A DECADE OF RESEARCH ON PHILIPPINE MAMMALS: PROGRESS AND CHALLENGES

LAWRENCE R. HEANEY

ABSTRACT

The mammal fauna of the Philippines is exceptionally rich in endemic mammals, and also has a very high proportion of endangered species. Research during the period 1990 to 2000 has resulted in an improved understanding of the basic systematics of the 172 native land-mammal species known to be present. Some of the recently-discovered species have been formally described (but others have not), and a few identification keys are now available (but more are badly needed). Studies of comparative morphology, karyotypes, and protein allozymes have yielded information on phylogenetic relationships, but this topic remains poorly investigated. Published faunal surveys have produced the first comprehensive inventories in the country yielding much crucial information on ecology and biogeography and the material for taxonomic studies, but many more are needed, and many unpublished surveys are not available.

Biogeographic analyses have demonstrated that distributions of mammals have been profoundly influenced by the extent of Pleistocene islands and by climatic variation along elevational gradients in the many mountains of the Philippines. Each Pleistocene island is a unique center of biodiversity, and many high mountains (or mountain ranges) are unique subcenters. Patterns of genetic variation within species match very well with these Pleistocene islands, suggesting that speciation and diversification within the Philippines is intimately tied to this geological history. Further studies are needed to integrate phylogenetic information with biogeographic and ecological data.

Ecological studies have demonstrated that species richness of some groups (e.g., bats) is highest in the lowlands, and that species richness of other groups (e.g., rodents) is highest at high elevations, often in lower mossy forest. Reproductive biology of fruit bats is well known from several studies, demonstrating that females of some small Philippine species are unique in being pregnant for 95% of their lives, but have low total

reproductive output. The reproductive biology of most Philippine mammals remains poorly known or unknown. Population ecology and community ecology are well-known at a few sites, but generally poorly known at this time. We do know that many natural communities are very species-rich and that densities are often very high, and that native and non-native species often have very different patterns of habitat use, feeding ecology, movement, and longevity.

Information on conservation status of mammals has improved greatly, with at least some information on distribution and abundance available for most species, and this allows us to estimate their decline in population due to destruction of habitat, and the relative vulnerability of most species. Recent studies of seed dispersal by fruit bats demonstrate their key role in naturally regenerating rain forest. Loss of about 94% of old-growth forest habitat has left many species highly vulnerable. The increase in number of protected areas (due in part to discovery of new species and biogeographic analysis) has improved the prospects for conservation, but more are needed. Current knowledge is sufficient to guide some crucial conservation efforts, but much essential information is not currently available.

Introduction

It is now generally recognized by both the scientific and the conservation communities that the Philippine Islands support one of the most species-rich, highly endemic, and highly endangered mammal faunas in the world (Groombridge, 1992; Mittermeier et al., 1997, 1999; Myers, 2000). The fact that this is recognized is due largely to research efforts that have taken place in the country during the last 20 years, and especially to the work done in the last decade. While there remain enormous gaps in our knowledge, enough is known to indicate that the Philippine mammal fauna has gone from one of the least-well known in the world to one of the better-known faunas in Asia, in terms of systematics, biogeography, ecology, and conservation status and priorities. The purpose of this paper is to identify the primary topics of research during the period of 1990 - 2000, and to identify the topics and issues that should be among the high priorities during the coming decade.

There are many formats that could be used for such a summary. In this paper, I will present information organized by research topic, rather than by taxon or by geographic region, simply because it reflects my own perspective. Within the four topical areas, I will primarily follow a taxonomic and/or geographic organization. In general, I refer only to published studies, because all others are effectively unavailable. While this review focuses on research published in the period of 1990 to 2000, I include a few crucial references from the late 1980s and a few publications currently in press.

Systematics

The most basic level of understanding for any fauna is the one that involves the ability to recognize species. Discussion of any other issue is made vastly more difficult when we do not know how to recognize or what name to use for an animal, and our ability to recognize the evolutionary relationships of species is key to many other topics of research; both of these topics can be approached through a variety of means, including morphological studies, karyological studies, and genetics.

