

# Barro Colorado Island, Panamá, Basic Research, and Conservation

Egbert Giles Leigh, Jr.  
Georgina de Alba

SMITHSONIAN TROPICAL RESEARCH INSTITUTE  
*Balboa, Panamá*

## INTRODUCTION

To design reserves for protecting biodiversity and preserving representative ecosystems, we must know (1) what factors limit the populations of various representative kinds of plants and animals, (2) what factors allow these populations to persist, (3) which species are particularly crucial to the integrity of their communities, and (4) how the integrity of these communities depends on events in their surroundings, or in the biosphere as a whole.

Social questions also confront conservationists. Biodiversity cannot be preserved if the hope of the rural poor is taken away, or if human populations continue outgrowing their resources. The preservation of ecosystems requires that local people be able to support themselves decently without destroying them. Speaking *practically*, right relationships between humans and nature cannot be based on grossly inequitable relationships among humans. This paper considers only the (equally essential) biological dimension of conservation.

This paper relates research on Barro Colorado Island (BCI) to problems connected with conserving tropical forest and its diversity. This research

yields no immediate prescriptions about how large a viable park must be, how many habitat types it must contain, etc. Indeed, research at many sites is needed to answer such questions. We merely identify factors which must be considered in making such decisions, and suggest where appropriate information may be found.

First, some background (from Windsor 1990): BCI is a 1,500-ha island isolated about 1913 from the surrounding mainland of central Panamá by the rising waters of Gatun Lake. BCI's rainfall has averaged 2,600 mm/yr over the last 60 years. A severe dry season extends from December into April or May; the median rainfall for the first 13 weeks of the year is 84 mm. BCI's vegetation is considered characteristic of fertile soil (Foster and Brokaw 1982, 1990). Human populations lived on BCI before the Spanish conquest (Piperno 1990). Mature forest has covered parts of BCI's central plateau uninterrupted for 2,000 years, but other parts of BCI probably were more thickly settled.

How can basic research on this island help answer our questions?

## ANIMALS

**Population regulation** Monitoring the timing and extent of flowering, fruiting, and leaf flush among BCI's plants, and studies of the behavior and demography of vertebrate frugivores and folivores in relation to seasonal changes in their food supply, suggest that the forest controls its vertebrate herbivores by seasonal shortages of fruit and new leaves (Leigh 1975, 1982; Leigh et al. 1982, 1990), even though parasites may eliminate overly malnourished individuals (Milton 1982, 1990), and predators eat surplus young (Smythe et al. 1982, 1990). Fruit is most abundant on BCI from March through May and from August into October (Foster 1982a). Fruit and new leaves are most scarce from late

October into the dry season. During this seasonal shortage, there is not enough fruit to feed the frugivores, a circumstance reflected in their behavior and demography (Table 1). As in Peru's Parque Manú (Terborgh 1986a, 1986b), each species which shares in the bounty when fruit abounds has its own specialty in the lean season, as if to avoid competitive displacement during this critical period (Zaret and Rand 1971). When fruit is rare, coatís, *Nasua narica*, hunt animals in the leaf litter; pacas, *Agouti paca*, browse seedlings; agoutís, *Dasyprocta punctata*, dig up seeds buried in the time of abundance, etc. (Smythe 1978).

Collectively, folivorous insects are most abundant soon after the rains begin, when leaf flush is in full swing (Wolda 1978, 1982, 1990; Smythe 1982, 1990). Insectivorous bats and birds tend to breed in this season of insect abundance (Bonaccorso 1979; Leigh and Windsor 1982, 1990). We know the population density or aggregate feeding rate of no kind of folivorous insect, not even leafcutter ants, *Atta* spp. Nevertheless, comparing the population sizes and feeding rates of insectivorous birds with estimates of insect folivory from damage to litter leaves suggests that BCI's birds eat enough folivorous insects to control their numbers (Leigh and Windsor 1982, 1990). One Australian eucalyptus forest depends demonstrably on its birds for protection against folivorous insects (Loyn 1987): is this equally true for tropical forests?

**What do different animal populations need to persist?** A species can only persist if it has enough suitable habitat to maintain a viable population, enough habitat types to meet its various needs, and access to enough of the resources it needs to assure it a living, secure from superior competitors, even in bad years (Leigh 1981, 1990; Karr 1982). White-lipped peccaries, *Tayassu pecari*, travel very widely in large herds.

**Table 1. Evidence that a seasonal shortage of fruit and new leaves controls BCI's populations of vertebrate herbivores**

### **1. Quantitative data**

- ◆ During the lean season, measured fruit supply is insufficient to feed, e.g., terrestrial frugivores (Smythe et al. 1982, 1990) and manakins, *Pipra mentalis* and *Manacus vitellinus* (Worthington 1982, 1990)
- ◆ Failure of September fruiting peak in 1970 caused mass starvation among BCI's mammals (Foster 1982b, 1990b)
- ◆ Mortality, reproductive activity and population density of squirrels, *Sciurus granatensis*, changes from year to year in accord with availability of principal foods in successive years (Giacalone et al. 1990)

### **2. Seasonal changes of behavior in relation to food supply**

- ◆ Species which share in the same abundance of fruit during the season of abundance each specialize to a different diet during the lean season; e.g., terrestrial frugivores (Smythe 1978)
- ◆ Animals are more easily trapped during the lean season; e.g., terrestrial frugivores (Smythe et al. 1982, 1990) and squirrels, *Sciurus granatensis* (J. Giacalone pers. comm.)
- ◆ Animals range further and take more risks to find food; e.g., terrestrial frugivores (Smythe et al. 1982, 1990) and coatis, *Nasua narica* (Russell, 1982, 1990)
- ◆ Animals show less care for their young in the lean season; e.g., agoutis, *Dasyprocta punctata* (Smythe 1978)

