

A FRAMEWORK FOR ASSESSMENT AND MONITORING OF SMALL MAMMALS IN A LOWLAND TROPICAL FOREST

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Abstract. Development projects in tropical forests can impact biodiversity. Assessment and monitoring programs based on the principles of adaptive management assist managers to identify and reduce such impacts. The small mammal community is one important component of a forest ecosystem that may be impacted by development projects. In 1996, a natural gas exploration project was initiated in a Peruvian rainforest. The Smithsonian Institution's Monitoring and Assessment of Biodiversity program cooperated with Shell Prospecting and Development Peru to establish an adaptive management program to protect the region's biodiversity. In this article, we discuss the role of assessing and monitoring small mammals in relation to the natural gas project. We outline the conceptual issues involved in establishing an assessment and monitoring program, including setting objectives, evaluating the results and making appropriate decisions. We also summarize the steps taken to implement the small mammal assessment, provide results from the assessment and discuss protocols to identify appropriate species for monitoring.

Keywords: adaptive management, assessment, development, monitoring, small mammals, tropical forests

1. Introduction

Managing forest ecosystems depends on the ability to comprehend changes caused by natural events and human actions in those ecosystems (Dallmeier, 1997). An assessment and monitoring program based on adaptive management principles can provide natural resource managers with the information to understand changes and make appropriate decisions regarding the use and maintenance of forest resources and biodiversity in the forest ecosystems (Spellerberg, 1992; Dallmeier and Comiskey, 1998). The small mammal community is one of several components of a forest ecosystem that managers may choose to investigate, depending on their objectives. In this article, we discuss the role of assessing and monitoring small mammals within an adaptive management framework. As an example, we describe a multi-taxa assessment and monitoring project developed to investigate the effects of natural gas exploration on a Peruvian rainforest. For the purposes of this study, we considered the following indigenous mammalian Orders as small mammals: Rodentia (families Muridae and Echimyidae), Chiroptera and Didelphimorphia.



In 1996, the Smithsonian Institution's Monitoring and Assessment of Biodiversity Program (SI/MAB) began a multi-taxa assessment and monitoring program in an unexplored Amazonian rainforest in southeastern Peru. The program was initiated because of the revival of a natural gas exploration project managed by Shell Prospecting and Development Peru (SPDP). Concerned about the possible effects on biodiversity, SI/MAB and SPDP collaborated to ensure wise use of natural resources and protection of biodiversity in the region (Dallmeier and Alonso, 1997). Following consultations with stakeholders, SI/MAB proposed a multi-taxa, biodiversity assessment and monitoring project in the forests surrounding four natural gas drilling sites to provide the data necessary for appropriate decisions and actions regarding development of the gas resource.

The company's project was located in the Lower Urubamba region, which lies at the confluence of the Urubamba, Camisea and Cashiriari rivers 50 kilometers (km) northwest of Manu National Park along the foothills of the Andes Mountains. The study area encompassed approximately 600 km² at approximately 12°S latitude and 73°W longitude. The dominant vegetation was non-flooded, old-growth, lowland tropical rainforest (Comiskey *et al.*, 2001); about one-half of the study area was dominated by the understory bamboo *Guadua sarcocarpa*. Dallmeier and Alonso (1997) provide further details regarding the study area.

Biotic and abiotic components of tropical forests exist in a complex web wherein changes in any one component may lead to changes in others. In the Lower Urubamba, as is the case in many tropical forests, the components of the forest and their interactions were poorly understood. SI/MAB proposed a multi-taxa approach. Over a two-year period, scientists assessed the vegetation, aquatic systems, arthropods, amphibians and reptiles, birds and mammals in the region. Based on this assessment, a system of monitoring was developed that would allow SPDP to evaluate management strategies and objectives designed to protect the region's biodiversity (Dallmeier and Alonso, 1997; Alonso and Dallmeier, 1998, 1999).

2. The Ecological Importance of Small Mammals

Small mammals are important elements of tropical forest ecosystems. They affect the structure, composition and dynamics of forest communities through activities such as seed dispersal (Brewer and Rejmanek, 1999), pollination (Janson *et al.*, 1981; Fleming and Sosa, 1994; Carthew and Goldingay, 1997), mycorrhizal dispersal (Janos *et al.*, 1995), impacts on insect populations (Yahner and Smith, 1991; Cook *et al.*, 1995) and as food for carnivorous animals (Greene, 1988; Wright *et al.*, 1994).

Seed dispersal and predation are two of the more influential effects that small mammals have on tropical forests. Tropical plant diversity is thought to be influenced by high mortality rates among seeds and seedlings when they fall near the parent (Janzen, 1970; Connell, 1971; Clark and Clark, 1984). The high mor-

tality rates are partially attributed to predation by small mammals, especially rodents, which can be voracious seed predators (Forget, 1992; Brewer and Rejmanek, 1999). However, small mammals also act as vectors for seed dispersal, thus providing plants with a mechanism to avoid high mortality (Janzen, 1970; Connell, 1971). Although non-volant small mammals have been shown to be effective seed dispersers in the neotropics (Smythe, 1970; Charles-Dominique *et al.*, 1981; Denslow and Moermond, 1982; Smythe, 1986; Janzen, 1986; Forget, 1990; Brewer and Rejmanek, 1999), this role has been attributed mostly to bats in both the neotropics (Fleming, 1979, 1981, 1988; Estrada and Fleming, 1986) and the paleotropics (Fujita and Tuttle, 1991; Shilton *et al.*, 1999). In Costa Rica, Fleming and Heithaus (1981) showed that bats defecate large numbers of non-related seeds of several species around fruiting plants and roost sites. This creates mixed-species seed shadows around fruit sources, which lowers seed and seedling mortality and helps to maintain high plant species diversity (Janzen, 1970). Furthermore, as dispersers, bats play an important role in successional and restoration processes by dispersing pioneer species in and around sites of human-caused disturbance (Thompson and Willson, 1978; Galindo, 1998; Medellin and Gaona, 1999). Bats have been shown to disperse *Cecropia* spp. and other neotropical pioneer species into abandoned cornfields, old fields and cacao plantations (Medellin and Gaona, 1999). In relation to dispersal, passage of seeds through the guts of frugivores often enhances germination rates (Traveset, 1998).