Several groups of mammals have been the subjects of recent taxonomic studies, including shrews (Heaney and Ruedi, 1994), primates (Fooden, 1991a, 1991b; Timm and Birney, 1992), bats (Ruedas et al., 1994), murid rodents (Musser and Heaney, 1992; Musser et al., 1998; Rickart and Heaney 1991; Rickart et al., 1998; Ruedas, 1995), cats (Groves, 1997b), wild pigs (Groves, 1997a), and deer (Grubb, 1993). A summary of the Philippine mammal fauna (Heaney, 1998) listed 201 species, including 22 marine mammals, 172 native terrestrial mammals, and 7 introduced, non-native species; this included 16 species (eleven not yet formally described) discovered since the previous checklist published in 1988 (Heaney et al., 1988). Much of the fundamental work of

describing new species and rigorously defining genera remains to be done, with perhaps the greatest challenges among the murid rodents and insectivorous bats. Identification of bats has been eased by a key to species (Ingle and Heaney, 1992), and two brief field keys to the bats and the non-flying mammals of Mindanao (Ingle et al., 1999; Heaney et al., 1999), but for all other groups and areas, no keys are available.

Our ability to assess the relationships among species, and to verify their distinctiveness, has been enhanced by recent karyological studies of bats (Rickart et al., 1988, 1999) and murid rodents (Rickart and Musser, 1993). These studies have helped to identify aspects of the process of speciation, but only a small number of species in the Philippines have been karyotyped thus far, and much remains to be done. Studies of genetics (based on protein allozyme) are still fewer, limited to some data on shrews (Heaney and Ruedi, 1994) and on two species of fruit bats (Peterson and Heaney, 1993), with no published studies yet taking advantage of the newer DNA sequencing technologies.

Phylogenies have been presented only for shrews (Heaney and Ruedi, 1994), fruit bats and murids (Heaney and Rickart, 1990), and these were limited in scope and robustness. This limits our ability to interpret many issues (e.g., biogeographic patterns, evolution of life history traits and other ecological patterns), and represents a substantial current shortcoming to our knowledge.

Faunistics and Biogeography

Knowledge of the fauna requires that we understand the distributions and habitat relationships of every species, and that we recognize the general patterns that are formed by the sum of distribution patterns of individual species - the topics that are involved in biogeography.

Intensive inventories of faunas on specific islands or mountains include those of Catanduanes Island (Heaney et al., 1991), Leyte, Biliran, and Maripipi Islands (Rickart et al., 1993), Sibuyan Island (Goodman and Ingle, 1993), Camiguin Island (Heaney and Tabaranza, 1997), Siquijor Island (Lepiten, 1997), the Sierra Madre of northeast Luzon (Mallari and Jensen, 1993; Danielsen et al., 1994), and Mt. Isarog in southern Luzon (Rickart et al., 1991; Heaney et al., 1999), Mt. Kitanglad (Heaney, 2001), and with brief studies on Mindoro (Gonzalez and Dans, 1999; Ocampo et al., 1999). Field studies were conducted in many other areas during the decade, but the results have not been published. Because many of these inventories have resulted in the discovery of previously unknown species of mammals, they demonstrate that we still have much to learn about even the most basic aspects of mammalian biodiversity in the country. Intensive inventories such as these are needed in every part of the country, since most provinces and islands have had very few species recorded (Heaney et al., 1998, in press).