### **3. Relationship of demography to food supply**

- ◆ Coatis who have never bred before delay breeding for a year in a year when food is short (Russell 1982, 1990)
- ◆ Death rates, especially among young, are higher in the lean season; e.g., agoutis, *Dasyprocta punctata* (Smythe 1978); howling monkeys, *Alouatta palliata* (Milton 1982, 1990, 1990b); and sloths, *Bradypus variegatus* (Montgomery and Sunquist 1978; Milton 1990b)
- ◆ Births are timed to produce young in the favorable season; e.g., iguanas, *Iguana iguana* (Burghardt et al. 1977; Rand and Greene 1982); coatis, *Nasua narica* (Russell 1982, 1990); insectivorous bats: *Saccopteryx bilineata* (Tannenbaum 1975); frugivorous bats, *Artibeus jamaicensis* (Morrison 1978); and others (Bonaccorso 1979)
- ◆ Birth rates are lower during the lean season; e.g., whitefaced monkeys, *Cebus capucinus* (Mitchell 1989); howling monkeys, *Alouatta palliata* (Milton 1982, 1990); and squirrels, *Sciurus granatensis* (Glanz et al., 1982, 1990)

Such herds disappeared from BCI in the 1930s, 20 years after its isolation (Glanz 1982, 1990a), although individuals have been reported since. Big cats need large territories: puma, *Felis concolor*, were photographed on BCI in the 1930s (Glanz 1982, 1990),

but the last sighting was in 1958 (Martin Moynihan, personal communication). The only jaguar, *Panthera onca*, ever recorded on BCI was seen in 1983. Is BCI too small to support such species indefinitely?

Many bird species of young second-growth have disappeared from BCI as its forest has aged (Willis 1974), as if BCI has too few kinds of habitat to maintain high bird diversity. Some bird species, which migrate to streamside habitats, have disappeared from BCI, which lacks permanent streams (Karr 1982). Similarly, isolating La Selva, in Costa Rica, from montane forest would eliminate those many species of birds which migrate seasonally from lowland forest up nearby mountainsides in response to changing fruit availability (Loiselle and Blake 1991). Finally, some species of large ant-following birds with very specialized feeding requirements have disappeared (Willis 1974), as if BCI were too small to assure them a reliable food supply.

In sum, animal diversity presupposes diversity of plants and vegetation types. The principle of competitive exclusion implies that species coexist only if their numbers are limited by different factors, say, different predators or availabilities of different foods or habitats. A rainforest's vertebrates, whether at BCI (Leck 1971; Jones 1977; Smythe 1978; Bonaccorso 1979), Manú (Terborgh 1983; Terborgh et al. 1990) or Gabon (Emmons 1980; Emmons et al. 1983), differ enough in diet or habitat, at least during the lean season, to ensure coexistence. The same probably applies to insects. The diverse rhythms of flowering, fruiting, and leaf flush among a rainforest's plants, and the lack of winter cold, ensures that fruit and insects are available all year round, even though selection by herbivores (Aide 1988) has shaped a forest-wide rhythm that controls the number of vertebrate herbivores (Leigh 1975, 1982). The continual, if uneven, supply of suitable food allows many more kinds of frugivorous and insectivorous mammals and birds in the tropics than in the temperate zone

(Emmons et al. 1983; Terborgh and Robinson 1986; Emmons 1989).

**Keystone species for animal populations** Of the 1,500+ plant species in Peru's Parque Manú, just 12 "keystone" species, including figs, *Ficus* spp., and palms, *Scheelea* spp. and *Astrocaryum* spp., provide food, tiding frugivores over the lean season. These 12 species set Manú's carrying capacity for frugivores (Terborgh 1986a, 1986b). On BCI, *Ficus insipida*, *Ficus yoponensis*, *Scheelea zonensis* and *Astrocaryum standleyanum* are keystone species with fruit in the lean season (Morrison 1978; Handley and Leigh 1991; Glanz et al. 1982, 1990). *Astrocaryum* seeds, moreover, are durable enough to bury against future shortages (Smythe 1989). Keystone species for BCI's smaller frugivores are not yet identified, but, as at Manú, they include pollen- and nectar-producers.

Are big cats (Felidae) keystone species which BCI lacks? They annually kill 8% of Manú's standing crop of mammals weighing over 1 kg, a predation pressure similar to the Serengeti's (Emmons 1987; Terborgh 1988, 1990), yet frugivores are as abundant there as at BCI (Terborgh 1986a). Do big cats merely stabilize prey populations, weeding out the weak, the sick and the surplus, as wolves (*Canis lupus*) do at Isle Royale? Or have big cats caused the differences between BCI and Manú mammal faunas (perhaps by thinning mammal populations enough to allow more species to coexist in the Manú)? Views on this subject differ widely (Glanz 1990; Janson and Emmons 1990).

## PLANTS

**Population regulation** Why there are so many kinds of tropical plants is one of biology's greatest mysteries (Leigh 1990; Leigh et al. in press).