Small mammals, both bats and non-volant species, are also responsible for pollination. Although mammals are not as effective at pollination as insects (Bawa, 1990), bats are more likely to be long-distance carriers of pollen (Heithaus *et al.*, 1974; Lemke, 1984). This capacity for long-distance distribution of pollen has been shown to affect the genetics of tropical tree populations over large areas (Hamrick and Loveless, 1989).

Many tropical plants require mutualistic relationships with fungi to form vesicular-arbuscular mycorrhizal fungi (Trappe, 1987). Such relationships enhance the ability of plants to take in many nutrients (Allen, 1991). In tropical forest soils where nutrients are often limited, mycorrhizal fungi can improve a plant's survival ability and increase plant growth (Janos, 1980a, 1985). This ultimately affects plant competition, successional patterns, forest structure, composition and diversity (Janos, 1980b, 1983, 1985; Connell and Lowman, 1989). Janos *et al.* (1995) demonstrate that rodents in a neotropical forest are effective dispersers of mycorrhizal fungi.

Small mammals have also been shown to affect forest dynamics through insect predation. Andersen and Folk (1993) describe a situation where a shrew (*Blarina brevicauda*) and a mouse (*Peromyscus leucopus*) reduced survivorship of weevils that fed on the acorns of oak trees (*Quercus* spp.). Predation by the small mammals on the weevils had a positive effect on oak populations, and thus could lead to impacts on forest composition and functioning.

All of these processes ultimately lead to greater reproductive success for plants (Fleming and Sosa, 1994). It has also been shown, however, that resource development activities can alter, fragment or contaminate small mammal habitats, dramatically affecting the distribution, abundance and diversity of the animals (Yahner, 1992; Granjon *et al.*, 1996; Adler *et al.*, 1997; Malcolm, 1997; Gascon and Lovejoy, 1998; Nupp and Swihart, 1998; Stevens and Husband, 1998). Changes in the small mammal community will lead to changes elsewhere in the forest. The loss of a keystone disperser can have major effects throughout the community because of the loss of mutualistic links (Gilbert, 1980; Janzen and Martin, 1982; Howe, 1984; Terborgh, 1986; Levey *et al.*, 1994). For this reason, resource managers need to consider the impacts of development on small mammals when setting management objectives. A clear understanding of small mammal population dynamics is essential for appropriate management in tropical forests.

3. The Adaptive Management Framework

Four inter-related components comprise the adaptive management framework: definition of goals and objectives, assessment and monitoring, evaluation and decision-making (Holling, 1978; Walters, 1986; Hilborn, 1992). Clear goals and objectives are needed to identify benchmarks for evaluating management strategies. The next step, assessment, provides the baseline data – which species are present and a measure of their abundance. The assessment can include descriptions of the habitat, inventories (including identification and classification of species), studies of natural history and the ecology of target taxa, and literature reviews (Spellerberg, 1991; Dallmeier and Comiskey, 1998). Monitoring consists of repeated measuring and sampling of species over time and comparing the results to the baseline (Hollawell, 1991). As a combined process, assessment and monitoring track the status of the target taxa and measure progress toward meeting management objectives. Thus, assessment and monitoring provide the evidence needed for project adaptation, continuation or cessation (Holling, 1978; Dallmeier and Comiskey, 1998; Elzinga *et al.*, 1998; Comiskey *et al.*, 2000).

3.1. SETTING THE OBJECTIVES

An assessment and monitoring program was developed based on a management strategy that sought to mitigate the potential impacts of natural gas exploration on the small mammal community. We set the following objectives: (1) obtain baseline information regarding the status and distribution of small mammals in the Lower Urubamba region, (2) compare the small mammal community of the region to that of other neotropical forests and (3) develop monitoring protocols for small mammals.

3.2. THE ASSESSMENT

The assessment provides the baseline data necessary for managers to evaluate the consequences of the use of forest resources (Spellerberg, 1992). As a first step, Rudran and Foster (1996) recommend conducting comprehensive inventories at a study site to confirm the presence of as many species as possible in the shortest amount of time. There are many techniques available for inventorying small mammals. Wilson *et al.* (1996b) and Bookhout (1994) provide excellent descriptions of many of these techniques, and Voss and Emmons (1996) discuss techniques and strategies proven effective for neotropical mammals. We conducted a comprehensive inventory of the small mammal species present in and around the well sites.

3.2.1. *Non-volant Mammals*

Trapping is typically the most effective means to assess the smaller rodents and marsupials present in an area (Voss and Emmons, 1996), and it results in voucher specimens. Because of the various behavioral adaptations and habitat and food preferences of small mammals, a variety of trap types, placement and baits is necessary to maximize the diversity of species captured. Because our objective was to determine the species present, we utilized a sampling design to maximize the potential number of species encountered. We established trap lines at the four sites in a systematic and biased fashion, subjectively selecting the locations to ensure adequate sampling of a large proportion of all micro-habitats occurring at each site. For example, we placed traps in transitional forests, stream sides, patches of bamboo and areas near logs, branches, rocky outcrops and cultivated areas. When estimating abundance, trap lines are placed at random and standardized for number of traps per trap station, number of trap stations per trap line and distance between trap stations (see monitoring section). Along each trap line, we established trap stations approximately every 10 meters (m). At each station, we set several types of traps, including snap traps (Victor brand rat traps) and live traps (Sherman and Tomahawk traps). We baited traps daily, each morning and evening, with a mixture of oats, peanut butter, vanilla, fruits or vegetables.

