and *Micoureus demerarae*) (see photo 6-3) were not found in intensively



PHOTO 6-2 Interior view of a logged forest in the Venezuelan Guayana (Imataca Forest Reserve). In this area the understory is characterized by a high density of colonizer plants and fallen trunks, where communities of nonvolant small mammals are dominated by semiarboreal/predator-omnivore marsupials (e.g., *Philander opossum*) and terrestrial/frugivore-omnivore rodents (e.g., *Proechimys* spp.). (J. Ochoa G.)



PHOTO 6-3 The semiarboreal marsupial *Micoureus demerarae* is among the group of small mammals showing reductions of population levels in some intensively logged forests of the Venezuelan Guayana Region. This species has preferences by food resources located at the canopy level.

(J. Ochoa G., Imataca Forest Reserve, Bolivar State)

disturbed areas and did not show significant lower abundances (Ochoa 1997a, 2000).

Edaphic conditions that affect forest productivity appear to have an effect on small mammal responses to logging (Emmons 1984). In southern Venezuela, sandy soils with low water and nutrient retention capabilities are the predominant edaphic conditions, primarily in the lowlands of the Guayana Shield (Mogollón and Comerma 1995). This results in low productivity in the understory of closed-canopy forests, with limited availability of some resources for primary terrestrial consumers (Emmons 1984; Voss and Emmons 1996). Following logging in these areas, the semiarboreal/omnivore-predator, the common gray four-eyed opossum (*Philander opossum*), occurred with a relative abundance that was 4.3 times higher than the value found in undisturbed areas (see figure 6-3), while primary consumers like spiny rats (*Proechimys* spp.) showed increases approaching 2.1 times (Ochoa 1997b, 2000). These same species occur in forests of the Venezuelan Andean foothills (characterized by alluvial soils with high fertility). On these more productive sites, however, the genus *Proechimys* was the dominant component in primary and secondary forests (see

figure 6-3). While site productivity may influence the carrying capacity in terms of animal density and biomass, opening of the forest canopy (and subsequent increases in understory growth following logging) appears to have a greater effect on small mammal populations than the site's inherent productivity potential. Finally, it is important to consider the implications of logging on trees with flowering cycles that provide key resources for nectar-feeding small mammals (Lumer and Schoer 1986; Terborgh 1986; Emmons and Feer 1990; Julien-Laferrere and Atramentowitz 1990). In many cases, marsupials and other small mammals depend on the nectar produced by valuable timber trees (e.g., *Ceiba pentandra*, *Eriotheca* spp., and *Pachira quinata*), especially during seasonal periods of low food availability (Julien-Laferrere and Atramentowitz 1990; Kikkawa and Dwyer 1992). Harvesting practices that remove a large percentage of these *keystone* resources may promote the local extinction (or reduction in population levels) of some nectar-feeding species that are highly dependent on these resources. Where these animals play critical roles in the reproduction of timber species (principally through pollination and secondary dispersal), overexploitation of trees may lead to a cascading collapse in their reproductive success through the loss of ecological services obtained by mutualistic associations with small mammals (Lumer and Schoer 1986; Gribel 1988).

Effects on Reproductive Behavior

The reproductive strategies of some Neotropical marsupials can be influenced by changes in patterns of food availability after forest disturbance (Julien-Laferrere and Atramentowitz 1990). Primary forests tend to vary widely in their food abundance for small mammals, with longer scarcity periods, lower densities of fruiting trees, and reduced reproductive effort for many plants compared to secondary forests (Charles-Dominique 1986). In response to these conditions, Julien-Laferrere and Atramentowitz (1990) found that the bare-tailed woolly opossum and the four-eyed opossum show more continuous reproductive patterns and higher juvenile survival rates in primary forests. These characteristics are thought to be a function of: 1) their ability to focus foraging efforts on a limited number of resources that are relatively abundant during periods of fruit scarcity (mainly nectar); and 2) their lower population densities compared to disturbed areas (see figure 6-3). When the arboreal strata is drastically reduced, fragmented, or even eliminated, the most specialized species (and those