The forest as a whole is limited by abundance of light, water, and nutrients. On BCI, upland forest equilibrates at a density of slightly

over 400 trees/ha  $\geq 10$  cm, and 4,800 stems/ha  $\geq 1$  cm, in diameter at breast height (Richard Condit, personal communication). However, trees are so long-lived that changes devastating for a forest's future diversity can pass unnoticed by any but the most practiced eye. We now think we understand the population dynamics of one of BCI's tree species, *Trichilia tuberculata*, the most common canopy tree on BCI's 50-ha Forest Dynamics Plot (Hubbell et al. 1990). This triumph was attained by mapping and recensusing all of this plot's 240,000 stems  $\geq 1$  cm thick, an immense project of unknown environmental impact.

This 50-ha plot has shown that few species specialize to particular habitats (such as slope vs. ridgetop) or particular sizes of treefall gap (Hubbell and Foster 1986), suggesting that habitat heterogeneity is not essential to (although, according to Gentry 1988, it often enhances) tree diversity.

*What do plant populations need to persist?* What factors help maintain the diversity of BCI's trees? The seeds of many (but not all) trees have better prospects when dispersed well away from the parent plant (Howe and Smallwood 1982), to avoid species-specific herbivores (Howe et al. 1985) or pathogens (Augspurger 1983) around the parent. *Virola surinamensis* seeds are 44 times more likely to become six-week-old seedlings when removed 45 m from the parent crown than when dropped under the parent (Howe et al. 1985). Pests can thus promote tree diversity by providing room for other species between a parent and its surviving young (Janzen 1970). Moreover, fruit production and recruitment of different tree species varies drastically, and contrastingly, from year to year (Hubbell and Foster 1990; Leigh 1990). Such "sorting in time" of reproductive success may help prevent competitive displacement (Chesson and Warner 1981),

thus promoting tree diversity. These contrasting reproductive responses must, in part, reflect contrasting responses to yearly differences in abundance of various pollinators, dispersers, and seedling-browsers. Indeed, the diversity of pollination and dispersal mechanisms (Foster 1982a, 1990a), exploiting the diversity of possible carriers, suggests a premium on novelty for its own sake, as if a novel reproductive response to environmental change favored persistence. If so, animal diversity is crucial to plant diversity.

Perhaps competitive exclusion is irrelevant to plant diversity (Huston 1979, Hubbell and Foster 1986). Are animals demonstrably essential for maintaining some plant populations? The seeds of the black palm, *Astrocaryum standleyanum*, can only escape destruction by weevils if agoutis peel their flesh and bury them (Smythe 1989). This instance is not isolated. Even after toucans, *Ramphastos* spp., disperse them, agoutis must bury seeds of *Virola surinamensis* (= *nobilis*) to save them from weevils (Forget and Milleron 1991). Islands of 1 ha or less near BCI, which were forested when isolated and not cleared since, have been largely taken over by four species of tree, *Protium panamense* (Burseraceae), *Swartzia simplex* (Leguminosae), *Oenocarpus mapora* (Palmae), and *Scheelea zonensis* (Palmae) (Putz et al. 1990; Leigh et al. in press). These islands lack mammals, so their seeds remain unburied. The seeds of the first three of these species are not infested by insects, while the bruchids which plague *Scheelea* early in its fruiting season disappear by October, leaving late-falling *Scheelea* seeds uninfested (Wright 1990). (On BCI, the latter fall during the lean season and are immediately eaten by mammals.) Are mammals crucial to the survival of many tree species?

The diversity of regeneration in the rain forest at Las Tuxtlas, Mex-

ico, where mammals are very rare, is much lower than in a much larger expanse of rainforest with roughly similar diversity and species composition of canopy trees, but with many more mammals, in Chiapas, Mexico (Dirzo and Miranda 1990, 1991). In the Neotropics, the least-seasonal forests have the highest tree diversity, the highest proportion of animal-dispersed trees, and the highest diversity of frugivorous animals (Emmons 1989). The first animals to be hunted out are potential seed dispersers. Such hunting imperils tropical tree diversity.

**Plant diversity and keystone animals** Many tree species at both the Taï Reserve, in the west of Côte d'Ivoire, and the Parc National Banco, near Abidjan, had seeds designed to be dispersed by elephants, *Loxodonta africana* (Alexandre 1978). On much of BCI, at least in some years, agoutis eat nearly all the seeds of *Dipteryx panamensis*. Young of this species are abundant only on certain peninsulas of BCI. Are agoutis rarer there, or are these young more abundant because more light reaches the forest floor of these peninsulas? This question is in dispute. On the mainland points near BCI, where there are fewer agoutis, and where the forest is younger and perhaps thinner, and at La Selva, *Dipteryx* regeneration seems quite adequate (De Steven and Putz 1984; Clark and Clark 1987). Similarly, agoutis may be keystone animals for maintaining BCI's tree diversity.

Are jaguars also keystone animals for plants? Agoutis are much more common on BCI than at Manú. BCI's lack of jaguars must play some role in this difference (Glanz 1990b). Again, on BCI agoutis eat so many seeds of *Dipteryx panamensis* (Leguminosae) that this species is regenerating only on certain peninsulas where agoutis are rare. At La Selva, and on the mainland points near BCI, where agoutis are rarer, *Dipteryx* regeneration seems quite

adequate (De Steven and Putz 1984; Clark and Clark 1987). Will *Dipteryx*—or other species—disappear from BCI for lack of jaguars?

**Global environmental change and plant responses** Atmospheric content of carbon dioxide (Hogan et al. 1991) and methane (Keller et al. 1990) is increasing, thanks to a variety of human activities. How will these changes affect rainforest plants? How should reserve design reflect these effects?