This sampling strategy provided a comprehensive list of the small mammal species present in the Lower Urubamba region. We base this conclusion on lists of expected species derived from long-term studies of the small mammal communities in other lowland tropical forests of southeastern Peru (Voss and Emmons, 1996), including nearby Manu National Park (Pacheco *et al.*, 1993; Table I). Overall, we confirmed the presence of 100 species of small mammals, including 35 non-volant species (17 Didelphimorphs, 13 Murid and 5 Echimyid rodents; Solari *et al.*, 2001). This suggests that by subjectively sampling small, non-volant mammals with a variety of traps, locations and baits, we recorded nearly all of the species expected to be present at the site.

TABLE I

Number of small mammal species by Order recorded at four neotropical sites in southeastern Peru (data modified from Voss and Emmons, 1996; Solari *et al.*, 2001)

Site	Sampling period (years)	Didelphimorphia	Chiroptera	Rodentia	
				Muridae	Echimyidae
Balta	3	11	56	10	6
Cocha Cashu/Pakitza	21	12	60	11	7
Cuzco Amazonico	2	9	44	11	5
Lower Urubamba region	2	17	65	13	5

3.2.2. *Bats*

Neotropical bat communities are extremely rich. Like small, non-volant mammals, bats exhibit a number of behaviors and habitat preferences. Therefore, sampling bats requires a variety of sampling strategies. Tuttle (1976), Kunz and Kurta (1988) and Wilson *et al.* (1996b) provide reviews of methods and materials available for sampling bats. We captured bats using mist nets at all sites. Voss and Emmons (1996) indicate that mist nets set in the forest understory can be effective in sampling many species of bats. Similar to the placement of the trap lines for small non-volant mammals, we set mist nets in a subjective manner across trails, streams and forest edges and at a variety of heights in the canopy to maximize the number of species encountered. Each night, we placed up to 15 mist nets at a site, leaving the nets open for 4 to 12 hours. We varied the sampling effort and net location to maximize the diversity of species captured.

As with the non-volant mammal sampling strategy, our bat sampling strategy proved to be effective in assessing the number of species present in the Lower Urubamba region. Overall, we confirmed the presence of 65 species of bats (Solari *et al.*, 2001), which makes the Lower Urubamba the richest bat community in southeastern Peru (Table I) and one of the richest in the neotropics (Voss and Emmons, 1996; Solari *et al.*, 2001).

3.2.3. *Voucher Specimens*

Voucher specimens are particularly important for those small mammals that are difficult to identify and poorly known and therefore are subject to taxonomic revision. For these reasons, voucher specimens are essential to lend credibility to an assessment (Reynolds *et al.*, 1996). Standardized methods for preserving, recording, documenting and archiving vouchers exist and are summarized by Yates (1985) and Yates *et al.* (1987, 1996).

We prepared voucher specimens as standard museum study skins and skulls or preserved them whole in 10% formalin. We deposited museum specimens at the Museo de Historia Natural, Universidad Nacional Mayor de San Marcos in Lima, Peru, and at the National Museum of Natural History, Smithsonian Institution, Washington, DC, U.S.A.

3.3. MONITORING

Implementing a monitoring program for all 101 small mammal species recorded thus far in the Lower Urubamba would be impractical. The needed financial and human resources would be prohibitive, and because little information exists concerning the natural history of many of these species, the data would be difficult to interpret. Based on the assessment and our objectives, we identified a subset of 35 species for monitoring that will allow us to evaluate the impacts of development (Table II).

There are several options available when selecting appropriate species to monitor. One is to monitor indicators, which are measurable surrogates for environmental endpoints (Noss, 1990). Indicator species are those whose presence and fluctuations are believed to reflect those of other species in the community (Landres *et al.*, 1988). There are multiple approaches to choosing indicator species (Noss, 1990, 1999; Simberloff, 1998). Fenton *et al.* (1992) and Wilson *et al.* (1996a) suggest the use of certain bat species as indicators of human-caused habitat disturbance in neotropical forests. They state that disturbed habitats contain a distinct subset of the species that might be available in undisturbed habitats. Their comparisons between disturbed and undisturbed habitats at six neotropical sites show that species such as *Phyllostomus hastatus*, *Desmodus rotundus* and *Carollia perspicillata* are more abundant in highly disturbed sites, and an increasing abundance of these species may indicate habitat disturbance. Conversely, taxa such as Emballonuridae, the insectivorous Phyllostominae and Vespertilionidae are more abundant in undisturbed habitats and could be used to indicate no habitat disturbance. Twenty species known to occur in the Lower Urubamba have been identified as indicators of habitat disturbance or lack of disturbance, and they were chosen as part of the monitoring program (Table II).