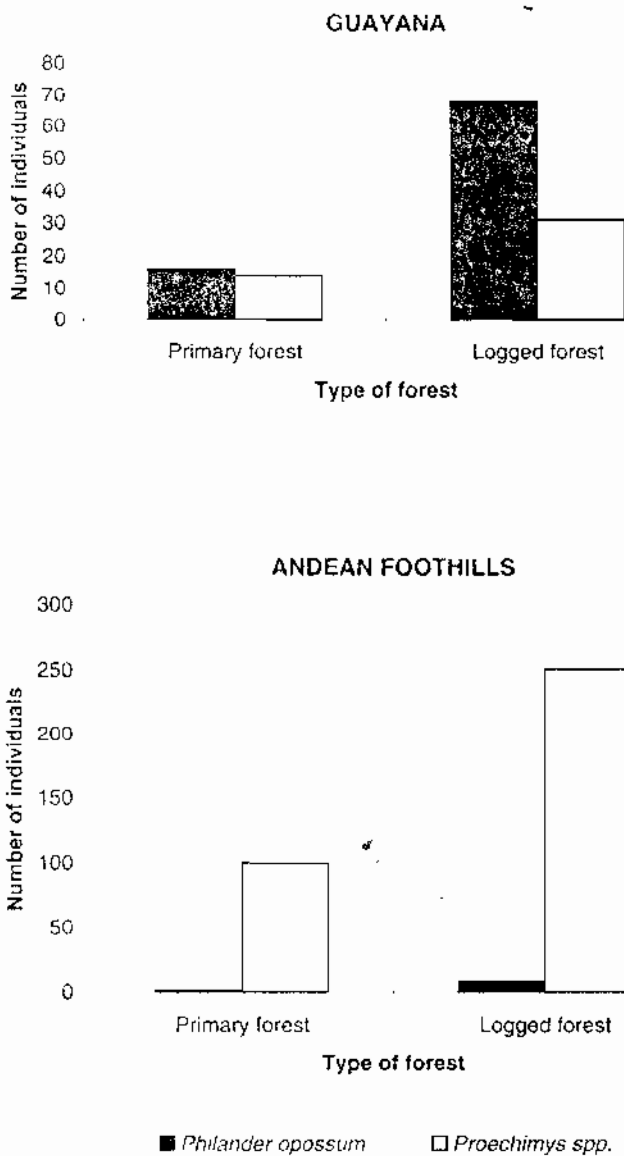


FIGURE 6-3 Relative abundance of *Philander opossum* (Didelphimorphia: Didelphidae) and *Proechimys* spp. (Rodentia: Echimyidae) in primary and logged forests in two biogeographic regions of Venezuela: Andean Foothills and Guiana Shield (based on 1,500 and 5,000 trap nights respectively; Ochoa et al. 1988; Ochoa 1997b).

generalists with a high level of resilience to forest disturbance) will probably be affected by significant trophic constraints and a drastic change in demographic patterns (Johns 1992b; Malcolm 1997).

Hunting Pressures

Logging activities are often associated with increases in hunting pressure by both local people and timber company personnel, who augment their economic income through trade or consumption of wildlife products—including an important number of mammals (Johns 1986b; Bisbal 1994; Frumhoff 1995; Ochoa 1997a; see chapters 15–17). In most Neotropical areas, mammal extraction is focused on medium to large-sized species (Redford and Robinson 1987, 1991). In some areas where large species have been overexploited, however, hunters target meat from marsupials and small rodents (including members of the families Didelphidae, Heteromyidae, Muridae and Echimyidae families: e.g., rice rats [*Oryzomys* spp.], spiny rats [*Proechimys* spp.], and the armored rat [*Hoplomys gymmurus*]; Suárez et al. 1995; chapters 15 and 16).

Depending on the locality, hunting patterns can influence the population status of certain taxa, leading to a significant reduction in the density and relative abundance of some species—especially where human settlements have exerted hunting pressures for a long time (Suárez et al. 1995) and wildlife use is translated into benefits for logging companies (Ochoa 1997a). These population changes may modify the patterns of community assemblages and some ecological processes within the forest (J. Ochoa unpublished data).

The Ecological Role of Marsupials and Small Rodents in Neotropical Forest Dynamic and Regeneration

An extensive area of Neotropical rain forest has been allocated for timber production, under management schemes that scarcely consider the dynamics of these ecosystems (Uhl and Vieira 1989; Johns 1992a; Whitmore and Sayer 1992). During the past two decades, field studies have demonstrated the importance of small mammals—including bats (see chapter 7)—as connective elements in a complex web of mutualis-

tic interactions, which help to maintain the taxonomic and structural diversity of forests (Uhl et al. 1981; Charles-Dominique 1986).

Seed dispersal and predation represent two of the most studied roles of marsupials and rodents in rain forests from the New World (Charles-Dominique et al. 1981; Gautier-Hion et al. 1985; Smythe 1986, 1987; Adler and Kestell 1998; see box 6-2). Many small mammals have trophic strategies closely associated with the consumption of fruits or their constituent parts. At the same time, an important number of plants depend on small mammals as seed dispersers or pollinators (Charles-Dominique 1986; see box 6-2). These mutualistic interactions are often associated with coevolutionary patterns and are strongly related to the population dynamics of many commercial trees (e.g., *Spondias mombin*, *Inga* spp., *Carapa guianensis*, *Erismia uncinatum* and *Protium* spp.). Features such as phenology and the reproductive patterns of plants, and morphology and the nutritional quality of fruits, maximize the efficiency of dispersing processes (Janson 1983; Gautier-Hion et al. 1985; Herrera 1984). These mammals have also developed a set of strategies to access scarce food resources and avoid competition with ecologically related species through strategies such as the consumption of size-differentiated fruits or the hoarding of fruits and seeds (Smythe 1986, 1987; Terborgh 1986; Fleming et al. 1987; Kikkawa and Dwyer 1992; see box 6-2).