Answering these questions must begin with plant physiology. Changing CO<sub>2</sub> levels affects photosynthetic rate and water use, and might increase plants' tolerance for higher temperatures (Hogan et al. 1991). How will these atmospheric changes affect plant-animal interactions? Among other things, we must understand the physiology underlying phenological rhythms of flowering, fruiting, and leaf flush in different rainforest plants. Synchronous fruiting, and synchronous leaf flush, helps protect seeds, seedlings, and new leaves from herbivores within a species (Augsburger 1982, 1990; Aide 1991) or in whole forests (Ashton et al. 1988). Speedy leaf flush, (Aide and Londoño 1989), or flushing leaves in the dry season when insects are rarer (Aide 1988), are also possible defenses against herbivory.

**Our devastating ignorance of plants** The greatest service of BCI's 50-ha Forest Dynamics Plot has been to reveal the depths of our ignorance of the lives of plants. Saplings whose nearest canopy neighbor is a conspecific grow more slowly, and die more rapidly, than those with nearest neighbors of different species (Hubbell and Foster 1990). Is this effect strong enough to enhance tree diversity? No one knows. The plot's common trees tended to grow more common, and rarer trees rarer, between the first two censuses (Welden et al. 1991). Does this reflect the later stages of a plant succession after the Spanish conquest eliminated BCI's

human populations (Piperno 1990)? Did the Amerindians actively *maintain* plant diversity (Irvine 1989)? Or do these changes reflect a continuing response to the onset 11,000 years ago of wetter conditions (Bush et al. in press)? These are tricky questions. The vegetation of eastern North America has been changing continuously since the last glaciers receded. These changes were considered evidence for disequilibrium in North American plant communities, but a more thorough study (Prentice et al. 1991) suggests that the vegetation has remained in equilibrium with a continuously changing climate.

More general questions remain unsettled. The potentially high pest pressure in tropical forests promotes effective plant dispersal. Dispersal is often enhanced by attractive fruits (Howe and Smallwood 1982). Calculations suggest that, if a tree's seeds disperse well beyond the "neighborhood" of the trees with whom the roots or leaves of their parent competes, it pays the parent to increase seed and fruit production, even by means which benefit neighboring trees; harming neighbors at the expense of slowing one's own growth or reproduction no longer pays (Wilson 1980; Leigh 1991). Many naturalists have consid-

ered tropical rainforest to be the apex of mutualism (Corner 1964; Jacobs 1988): the nature and extent of its interdependences have hardly begun to be explored. Are insect pests, through their effect on seed dispersal, crucial to the diversity and productivity of tropical forests, the complex interdependencies among their species, and the luxuriance of their mammal populations?

### CONCLUDING REMARKS

We understand something of what factors affect the diversity of vertebrates and perhaps—despite our stunning ignorance of them—even insects. At bottom, however, animal diversity presupposes plant diversity (Hutchinson 1959).

Therefore, our abysmal ignorance of tropical plants may be the stumbling-block for formulating appropriate long-term conservation strategies. Our ignorance of plants, however, is no excuse for neglecting animals, for we know least about the many ways plants depend on animals (Table 2). Alexandre's (1978) demonstration that elephants are keystone animals for West African plant diversity was nearly universally ignored. The corresponding role of agoutis for BCI's forests is a remarkably recent discovery.

---

**Table 2. How tropical plants depend on animals: What we know (·), what we must learn (∞), and management implications (§)**

◆ **Animals pollinate plants.**

- ◆ Animal pollinators allow scattered individuals to outcross, permitting high tree diversity (Regal 1977).
- ◆ Birds, bats, and insects serve as pollinators (Appanah 1990; Bawa 1990; Schatz 1990).
- ◆ Some pollinating birds (Feinsinger 1980), bats (Lee 1980) and insects (Williams 1958) migrate.
- ◆ The bats in Malaysia which pollinate durians also eat mangrove pollen. The destruction of mangrove habitats and bat caves in Malaysia thus imperils its durian industry.
- ◆ What proportion of pollinators migrate? We must identify migrant pollinators.

**Table 2 (continued)**

- ◆ We must protect alternate habitats and resources of migrating pollinators.
- ◆ **Animals protect plants against herbivores and pathogens.**
  - ◆ Are insectivorous birds needed to protect a forest's trees from defoliation by insects?
  - ◆ Excluding insectivorous birds leads to defoliation and death of Australian *Eucalyptus* forest (Loyn 1987).
  - ◆ On BCI, excluding insectivorous birds allows insect populations to build up in aerial tangles of *dead* leaves (Gradwohl and Greenberg 1982).
  - ◆ Rough calculations suggest that half the "consuming biomass" of a tropical forest's leaf-eating insects are destined to be eaten by birds (Leigh and Windsor 1982, 1990).
  - ◆ Management practices (such as using insecticides) which kill insectivorous birds should be avoided.
  - ◆ Animals help seeds escape species-specific pests by dispersing seeds away from their parents (Janzen 1970).
  - ◆ In the most diverse rainforest, over 90% of tree species are dispersed by animals (Gentry 1982; Emmons 1989).
  - ◆ Some plants cannot replace themselves unless their seeds are dispersed. On BCI, Panamá, seeds of *Virola surinamensis* must be dispersed to survive (Howe et al. 1985). In Guanacaste, Costa Rica, seeds of *Hymenaea courbaril* must be dispersed by agoutis (Hallwachs 1986). In Côte d'Ivoire, seeds of *Saccoglottis gabonensis* must be dispersed by elephants (Alexandre 1978).
  - ◆ On BCI, seeds of *Astrocaryum standleyanum* (Smythe 1989) and *Virola surinamensis* (Forget and Milleron 1991) must be buried by agoutis to be saved from destruction by insects.
  - ◆ On BCI, *Virola surinamensis* regeneration depends on the intervention of both toucans and agoutis (Forget and Milleron 1991).
  - ◆ Some dispersers, like toucans, migrate (Foster 1982b); some are prize game, like agoutis (Smythe 1978), some need special nest sites, like hornbills which nest in dead trees (Jacobs 1988).
  - ◆ What species require their seeds to be dispersed or buried by animals in order to regenerate? We must identify crucial dispersers and "protectors," especially those which migrate, those prized by hunters, and those with unusual requirements.
  - ◆ We must protect crucial dispersers, and the alternative habitats and foods they require (Terborgh 1990b).
- ◆ **Animals facilitate the coexistence of different kinds of plants.**
  - ◆ Insect pests keep at least some tree species rare, making room for others (Janzen 1970; Howe 1990).
  - ◆ Each tree species attracts different defoliators, pollinators, and dispersers (Janzen 1981, 1983), which respond differently to the climate differences of successive years, causing their host plants to respond differently as well (Leigh 1990).
  - ◆ These different reproductive responses create a "sorting in time" of reproductive success.
  - ◆ Theory predicts that this sorting facilitates coexistence of different species (Chesson and Warner 1981).