Another monitoring approach focuses on keystone species, which are species having major effects on ecological processes and community diversity (Paine, 1966; Menge *et al.* 1994; Simberloff, 1998). keystones can also be viewed as guilds or groups of functionally equivalent species (Krebs, 1994). Root (1967) states that by focusing on specific functional groups, we do not need to study the entire set of species present in a community. Instead we can concentrate on manageable units. In the Lower Urubamba, we chose seven species of frugivorous bats (Table II) that affect the dynamics of tropical forests through seed dispersal and pollination. Their roles have been reviewed by Fleming and Heithaus (1981), Howe (1986), Fleming *et al.* (1987) and Levey *et al.* (1994). Any changes in the abundance

TABLE II

List of small mammal species known to occur in the Lower Urubamba region, Peru (Solari *et al.*, 2001) identified for monitoring (species listed by Order, with their classification for monitoring noted)

Species	Monitoring class ^a
Didelphimorphia	
<i>Caluromysiops irrupta</i>	re
<i>Marmosa andersoni</i>	re
<i>Marmosops noctivagus</i>	c
<i>Monodelphis emiliae</i>	re
Rodentia	
<i>Oecomys bicolor</i>	c
<i>Oryzomys megacephalus</i>	c
<i>Oryzomys macconnelli</i>	c
<i>Oryzomys nitidus</i>	c
<i>Proechimys simonsi</i>	c
Chiroptera	
<i>Artibeus lituratus</i>	c, f
<i>Artibeus obscurus</i>	c, f
<i>Artibeus planirostris</i>	c, f
<i>Carollia brevicauda</i>	c, f
<i>Carollia castanea</i>	c, f
<i>Carollia perspicillata</i>	c, dh, f
<i>Desmodus rotundus</i>	dh
<i>Eptesicus brasiliensis</i>	uh
<i>Micronycteris megalotis</i>	uh
<i>Micronycteris minuta</i>	uh
<i>Mimon crenulatum</i>	uh
<i>Myotis albescens</i>	uh
<i>Myotis nigricans</i>	uh
<i>Myotis riparius</i>	uh

^a Monitoring class categories: c = common in the region, based on trapping frequency (Solari *et al.*, 2001); therefore it is possible to collect adequate data on abundance; dh and uh = indicator of disturbed or undisturbed habitat (Fenton *et al.*, 1992; Wilson *et al.*, 1996a); f = frugivorous (Emmons and Feer, 1997) and therefore critical for ecological processes that drive forest dynamics; re = rare or endemic and therefore of particular conservation concern.

TABLE II
(continued)

Species	Monitoring class ^a
Chiroptera (continued)	
<i>Myotis simus</i>	uh
<i>Peropteryx kappleri</i>	uh
<i>Peropteryx macrotis</i>	uh
<i>Phyllostomus elongatus</i>	uh
<i>Phyllostomus hastatus</i>	dh
<i>Platyrrhinus brachycephalus</i>	c, f
<i>Rhynchonycteris naso</i>	uh
<i>Saccopteryx bilineata</i>	uh
<i>Saccopteryx leptura</i>	uh
<i>Tonatia brasiliense</i>	uh
<i>Tonatia saurophila</i>	uh
<i>Tonatia sylvicola</i>	uh

^a Monitoring class categories: c = common in the region, based on trapping frequency (Solari *et al.*, 2001); therefore it is possible to collect adequate data on abundance; dh and uh = indicator of disturbed or undisturbed habitat (Fenton *et al.*, 1992; Wilson *et al.*, 1996a); f = frugivorous (Emmons and Feer, 1997) and therefore critical' for ecological processes that drive forest dynamics; re = rare or endemic and therefore of particular conservation concern.

and composition of frugivorous bats caused by a development project may lead to changes in the composition of regional flora, which may then lead to changes in regional fauna.

Rudran and Foster (1996) suggest monitoring target species, those that are the most abundant, easiest to detect or most in need of conservation. The first two criteria assure adequate data for drawing conclusions from the monitoring program. The third criterion is likely to garner support from project stakeholders, but because species in need of conservation usually are not abundant, it may be difficult to collect sufficient data to detect changes in their abundance. By monitoring common species such as rodents from the genera *Oecomys*, *Oryzomys* and *Proechimys* (Table II), it is likely that we can gather sufficient data to evaluate management objectives. For example, one of our management objectives is to regulate the amount of forest edge created by managing the scale of human activity centers in the rainforest. This means we need to focus on the abundance of common species over time in relation to the amount of forest edge and evaluate our management strategy based on whether we detect changes in abundance. In addition, we will be gathering more data regarding the ecology of these common species. Ultimately,

the data will support or refute the value of such species as indicators, making the monitoring program more effective, providing much needed information to assist other projects in the region and adding to the knowledge of tropical forest ecology.

We also chose to monitor three rare species of conservation importance (Table II). Because of the difficulties in gathering adequate data on their abundance, we do not recommend a monitoring program that focuses intensively on rare species.

Once managers and researchers decide which species to monitor, they must then collect information on the abundance of those species. This becomes the first monitoring or sampling period. For both non-volant species and bats, the basic techniques chosen for the Lower Urubamba region will remain the same during the monitoring phase, although it is necessary to standardize the methodology and meet statistical requirements. It is important that the study is designed properly to ensure that results will be statistically valid and comparable to future results. Cochran (1977) provides detailed explanations on sampling design, and Conroy and Nichols (1996) provide an overview.

3.4. EVALUATION

The evaluation provides an opportunity for researchers and managers to reflect on the species and techniques chosen for the monitoring program and to examine the data collected to that point. They can then decide whether the chosen strategies are the most appropriate or whether a new direction must be taken. In the Lower Urubamba region, our preliminary survey design provided the necessary data to meet our objectives. During the steps leading up to monitoring, we continually revisited the evaluation phase, allowing for evolution of our management strategies and objectives as well as the design of our monitoring program.

3.5. DECISION MAKING

Although the adaptive management process is cyclical and continuous, the decision-making stage is the ultimate phase. If the data indicate that trends in the populations under examination fall within acceptable ranges and managers feel that the sampling design is appropriate and capable of detecting real changes, then monitoring should continue without modification. If population values fall outside of the acceptable range, then managers need to make decisions that will either alter the monitoring strategy, alter the objectives of the project or adapt the management plan (Dallmeier and Comiskey, 1998; Comiskey *et al.*, 2000).