Box 6-2 *Implications of logging on seed dispersal and predation by rodents in the lowland rain forests of central Guyana.*

(David S. Hammond and Raquel Thomas)

Rodents regulate the recruitment of trees by selectively preying and/or dispersing seeds. By selecting the seeds of certain species over others, they can actively influence the competitive hierarchy which establishes the relative recruitment success of co-occurring canopy tree species.

Timber tree species in the Guianas tend to have relatively large seeds. More than 50 percent of the eighty-seven timber species currently harvested in Guyana are dispersed by mammals—an estimated 28 percent being solely dispersed by rodents, especially by red-rumped agouti (*Dasyprocta agouti*), red acouchy (*Myoprocta acouchi*), Cuvier's spiny rat (*Proechimys cuvieri*), and the Guyanian spiny rat (*P. guyanensis*) (Hammond et al. 1996). The dispersal or burial of seeds by rodents often results in enhanced recruitment. One of Guyana's most important timber tree species, Greenheart (*Chlorocardium rodiei*; Lauraceae) has very large seeds that fall beneath dense aggregations of adult stems during the main fruiting period from January to April. The seeds (and later seedlings) are attacked by a bark beetle (Scolytidae), which reduces per capita survivorship significantly beneath parent trees in comparison to sites at greater distances (Hammond et al. in press). Though most Greenheart

stems are found in aggregations, the minority of offspring recruiting away from these clumps sustain the regeneration of this species—especially given that most harvesting is directed to these densely stocked areas (i.e., high advanced regeneration mortality due to incremental damage during logging). At the same time, the extremely prolonged germination of Greenheart seeds makes them an ideal resource for seed-eating rodents during periods between high fruit production. Most Greenheart seeds were found to be consumed during the period when overall resource availability was lowest, suggesting that this species is not a preferred resource, but one that is used during periods of scarcity by at least five species of rodents. Seed losses incurred through rodent foraging during periods of scarcity is a minor trade-off for the tree, however, in light of the important role rodents play in establishing new Greenheart regeneration when cached seeds are later forgotten.

The healthiest stems of Greenheart are the individuals typically harvested. This also means that the most reproductively active adult trees are also removed from the population—an activity that can lead to a precipitous decline in the number of seeds of these species that are available each year. Many rodents are also territorial, and this spatial segregation can mean that some intensively logged areas can no longer support the pre-harvest inhabitants. After logging at one 15 ha study site, the estimated abundance of acouchys (*Myoprocta* spp.)—accounting for changes in visibility—was lower than in a same-sized, unlogged plot with nearly identical abundances of the most common tree species (Hammond et al. 1992). A conservative approach to Greenheart seed tree retention would maximize the seed stock available for maintaining seed-dispersing rodents during periods of resource scarcity.

Size plays an important role in determining which animals will attempt to consume a fruit or seed. Generally, a greater number of species can consume the smaller seeds. The fact that many larger-bodied rodent species specialize in consuming large seeds is likely a product of the reduced competition for these resources. Small rodent species (such as those in the Muridae) are able to efficiently consume much smaller-seeded species, many of which profit from heavy disturbance. Seed dispersal by these small rodents can lead to a rise in the abundance of small-seeded colonizing plant species (Forget and Hammond in press).

Few applied studies have been carried out to determine the role of seed-consuming rodents in the regulation of timber tree recruitment after logging and the impact that logging intensity can have on the habitability of the site by these animals. Rodents, along with bats, represent the greatest diversity of tropical forest dwelling mammals. Attempts to preserve this diversity need to consider the conservation and role of these species in timber management.

Marsupials are commonly frugivorous and include species that exploit the understory and arboreal strata in Neotropical forests (Emmons and Feer 1990). They consume fleshy fruits of different sizes (Charles-Dominique et al. 1981), particularly those belonging to colonizer plants (*Cecropia* spp. and *Solanum* spp.) that produce numerous small seeds (Charles-Dominique 1986). In most cases, passage of seeds through the digestive tracts of the disperser agent represents an essential

step in increasing the germination capacity and reproductive success of some pioneer plants (Fleming and Heithaus 1981; Fleming 1988).

In contrast to marsupials, small, forest-dwelling rodents prefer seeds of unripe and hard fruits (usually small or medium-sized), which are carried to feeding sites (Charles-Dominique 1981; Gautier-Hion et al. 1985). In this case, the successful contribution of these mammals as disperser agents depends on the proportion of transported seeds that find suitable microhabitats for germination, or whose viability is not affected by predation (Gautier-Hion et al. 1985; Smythe 1986).