**Table 2 (continued)**

- ◆ Does this "sorting in time" of reproductive success contribute substantially to tropical tree diversity?
  - ◆ If so, animal diversity must be protected for the sake of plant diversity.
  - ◆ **Do pests favor evolution of higher fruit production and increased populations of game animals?**
    - ◆ Insect pests favor dispersal of a tree's seeds far beyond the "neighborhood" of adult trees with which their parent's roots or crown competes directly (Janzen 1970).
    - ◆ Seed dispersal thus promotes reproductive competition between different neighborhoods (trait-groups) of adult trees (Wilson 1980).
    - ◆ Theory predicts that competition among neighborhoods favors increased seed and fruit production, even by means which also benefit neighboring trees, and selects against "spiteful" competition which reduces the agent's own growth rate in order to harm or kill competitors (Wilson 1980).
    - ◆ How might a tree benefit its neighbors by increasing its own growth rate and fruit production?  
(Perhaps by making leaves which rot and release nutrients more readily when they fall, or by using types of mycorrhizae that neighbors can share: Leigh 1991).
    - ◆ What are the observable effects of this theoretical competition among neighborhoods?
    - ◆ It is essential to consider evolutionary as well as ecological consequences of management decisions.
- 

We need to understand the natural history of tropical forest. Autecological studies of especially interesting species will not suffice. We need field stations where many students work independently on different organisms and share their results. Low-budget student projects at the primitive, ill-equipped Manú (Terborgh 1983, 1990; Terborgh et al. 1990), have been especially spectacular. (The Manú's lack of financial support is the most stunning condemnation we know of the funding priorities of both the U.S. National Science Foundation and non-governmental organizations.) Such arrangements would facilitate the identification and study of the interactions which maintain the integrity of ecosystems (Karr 1990).

Research at a single site, even one with the Manú's pristine glory, can-

not provide a sufficient basis for conservation strategies appropriate to all habitats. For example, BCI's agoutis bury seeds dispersed by other animals (Forget and Milleron 1991), but agoutis of Costa Rica's dry forest disperse seeds (Hallwachs 1986). Migration patterns—in birds (Loiselle and Blake 1991), butterflies (Williams 1958), moths (Smith 1976, 1990), and bats (Handley et al. 1991)—will differ from site to site. Local research stations are needed to establish conservation policies appropriate for local conditions (Rubinoff and Leigh 1990).

#### **ACKNOWLEDGMENTS**

We are most grateful to Olga Linares for encouragement, and to George Angehr, Joseph Wright, Robin Foster, and Elizabeth Leigh for helpful and timely criticism.