4. Conclusion

The methodologies for sampling and monitoring small mammals are well developed, tested and easy to use. However, interpreting the data in an adaptive management framework and understanding the responses of populations of small mammals

to changes in their environment can be challenging, especially when there is little natural history information regarding the species of interest. For example, one potential effect of the gas exploration project in the Lower Urubamba region is habitat fragmentation. Habitat fragmentation affects small mammals by lowering diversity (Adler *et al.*, 1997; Stevens and Husband, 1998), lowering abundance (Granjon *et al.*, 1996; Nupp and Swihart, 1998) and leading to large fluctuations in population abundance (Adler *et al.*, 1997). However, for some species of small mammals, fragmentation has been shown to increase diversity (Gascon and Lovejoy, 1998) and abundance (Adler *et al.*, 1997; Yahner, 1992; Nupp and Swihart, 1998). In still other studies, fragmentation has been shown to have no effects on small mammal populations (Heske, 1995; Bayne and Hobson, 1998; Mahan and Yahner, 1998). Furthermore, small mammal populations have been known to experience oscillations under conditions of no human impact (Krebs, 1996). Because there is such variability in the responses of small mammals to environmental changes, interpretation of monitoring results can be a challenging task. To assess fully the impacts of fragmentation, or in our case the gas project, researchers may have to rely on intensive (large sample sizes) and extensive (investigation of the ecology of many species) field studies.

Our initial determination in the Lower Urubamba region was that the gas exploration project was having little to no effect on small mammal populations (Solari *et al.*, 2001). We based this impression on the extremely high diversity of the small mammal community surrounding the project and its similarities to small mammal communities in other protected areas in the region. Because responses by small mammal populations to human-induced habitat alteration are often contradictory, it is important that scientists critically evaluate the role of small mammals as indicators of ecosystem health and select appropriate species for monitoring.

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References

- Adler, G. H., Arboledo, J. J. and Travi, B. L.: 1997, 'Diversity and abundance of small mammals in degraded tropical dry forest of northern Colombia', *Mammalia* **61**(3), 361–370.
- Allen, M. F.: 1991, *The Ecology of Mycorrhizae*, Cambridge University Press, Cambridge, U.K.

- Alonso, A. and Dallmeier, F. (eds): 1998, *Biodiversity Assessment and Long-term Monitoring of the Lower Urubamba Region, Peru: Cashiriari 3 Well Site and the Camisea and Urubamba Rivers*, SI/MAB Series #2, Smithsonian Institution/MAB Biodiversity Program, Washington, DC.
- Alonso, A. and Dallmeier, F. (eds): 1999, *Biodiversity Assessment and Long-term Monitoring of the Lower Urubamba Region, Peru: Pagoreni Well Site, Assessment and Training*, SI/MAB Series #3, Smithsonian Institution/MAB Biodiversity Program, Washington, DC.
- Andersen, D. C. and Folk, M. L.: 1993, 'Blarina brevicauda and Peromyscus leucopus reduce overwinter survivorship of acorn weevils in an Indiana hardwood forest', *J. Mammal.* **74**(3), 656–664.
- Bawa, K. S.: 1990, 'Plant-pollinator interactions in tropical rain forests', *Ann. Rev. Ecol. System.* **21**, 399–421.
- Bayne, E. M. and Hobson, K. A.: 1998, 'The effects of habitat fragmentation by forestry and agriculture on the abundance of small mammals in the southern boreal mixed wood forest', *Can. J. Zool.* **76**(1), 62–69.
- Bookhout, T. A. (ed.): 1994, *Research and Management Techniques for Wildlife and Habitats*, 5th ed., The Wildlife Society, Bethesda, MD.
- Brewer, S. W. and Rejmanek, M.: 1999, 'Small rodents as significant dispersers of tree seeds in a neotropical forest', *J. Veg. Sci.* **10**(2), 165–174.
- Carthew, S. M. and Goldingay, R. L.: 1997, 'Non-flying mammals as pollinators', *Trends Ecol. Evol.* **12**(3), 104–108.
- Charles-Dominique, P., Atramentowicz, M., Charles-Dominique, M., Gérard, H., Hladik, A., Hladik, C. M. and Prévost, M. F.: 1981, 'Les mammifères frugivores arboricoles nocturnes d'une forêt guyanaise: Interrelations plantes-animaux', *Rev. Ecol. Terre Vie* **35**, 341–435.
- Clark, D. A. and Clark, D. B.: 1984, 'Spacing dynamics of a tropical rain forest tree: Evaluation of the Janzen-Connell model', *Amer. Natur.* **124**, 769–788.
- Cochran, W. G.: 1977, *Sampling Techniques*, 3rd ed., Wiley, New York.
- Comiskey, J. A., Campbell, P., Alonso, A., Mistry, S., Dallmeier, F., Nuñez, P., Beltran, H., Baldeon, S., Nauray, W., de la Colina, W., Acurio, L. and Udvardy, S.: 2001, 'Vegetation Assessment of the Lower Urubamba Region, Peru', in F. Dallmeier, A. Alonso and P. Campbell (eds), *Biodiversity of the Lower Urubamba Region, Peru*, SIMAB Series 7, Smithsonian Institution/MAB Biodiversity Program, Washington, DC.
- Comiskey, J. A., Dallmeier, F. and Alonso, A.: 2000, 'Framework for Assessment and Monitoring of Biodiversity', in S. Levin (ed.), *Encyclopedia of Biodiversity*, Vol. 1, Academic Press, London.
- Connell, J. H.: 1971, 'On the Role of Natural Enemies in Preventing Competitive Exclusion in Some Marine Animals and Rain Forest Trees', in P. J. den Boer and G. R. Gradwell (eds), *Dynamics of Populations: Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations*, Oosterbeek, 1970, Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Connell, J. H. and Lowman, M. D.: 1989, 'Low-diversity tropical rain forests: Some possible mechanisms for their existence', *Amer. Natur.* **134**, 88–119.
- Conroy, M. J. and Nichols, J. D.: 1996, 'Designing a Study to Assess Mammalian Diversity', in D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran and M. S. Foster (eds), *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*, Smithsonian Institution Press, Washington, DC.
- Cook, S. P., Smith, H. R., Hain, F. P. and Hastings, F. L.: 1995, 'Predation of gypsy moth (Lepidoptera: Lymantriidae) pupae by invertebrates at low small mammal population densities', *Environ. Entomol.* **24**(5), 1234–1238.
- Dallmeier, F.: 1997, 'Biodiversity Assessment and Monitoring for Adaptive Management', in F. Dallmeier and A. Alonso (eds), *Biodiversity Assessment and Long-term Monitoring of the Lower Urubamba Region, Peru: San Martin 3 and Cashiriari 2 Well Sites*, SI/MAB Series #1, Smithsonian Institution/MAB Biodiversity Program, Washington, DC.