Seed predation has been recorded for several small Neotropical rodents belonging to the Sciuridae, Heteromyidae, Muridae and Echimyidae families (Emmons and Feer 1990; Nowak 1991). These mammals may act as important regulators of tree composition and density (Terborgh 1992a), and represent key elements for the management of forests (see box 6-2). Among them, the genus *Proechimys* has been considered one of the main seed predators-dispersers in Neotropical rain forests (Smythe 1986, 1987; Adler and Kestell 1998) due to its high population densities across a broad geographic range (Handley 1976; Emmons 1982; Janson and Emmons 1990; Malcolm 1990) (see photo 6-4).

Even species that are primarily seed predators can positively influence the regeneration potential of secondary forests. Spiny rats, for instance, disperse the mycorrhizal sporocarpus (e.g., *Sclerocystis coremioides*) and spores (e.g., *Glomus* spp.) (Emmons 1984; Janos et al 1995). This role has been studied for other small rodents (including the Neotropical genera, *Oryzomys* and *Mesomys*), demonstrating their contributions to forest conservation (Janos et al 1995; Johnson 1996).

Recommendations for Conserving Small Mammals in Logged Landscapes

Although most small mammals appear relatively adaptable to logging disturbance, strategies for forest management and conservation must consider that some species may be at risk—especially the arboreal frugivores-granivores and those taxa with limited range distributions. The loss of these mammals, and the additions of some savanna-secondary forest colonizing species in intensively disturbed forests, will cause changes in ecological processes that could negatively influence the regeneration success of important timber trees.



PHOTO 6-4 The terrestrial rodents of the genus *Proechimys* are considered among those mammals with a high influence on Neotropical rain forest regeneration. They are seed predators, but at the same time they contribute with dispersion of micorrhizae and seeds produced by many timber tree species. (P. J. Soriano)

A prudent approach would be to tread as lightly as possible during logging, to avoid significant impacts on mammal communities and other biodiversity components typically inhabiting primary forests (see chapters 21 and 24). This issue is especially important until we know more about how these communities respond to logging activities, mainly in those regions with the highest diversity.

Technical criteria in forest policies adopted by governments and logging industries must be focused on the protection of small mammal communities, if the long-term productivity, health, and economic value of production forests are to persist. Possible approaches include the creation of primary forest corridors in association with areas managed for timber (Ochoa 1993; MARNR 1995; see chapters 20 and 23). Several authors have explored reducing the impacts of logging on forest biodiversity (Johns 1986b; Thiollay 1992; Whitmore and Sayer 1992; Hernández et al 1994; Frumhoff 1995; Mason 1996; Greiser Johns 1997; Ochoa 1997b, 1998, 2000; Miranda et al. 1998; see chapters 21 and 24). These approaches include:

- Designing plans for selective tree cutting and log removal that minimize the level of disturbance to the residual vegetation structure and composition

- Taking into account the ecological role of commercial trees in providing key resources for marsupials and rodents (e.g., seeds and roosts in mature trees), thereby ensuring an adequate number of residual stems for both regeneration and mutualistic interaction purposes
- Using silvicultural methods based on an evaluation of their implications on primary forest regeneration and biodiversity conservation (see chapter 22)
- Controlling and monitoring hunting activities

Success of these initiatives will depend on technical and scientific cooperation from all stakeholder groups, including governmental agencies, research institutions, the logging industry, and local people. The integration of these sectors represents a basic step towards implementation of management models based on the conservation and sustainable use of Neotropical rain forests.

Long-term field inventories and monitoring efforts are also needed to understand the composition and structure of small mammal communities inhabiting Neotropical rain forests—especially those areas with high extractive pressures and/or low available biological information (Malcolm 1990, 1991; Patterson 1991; Woodman et al. 1995, 1996; Voss and Emmons 1996). These inventories serve as the foundation for additional ecological research and conservation planning. Such projects are likely to be difficult to implement in Latin American countries—at least in the short term—where financial constraints, an absence of institutional policies that promote forest evaluations, and a limited number of local taxonomic experts exist.

The analysis of plant-animal interactions as regulatory mechanisms and their importance in the regeneration and maintenance of primary forests (especially timber species), represent a crucial aspect for success of forestry management activities and the recovery of areas with high levels of disturbance (Frumhoff 1995). It is necessary to identify and assess those small mammal groups with a major influence on key ecological processes—including seed dispersion and predation—and pollination of those tree species with a high commercial value. Based on long-term monitoring programs, these evaluations must identify the levels of disturbance beyond which some marsupials and rodents are irreversibly affected (Blockhus et al. 1992; Johns 1992b; see chapter 19).

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