- Aide, T. M. 1988. Herbivory as a selective agent on the timing of leaf flush in a tropical understory community. *Nature* 336:574-575.
- . 1991. Synchronous leaf production and herbivory in juveniles of *Gustavia superba*. *Oecologia* 88:511-514.
- Aide, T. M., and E. C. Londoño. 1989. The effects of rapid leaf expansion on the growth and survivorship of a lepidopteran herbivore. *Oikos* 55:66-70.
- Alexandre, D.-Y. 1978. Le rôle disséminateur des éléphants en forêt de Taï, Côte-d'Ivoire. *La Terre et la Vie* 32: 47-71.
- Allen, D. L. 1979. *Wolves of Minong: Their Vital Role in a Wild Community*. Houghton Mifflin, Boston.
- Appanah, S. 1990. Plant-pollinator interactions in Malaysian rain forests. Pp. 85-101 in Bawa and Hadley (1990).
- Ashton, P. S., T. J. Givnish, and S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* 132:44-66.
- Augsburger, C. K. 1982. A cue for synchronous flowering. Pp. 133-150 in Leigh et al. (1982).
- . 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759-771.
- . 1990. Una señal para la floración sincrónica. Pp. 201-218 in Leigh et al. (1990).
- Bawa, K. S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21:399-422.
- Bawa, K. S., and M. Hadley (eds.). 1990. *Reproductive Ecology of Tropical Forest Plants*. Parthenon, Park Ridge, New Jersey.
- Bonaccorso, F. J. 1979. Foraging and reproduction ecology in a Panamanian bat community. *Bulletin of the Florida State Museum, Biological Sciences* 24:359-408.
- Burghardt, G. M., H. W. Greene, and A. S. Rand. 1977. Social behavior in hatchling green iguanas: Life in a reptile rookery. *Science* 195:689-691.
- Bush, M. B., D. R. Piperno, P. A. Colinvaux, P. E. De Oliveira, L. A. Krissek, and M. C. Miller. In press. A 14,300 year paleoecological profile of a lowland tropical lake in Panama. *Ecological Monographs*.
- Chesson, P. L., and R. R. Warner. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117:923-943.
- Clark, D. B., and D. A. Clark. 1987. Population ecology and microhabitat distribution of *Dipteryx panamensis*, a neotropical rain forest emergent tree. *Biotropica* 19:236-244.
- Corner, E. J. H. 1964. *The Life of Plants*. World Press, Cleveland.
- De Steven, D., and F. E. Putz. Impact of mammals on early recruitment of a tropical canopy tree, *Dipteryx panamensis*, in Panama. *Oikos* 43:207-216.
- Dirzo, R., and A. Miranda. 1990. Contemporary Neotropical defaunation and forest structure, function and diversity—a sequel to John Terborgh. *Conservation Biology* 4:444-447.
- . 1991. Altered patterns of herbivory and diversity in the forest understory: A case study of the possible consequences of contemporary defaunation. Pp. 273-287 in P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson (eds.). *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*. John Wiley, New York.
- Emmons, L. H. 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* 50:31-54.
- . 1987. Comparative feeding ecology of felids in a neotropical rainforest. *Behavioral Ecology and Sociobiology* 20:271-283.
- . 1989. Tropical rain forests: Why they have so many species and how we may lose this biodiversity without cutting a single tree. *Orion Nature Quarterly* 8(3): 8-14.
- Emmons, L. H., A. Gautier-Hion, and G. Dubost. 1983. Community structure of the frugivorous-folivorous forest mammals of Gabon. *Journal of Zoology* 199:209-222.

- Feinsinger, P. 1980. Asynchronous migration patterns and the coexistence of tropical hummingbirds. Pp. 411-419 in A. Keast and E. S. Morton (eds.). *Migrant Birds in the Neotropics*. Smithsonian Institution Press, Washington, D.C.
- Forget, P.-M., and T. Milleron. 1991. Evidence for secondary seed dispersal by mammals in Panama. *Oecologia* 87:596-599.
- Foster, R. B. 1982a. The seasonal rhythm of fruitfall on Barro Colorado Island. Pp. 151-172 in Leigh et al. (1982).
- . 1982b. Famine on Barro Colorado Island. Pp. 201-212 in Leigh et al. (1982).
- . 1990a. Ciclo estacional de caída de frutos en la isla de Barro Colorado. Pp. 219-241 in Leigh et al. (1990).
- . 1990b. Hambruna en la isla de Barro Colorado. Pp. 271-283 in Leigh et al. (1990).
- Foster, R. B., and N. V. L. Brokaw. 1982. Structure and history of the vegetation on Barro Colorado Island. Pp. 67-81 in Leigh et al. (1982).
- . 1990. Estructura e historia de la vegetación de la isla de Barro Colorado. Pp. 113-127 in Leigh et al. (1990).
- Gentry, A. H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15:1-84.
- . 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75:1-34.
- Giacalone, J., W. E. Glanz, and E. G. Leigh, Jr. 1990. Adición: fluctaciones poblacionales a largo plazo de *Sciurus granatensis* en relación con la disponibilidad de frutos. Pp. 331-335 in Leigh et al. (1990).
- Glanz, W. E. 1982. The terrestrial mammal fauna of Barro Colorado Island: Censuses and long-term changes. Pp. 455-468 in Leigh et al. (1982).
- . 1990a. Fauna de mamíferos terrestres de la isla de Barro Colorado: Censos y cambios a largo plazo. Pp. 523-536 in Leigh et al. (1990).
- . 1990b. Neotropical mammal densities: How unusual is the community on Barro Colorado Island, Panama? Pp. 287-313 in A. H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven.
- Glanz, W. E., R. W. Thorington, Jr., J. Giacalone-Madden, and L. R. Heaney. 1982. Seasonal food use and demographic trends in *Sciurus granatensis*. Pp. 239-252 in Leigh et al. (1982).
- . 1990. Utilización estacional de alimentos y tendencias demográficas de *Sciurus granatensis*. Pp. 317-330 in Leigh et al. (1990).
- Gradwohl, J., and R. Greenberg. 1982. The effect of a single species of avian predator on the arthropods of aerial leaf litter. *Ecology* 63:581-583.
- Hallwachs, W. 1986. Agoutis (*Dasyprocta punctata*): The inheritors of guapinol (*Hymenaea courbaril*: Leguminosae). Pp. 285 - 304 in A. Estrada and T. H. Fleming (eds.), *Frugivores and Seed Dispersal*. W. Junk, Dordrecht.
- Handley, C. O., Jr., and E. G. Leigh, Jr. 1991. Foraging behavior. Pp. 137-140 in Handley et al. (1991).
- Handley, C. O., Jr., D. E. Wilson, and A. L. Gardner (eds.). 1991. Demography and natural history of the common fruit bat, *Artibeus jamaicensis*, on Barro Colorado Island, Panamá. *Smithsonian Contributions to Zoology* 511:1-173.
- Hogan, K. P., A. P. Smith, and L. H. Ziska. 1991. Potential effects of elevated CO<sub>2</sub> and changes in temperature on tropical plants. *Plant, Cell and Environment* 14:763-778.
- Howe, H. F. 1990. Seed dispersal by birds and mammals: Implications for seedling demography. Pp. 191-218 in Bawa and Hadley (1990).
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201-228.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66:781-791.
- Hubbell, S. P., R. Condit, and R. B. Foster. 1990. Presence and absence of density dependence in a neotropical tree community. *Philosophical Transactions of the Royal Society of London, Series B*, 330:269-281.