- Dallmeier, F. and Alonso, A. (eds): 1997, *Biodiversity Assessment and Long-term Monitoring of the Lower Urubamba Region Peru: San Martin 3 and Cashiriari 2 Well Sites*. SI/MAB Series #1, Smithsonian Institution/MAB Biodiversity Program, Washington, DC.
- Dallmeier, F. and Comiskey, J. A.: 1998, 'Forest Biodiversity Assessment, Monitoring, and Evaluation for Adaptive Management', in F. Dallmeier and J. A. Comiskey (eds), *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies*, Man and the Biosphere Series, Vol. 20, UNESCO, Paris, and Parthenon Publishing Group, New York.
- Denslow, J. S. and Moermond, T. C.: 1982, 'The effect of accessibility on rates of fruit removal from tropical shrubs: An experimental study', *Oecologia* **54**, 170–176.
- Elzinga, C. L., Salzer, D. W. and Willoughby, J. W.: 1998, *Measuring and Monitoring Plant Populations*, United States Bureau of Land Management, Denver.
- Emmons, L. H. and Feer, F.: 1997, *Neotropical Rainforest Mammals: A Field Guide*, 2nd ed., University of Chicago Press, Chicago.
- Estrada, A. and Fleming, T. H. (eds): 1986, *Frugivores and Seed Dispersal*, W. Junk, Dordrecht.
- Fenton, M. B., Acharya, L., Audet, D., Hickey, M. B. C., Merriman, C., Obrist, M. K., Syme, D. M. and Adkins, B.: 1992, 'Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the neotropics', *Biotropica* **24**(3), 440–446.
- Fleming, T. H.: 1979, 'Do tropical frugivores compete for food?', *Amer. Zool.* **19**, 1157–1172.
- Fleming, T. H.: 1981, 'Fecundity, fruiting pattern and seed dispersal in *Piper amalago* (Piperaceae), a bat-dispersed tropical shrub', *Oecologia* **51**, 42–46.
- Fleming, T. H.: 1988, *The Short-tailed Fruit Bat: A Study in Plant-animal Interactions*, University of Chicago Press, Chicago.
- Fleming, T. H., Breitwisch, R. and Whitesides, G. H.: 1987, 'Patterns of tropical vertebrate frugivore diversity', *Ann. Rev. Ecol. System.* **18**, 91–109.
- Fleming, T. H. and Heithaus, E. R.: 1981, 'Frugivorous bats, seed shadows, and the structure of tropical forests', *Biotropica* **13**(suppl.), 45–53.
- Fleming, T. H. and Sosa, V. J.: 1994, 'Effects of nectarivorous and frugivorous mammals on reproductive success of plants', *J. Mammal.* **75**(4), 845–851.
- Forget, P. M.: 1990, 'Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana', *J. Trop. Ecol.* **6**(4), 459–468.
- Forget, P. M.: 1992, 'Regeneration ecology of *Eperua grandiflora* (Caesalpiniaceae), large-seeded tree in French Guiana', *Biotropica* **24**(2A), 146–156.
- Fujita, M. S. and Tuttle, M. D.: 1991, 'Flying foxes (Chiroptera: Pteropodidae): Threatened animals of key ecological and economic importance', *Conserv. Biol.* **5**(4), 455–463.
- Galindo, G. J.: 1998, 'Seed dispersion by fruit bats: Its importance in the conservation and regeneration of tropical forests', *Acta Zool. Mex. Nueva Ser.* **73**, 57–74.
- Gascon, C. and Lovejoy, T. E.: 1998, 'Ecological impacts of forest fragmentation in central Amazonia', *Zoology (Jena)* **101**(4), 273–280.
- Gilbert, L. E.: 1980, 'Food Web Organization and the Conservation of Neotropical Diversity', in M. Soulé and B. Wilcox (eds), *Conservation Biology: An Evolutionary-ecological Perspective*, Sinauer Associates, Sunderland, Massachusetts.
- Granjon, L., Cosson, J. F., Judas, J. and Ringuelet, S.: 1996, 'Influence of tropical rainforest fragmentation on mammal communities in French Guiana: Short-term effects', *Acta Oecol.* **17**(6), 673–684.
- Greene, H. W.: 1988, 'Species Richness in Tropical Predators', in F. Almeda and C. M. Pringle (eds), *Diversity and Conservation of Tropical Rainforests*, California Academy of Science, San Francisco.
- Hamrick, J. and Loveless, L.: 1989, 'Genetic Structure of Tropical Tree Populations: Associations with Reproductive Biology', in J. H. Bock and Y. B. Linhart (eds), *The Evolutionary Ecology of Plants*, Westview Press, Boulder, Colorado.

- Heithaus, E. R., Opler, P. A. and Baker, H. G.: 1974, 'Bat activity and pollination of *Bauhinia pauletia*: Plant-pollinator coevolution', *Ecology* **55**, 412–419.
- Hellawell, J. M.: 1991, 'Development of a Rationale for Monitoring', in F. B. Goldsmith (ed.), *Monitoring for Conservation and Ecology*, Conservation Biology Series 3, Chapman and Hall, London.
- Heske, E. J.: 1995, 'Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: Is there an edge effect?', *J. Mammal.* **76**(2), 562–568.
- Hilborn, R.: 1992, 'Can fisheries learn from experience?', *Fisheries* **17**(4), 6–14.
- Holling, C. S. (ed.): 1978, *Adaptive Environmental Assessment and Management*, John Wiley and Sons, New York.
- Howe, H. F.: 1984, 'Implications of seed dispersal by animals for tropical reserve management', *Biol. Conserv.* **30**, 261–281.
- Howe, H. F.: 1986, Seed Dispersal by Fruit-eating Birds and Mammals, in R. D. Murray (ed.), *Seed Dispersal*, Academic Press, New York.
- Janos, D. P.: 1980a, 'Vesicular-arbuscular mycorrhizae affect lowland tropical rain forest plant growth', *Ecology* **61**, 151–162.
- Janos, D. P.: 1980b, 'Mycorrhizae influence tropical succession', *Biotropica* **12**(suppl.), 56–64.
- Janos, D. P.: 1983, Tropical Mycorrhizas, Nutrient Cycles and Plant Growth, in S. L. Sutton, T. C. Whitmore and A. C. Chadwick (eds), *Tropical Rain Forest: Ecology and Management*, Blackwell Scientific, Oxford.
- Janos, D. P.: 1985, Mycorrhizal Fungi: Agents or Symptoms of Tropical Community Composition?, in R. Molina (ed.), *Proceedings of the Sixth North American Conference on Mycorrhizae*, Forest Research Laboratory, Corvallis, Oregon.
- Janos, D. P., Sahley, C. T. and Emmons, L. H.: 1995, 'Rodent dispersal of vesicular-arbuscular mycorrhizal fungi in Amazonian Peru', *Ecology* **76**(6), 1852–1858.
- Janson, C. H., Terborgh, J. W. and Emmons, L. H.: 1981, 'Non-flying mammals as pollinating agents in the Amazonian forest', *Biotropica* **13**(suppl.), 1–6.
- Janzen, D. H.: 1970, 'Herbivores and the number of tree species in tropical forests', *Amer. Natur.* **104**, 501–528.
- Janzen, D. H.: 1986, 'Mice, Big Mammals and Seeds: It Matters Who Defecates What Where', in A. Estrada and T. H. Fleming (eds), *Frugivores and Seed Dispersal*, W. Junk, Dordrecht.
- Janzen, D. H. and Martin, P. S.: 1982, 'Neotropical anachronisms: The fruits the Gomphotheres ate', *Science* **215**, 19–27.
- Krebs, C. J.: 1994, *Ecology: The Experimental Analysis of Distribution and Abundance*, 4th ed., Harper Collins College Publishers, New York.
- Krebs, C. J.: 1996, 'Population cycles revisited', *J. Mammal.* **77**(1), 8–24.
- Kunz, T. H. and Kurta, A.: 1988, 'Capture Methods and Holding Devices', in T. H. Kunz (ed.), *Ecological and Behavioral Methods for the Study of Bats*, Smithsonian Institution Press, Washington, DC.
- Landres, P. B., Verner, J. and Thomas, J. W.: 1988, 'Ecological uses of vertebrate indicator species: A critique', *Conserv. Biol.* **2**, 316–328.
- Lemke, T. O.: 1984, 'Foraging ecology of the long nosed bat *Glossophaga soricina*, with respect to resource availability', *Ecology* **65**, 538–548.
- Levey, D. J., Moermond, T. C. and Sloan Denslow, J.: 1994, 'Frugivory: An Overview', in L. A. McDade, K. S. Bawa, H. A. Hespenheide and G. S. Hartshorn (eds), *La Selva: Ecology and Natural History of a Neotropical Rain Forest*, The University of Chicago Press, Chicago.
- Malcolm, J. R.: 1997, 'Biomass and Diversity of Small Mammals in Amazonian Forest Fragments', in W. F. Laurance and R. O. Bierregaard Jr. (eds), *Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities*, University of Chicago Press, Chicago.