- Hubbell, S. P., and R. B. Foster. 1986. Commonness and rarity in a neotropical forest: implications for tropical tree conservation. pp. 205-231 in M. Soulé, ed. *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer, Sunderland, Massachusetts.
- . 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. Pp. 522-541 in A. H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81-101.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals. *American Naturalist* 94:145-159.
- Irvine, D. 1989. Succession management and resource distribution in an Amazonian rain forest. *Advances in Economic Botany* 7:223-237.
- Jacobs, M. 1988. *The Tropical Rain Forest*. Springer-Verlag, Berlin.
- Janson, C. H., and L. H. Emmons. 1990. Ecological structure of the non-flying mammal community at Cocha Cashu Biological Station, Manu National Park, Peru. Pp. 314-338 in A. H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forest. *American Naturalist* 104:501-528.
- . 1981. Patterns of herbivory in a tropical deciduous forest. *Biotropica* 13:271-282.
- . 1983. Food webs: Who eats what, why, how, and with what effects in a tropical forest? Pp. 167-181 in F. B. Golley (ed.), *Tropical Rain Forest Ecosystems, A.: Structure and Function*. Elsevier, Amsterdam.
- Jones, S. E. 1977. Coexistence in mixed species antwren flocks. *Oikos* 29:366-375.
- Karr, J. R. 1982. Avian extinctions on Barro Colorado Island, Panama: A reassessment. *American Naturalist* 119:220-239.
- . 1990. Biological integrity and the goal of environmental legislation: Lessons for conservation biology. *Conservation Biology* 4:244-250.
- Keller, M., M. E. Mitre, and R. F. Stallard. 1990. Consumption of atmospheric methane in soils of central Panama: Effects of agricultural development. *Global Biogeochemical Cycles* 4:21-27.
- Leck, C. F. 1971. Overlap in the diet of some neotropical birds. *The Living Bird* 89-106.
- Lee, D. 1980. *The Sinking Ark: Environmental Problems in Malaysia and Southeast Asia*. Heinemann, Kuala Lumpur.
- Leigh, E. G., Jr. 1975. Structure and climate in tropical rain forest. *Annual Review of Ecology and Systematics* 6:67-86.
- . 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90:213-239.
- . Jr. 1982. Estructura y clima en la pluvisilva tropical. Pp. 161-175 in G. A. de Alba and R. W. Rubinoﬀ (eds.), *Evolución en los Tropicos*. Smithsonian Tropical Research Institute and Editorial Universitaria, Panamá.
- . 1990. Introducción: ¿Por qué hay tantos tipos de árboles tropicales? Pp. 75-99 in Leigh et al. (1990).
- . 1991. Genes, bees and ecosystems: The evolution of a common interest among individuals. *Trends in Ecology and Evolution* 6:257-262.
- Leigh, E. G., Jr., A. S. Rand, and D. M. Windsor (eds.). 1982. *The Ecology of a Tropical Forest*. Smithsonian Institution Press, Washington, D.C.
- . 1990. *Ecología de un Bosque Tropical*. Smithsonian Tropical Research Institute, Balboa, Panamá.
- Leigh, E. G., Jr., and D. M. Windsor. 1982. Forest production and regulation of primary consumers on Barro Colorado Island. Pp. 111-122 in Leigh et al. (1982).
- . 1990. Producción del bosque y regulación de consumidores primarios de la isla de Barro Colorado. Pp. 179-190 in Leigh et al. (1990).
- Leigh, E. G., Jr., S. J. Wright, F. E. Putz, and E. A. Herre. In press. The decline of tree diversity on newly isolated tropical islands: A test of a null hypothesis and some implications. *Evolutionary Ecology*.

- Loiselle, B. A., and J. G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. *Ecology* 72:180-193.
- Loyn, R. H. 1987. The bird that farms the dell. *Natural History* 87(6):54-60.
- Milton, K. 1982. Dietary quality and demographic regulation in a howler monkey population. Pp. 273-289 in Leigh et al. (1982).
- Milton, K. 1990a. Calidad dietética y regulación demográfica de una población de monos aulladores *Alouatta palliata*. Pp. 357-373 in Leigh et al. (1990).
- . 1990b. Annual mortality patterns of a mammal community in central Panama. *Journal of Tropical Ecology* 6:493-499.
- Mitchell, B. J. 1989. *Resources, Group Behavior and Infant Development in White-faced Capuchin Monkeys*, *Cebus capucinus*. Ph.D. Dissertation, University of California, Berkeley.
- Montgomery, G. G., and M. E. Sunquist. 1978. Habitat selection and use by two-toed and three-toed sloths. Pp. 329-357 in G. G. Montgomery (ed.), *The Ecology of Arboreal Folivores*. Smithsonian Institution Press, Washington, D.C.
- Morrison, D. W. 1978. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* 59:716-723.
- Piperno, D. R. 1990. Fitólitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla de Barro Colorado. Pp. 153-156 in Leigh et al. 1990.
- Prentice, I. C., P. J. Bartlein, and T. Webb III. 1991. Vegetation and climate change in eastern North America since the last glacial maximum. *Ecology* 72:2038-2056.
- Putz, F. E., E. G. Leigh, Jr., and S. J. Wright. 1990. Solitary confinement in Panama. *Garden* 14(2):18-23.
- Rand, A. S., and H. W. Greene. 1982. Latitude and climate in the phenology of reproduction in the Green Iguana, *Iguana iguana*. Pp. 150-161 in G. M. Burghardt and A. S. Rand (eds.), *Iguanas of the World: Their Behavior, Ecology and Conservation*. Noyes, Park Ridge, New Jersey.
- Regal, P. J. 1977. Ecology and evolution of flowering plant dominance. *Science* 196:622-629.
- Rubinoff, I., and E. G. Leigh, Jr. 1990. Dealing with diversity: The Smithsonian Tropical Research Institute and tropical biology. *Trends in Ecology and Evolution* 5:115-118.
- Russell, J. K. 1982. Timing of reproduction by coatis (*Nasua narica*) in relation to fluctuations in food. Pp. 413-431 in Leigh et al. (1982).
- Sabatier, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Écologie (La Terre et la Vie)* 40:289-329.
- Schatz, G. E. 1990. Some aspects of pollination biology in Central American forests. Pp. 69-84 in Bawa and Hadley (1990).
- Smith, N. G. 1972. Migrations of the day-flying moth *Urania* in Central and South America. *Caribbean Journal of Science* 12(1-2): 45-58.
- Smith, N. G. 1990. El porqué de la migración del lepidóptero diurno *Urania fulgens* (Uraniidae: Geometroidea). Pp. 415-431 in Leigh et al. (1990).
- Smythe, N. 1970. Relationships between fruiting seasons and seed dispersal methods in a neotropical forest. *American Naturalist* 104:25-35.
- . 1978. The natural history of the central American agouti (*Dasyprocta punctata*). *Smithsonian Contributions to Zoology* 257:1-52.
- . 1982. The seasonal abundance of night-flying insects in a Neotropical forest. Pp. 309-318 in Leigh et al. (1982).
- . 1989. Seed survival in the palm *Astrocaryum standleyanum*: Evidence for dependence on its seed dispersers. *Biotropica* 21:50-56.
- . 1990. Abundancia estacional de insectos nocturnos en un bosque neotropical. Pp. 393-402 in Leigh et al. (1990).
- Smythe, N., W. E. Glanz, and E. G. Leigh, Jr. 1982. Population regulation in some terrestrial frugivores. Pp. 227-238 in Leigh et al. (1982).
- . 1990. Regulación de la población de algunos frugívoros terrestres. Pp. 305-316 in Leigh et al. (1990).
- Terborgh, J. W. 1983. *Five New World Primates*. Princeton University Press, Princeton, New Jersey.

- . Community aspects of frugivory in tropical forests. Pp. 371-384 in A. Estrada and T. H. Fleming (eds.), *Frugivores and Seed Dispersal*. W. Junk, Dordrecht.
- . 1986b. Keystone plant resources in the tropical forest. Pp. 330-344 in M. Soulé, ed. *Conservation Biology*. Sinauer, Sunderland, MA.
- . 1988. The big things that run the world—A sequel to E. O. Wilson. *Conservation Biology* 2:402-403.
- . 1990. An overview of research at Cocha Cashu Biological Station. Pp. 48-59 in A. H. Gentry (ed.), *Four Neotropical Rainforests*. Yale University Press, New Haven.
- . 1990b. Seed and fruit dispersal—Commentary. Pp. 181-190 in Bawa and Hadley (1990).
- Terborgh, J. W., and S. K. Robinson. 1986. Guilds and their utility in ecology. Pp. 65-90 in J. Kikkawa and D. Anderson (eds.), *Community Ecology: Pattern and Process*. Blackwell Scientific Publications, Oxford.
- Terborgh, J. W., S. K. Robinson, T. A. Parker III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60:213-238.
- Welden, C. W., S. W. Hewett, S. P. Hubbell, and R. B. Foster. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology* 72:35-50.
- Williams, C. B. 1958. *Insect Migrations*. Collins, London.
- Willis, E. O. 1974. Populations and local extinctions of birds on Barro Colorado Island, Panamá. *Ecological Monographs* 44:153-169.
- Wilson, D. S. 1980. *The Natural Selection of Populations and Communities*. Benjamin/Cummings, Menlo Park, California.
- Windsor, D. M. 1990. Climate and moisture variability in a tropical forest: Long-term research from Barro Colorado Island, Panamá. *Smithsonian Contributions to the Earth Sciences* 29:1-145.
- Wolda, H. 1978. Seasonal fluctuations in rainfall, food and abundance of tropical insects. *Journal of Animal Ecology* 47:369-381.
- . 1982. Seasonality of Homoptera on Barro Colorado Island. Pp. 319-330 in Leigh et al. (1982).
- . 1990. Estacionalidad de los Homoptera de la isla de Barro Colorado. Pp. 403-414 in Leigh et al. (1990).
- Worthington, A. H. 1982. Population sizes and breeding rhythms of two species of manakins in relation to food supply. Pp. 213-225 in Leigh et al. (1982).
- . 1990. Comportamiento de forrajeo de dos especies de saltarines en respuesta a la escasez de frutos. Pp. 285-304 in Leigh et al. (1990).
- Wright, S. J. 1990. Cumulative satiation of a seed predator over the fruiting season of its host. *Oikos* 58:272-276.
- Zaret, T. M., and A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. *Ecology* 52:336-342.