- Mahan, C. G. and Yahner, R. H.: 1998, 'Lack of population response by eastern chipmunks (*Tamias striatus*) to forest fragmentation', *Amer. Midl. Natur.* **140**(2), 382–386.
- Medellin, R. A. and Gaona, O.: 1999, 'Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico', *Biotropica* **31**(3), 478–485.
- Menge, B. A., Berlow, E. L., Blanchette, C. A., Navarrette, S. A. and Yamada, S. B.: 1994, 'The keystone species concept: Variation in interaction strength in a rocky intertidal habitat', *Ecol. Monogr.* **64**, 249–286.
- Noss, R. F.: 1990, 'Indicators for monitoring biodiversity: A hierarchical approach', *Cons. Biol.* **4**(4), 355–364.
- Noss, R. F.: 1999, 'Assessing and monitoring forest biodiversity: A suggested framework and indicators', *For. Ecol. Manage.* **115**, 135–146.
- Nupp, T. E. and Swihart, R. K.: 1998, 'Effects of forest fragmentation on population attributes of white-footed mice and eastern chipmunks', *J. Mammal.* **79**(4), 1234–1243.
- Pacheco, V., Patterson, B. D., Patton, J. L., Emmons, L. H., Solari, S. and Ascorra, C. F.: 1993, 'List of Mammal Species Known to Occur in Manu Biosphere Reserve, Peru', *Publicaciones del Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (A)* **44**, 1–12.
- Paine, R. T.: 1966, 'Food web complexity and species diversity', *Amer. Natur.* **100**, 65–75.
- Reynolds, R. P., Crombie, R. I., McDiarmid, R. W. and Yates, T. L.: 1996, 'Voucher Specimens', in D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran and M. S. Foster (eds), *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*, Smithsonian Institution Press, Washington, DC.
- Root, R. B.: 1967, 'The niche exploitation pattern of the blue-gray gnatcatcher', *Ecol. Monogr.* **37**, 317–350.
- Rudran, R. and Foster, M.: 1996, 'Conducting a Survey to Assess Mammalian Diversity', in D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran and M. S. Foster (eds), *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*, Smithsonian Institution Press, Washington, DC.
- Shilton, L. A., Altringham, J. D., Compton, S. G. and Whittaker, R. J.: 1999, 'Old world fruit bats can be long distance seed dispersers through extended retention of viable seeds in the gut', *Proc. Roy. Soc. of London Ser. B Biol. Sci.* **266**(1416), 219–223.
- Simberloff, D.: 1998, 'Flagships, umbrellas, and keystones: Is single-species management passé in the landscape era?', *Biol. Conserv.* **83**(3), 247–257.
- Smythe, N.: 1970, 'Relationships between fruiting season and seed dispersal methods in a neotropical forest', *Amer. Natur.* **104**, 25–35.
- Smythe, N.: 1986, 'Competition and resource partitioning in the guild of neotropical terrestrial frugivorous mammals', *Ann. Rev. Ecol. System.* **17**, 169–188.
- Solari, S., Vivar, E., Velazco, P., Rodriguez, J. J., Wilson, D., Baker, R. and Mena, J. L.: 2001, 'The Small Mammal Community in the Neotropical Rainforests of the Lower Urubamba River Valley, Peru', in F. Dallmeier, A. Alonso and P. Campbell (eds), *Biodiversity of the Lower Urubamba Region, Peru*, SIMAB Series 7, Smithsonian Institution/MAB Biodiversity Program, Washington, DC.
- Spellerberg, I. F.: 1991, *Monitoring Ecological Change*, Cambridge University Press, Cambridge.
- Spellerberg, I. F.: 1992, *Evaluation and Assessment for Conservation*, Chapman and Hall, London.
- Stevens, S. M. and Husband, T. P.: 1998, 'The influence of edge on small mammals: Evidence from Brazilian Atlantic forest fragments', *Biol. Conserv.* **85**(1–2), 1–8.
- Terborgh, J.: 1986, 'Keystone Plant Resources in the Tropical Forest', in M. E. Soulé (ed.), *Conservation Biology: The Science of Scarcity and Diversity*, Sinauer Associates, Sunderland, Massachusetts.
- Thompson, J. N. and Willson, M. F.: 1978, 'Disturbance and the dispersal of fleshy fruits', *Science* **200**, 1161–1163.

- Trappe, J. M.: 1987, 'Phylogenetic and Ecologic Aspects of Mycotrophy in the Angiosperms from an Evolutionary Standpoint', in G. R. Safir (ed.), *Ecophysiology of VA Mycorrhizal Plants*, CRC Press, Boca Raton, Florida.
- Traveset, A.: 1998, 'Effect of seed passage through vertebrate frugivores' guts on germination: Review', *Persp. Plant Ecol. Evol. System.* **1**(2), 151–190.
- Tuttle, M. D.: 1976, 'Collecting Techniques', in R. J. Baker, J. K. Jones Jr. and D. C. Carter (eds), *Biology of Bats of the New World Family Phyllostomatidae*, Part I, Special Publication of the Museum of Texas Tech University, Lubbock, Texas.
- Voss, R. S. and Emmons, L. H.: 1996, 'Mammalian diversity in neotropical lowland rainforests: A preliminary assessment', *Bull. Amer. Mus. Nat. Hist.* **230**, 1–115.
- Walters, C. J.: 1986, *Adaptive Management of Renewable Resources*, McGraw Hill, New York.
- Wilson, D. E., Ascorra, C. F. and Solari, S.: 1996a, 'Bats as Indicators of Habitat Disturbance', in D. E. Wilson and A. Sandoval (eds), *Manu: The Biodiversity of Southeastern Peru*, Smithsonian Institution Press, Washington, DC.
- Wilson, D. E., Cole, F. R., Nichols, J. D., Rudran, R. and Foster, M. S. (eds): 1996b, *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*, Smithsonian Institution Press, Washington, DC.
- Wright, S. J., Gompper, M. E. and Deleon, B.: 1994, 'Are large predators keystone species in neotropical forests? The evidence from Barro Colorado Island', *Oikos* **71**(2), 279–294.
- Yahner, R. H.: 1992, 'Dynamics of a small mammal community in a fragmented forest', *Amer. Mid. Natur.* **127**(2), 381–391.
- Yahner, R. H. and Smith, H. R.: 1991, 'Small mammal abundance and habitat relationships on deciduous forested sites with different susceptibility to gypsy moth defoliation', *Environ. Manage.* **15**(1), 113–120.
- Yates, T. L.: 1985, 'The role of voucher specimens in mammal collections: Characterization and funding responsibilities', *Acta Zool. Fennica* **170**, 81–82.
- Yates, T. L., Barber, W. R. and Armstrong, D. M.: 1987, 'Survey of North American collections of recent mammals', *J. Mammal.* **68**(suppl.), 1–76.
- Yates, T. L., Jones, C. and Cook, J. A.: 1996, 'Appendix 3: Preservation of Voucher Specimens', in D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran and M. S. Foster (eds), *Measuring and Monitoring Biological Diversity: Standard Methods for Mammals*, Smithsonian Institution Press, Washington, DC.