Analyses of biogeographic patterns among fruit bats (Heaney, 1991b) have shown that these animals likely entered the Philippines from both the Southeast Asian mainland and New Guinea/Australia, that most of the Pleistocene islands in the Philippines have unique species, and that species richness is related to island area. Much evidence supports the hypothesis that there are strong interactions between elevational patterns and distributional patterns among fruit bats and murid rodents, such that species that live in the lowlands tend to be widespread on many Pleistocene islands (defined as those connected to each other during periods of low sea level; Heaney, 1991a) within the archipelago, whereas those in the highlands usually are restricted to a single

Pleistocene island and often show evidence of speciation within a given Pleistocene island (Heaney and Rickart, 1990). Each of these Pleistocene islands is a separate center of endemism, with 40-90% of the non-flying mammals unique to the Pleistocene island (Heaney, 1993; Heaney and Regalado, 1998). Patterns of genetic variation within two species of fruit bats match the general biogeographic patterns very closely (Peterson and Heaney, 1993). Independent patterns of variation in karyotypes within several groups of bats strongly reflect biogeographic patterns (Rickart et al., 1999). A general model of island biogeography suggests that species richness on any given island is influenced by direct colonization from other islands (and occasionally the continent), by extinction, and by phylogenetic diversification within the archipelago, with local phylogenesis potentially accounting for up to about 75% of the biodiversity of a given group (Heaney, 2000). During the coming years, biogeographic analysis needs to focus on poorly-known parts of the country (such as the Batanes, Babuyan, and Sulu groups and the mountains of Mindoro, Palawan, northern Luzon, Panay, and southern and western Mindanao), on integrative studies of phylogeny and distribution (= "phylogeography"), on measuring rates and mechanisms of natural colonization, speciation, and extinction, and on integrating biogeographic data with ecological data on such topics as elevational distribution, life history traits, habitat use, foraging ecology, and community structure. These studies should include species of large and small body size, flying and non-flying species, and high and low elevation habitats in order to detect and document the major patterns.

Ecology

Much of what has been learned about the ecology of Philippine mammals has taken place in the context of studies of how they are distributed along elevational gradients. It is now recognized that such gradients play a key role in determining the distribution and abundance of all species (Rickart, 1993), perhaps associated with the vegetation changes that accompany the extreme variation in rainfall (usually ca. 2 m in the lowlands, and up to 12 m per year in mossy forest; Balete and Heaney, 1997). The initial studies of fruit bats, shrews, and rodents on Negros and Leyte islands (Heideman et al., 1987; Heaney et al., 1989) have been followed by those on Mt. Isarog, southern Luzon (Rickart et al., 1991; Balete and Heaney, 1997; Heaney et al., 1999), on Camiguin Island (Heaney and Tabaranza, 1997), and on Mt. Kitanglad (Heaney, 2001). These studies have demonstrated that species richness of fruit bats, and probably insectivorous bats, is highest in the lowland rain forest and declines steadily with increasing elevation. They have also demonstrated that small mammal diversity (shrews and rodents) is low in the lowlands, increases to about 1800 m elevation, and (when the mountain is higher) decreases at progressively higher elevation. This latter pattern of a mid-elevation peak in diversity is increasingly being recognized as a common pattern in many parts of the world (Heaney, 2001). Limited data suggest that mammal faunas on small, depauperate islands may not show these same patterns; further, it is unclear how differences in annual precipitation may affect the specific pattern; and there are many, poorly-evaluated hypotheses as to why these two patterns exist (Heaney, 2001). Much research will be needed to resolve these questions.

There are certain habitats or resources that are critically important to the ecology of some species; for example, it is likely that caves are essential for the survival of many of the species of both fruit and insect-eating bats. However, no

studies of either caves or other equivalent crucial resources have yet been published.

The reproductive biology of Philippine mammals is generally poorly known, with one dramatic exception - the small fruit bats. Through a series of papers by Heideman and his colleagues (Heideman, 1989, Heideman et al., 1993, Heideman and Powell, 1998), we now know that the small endemic genera (*Haplonycteris* and *Otopteropus*) are unique among all mammals in their reproductive patterns. Females become pregnant at about 9 months of age, and these young adults and all adult females in a population each give birth to a single young during a single 10-day period, mate and become pregnant about two weeks after birth, and are pregnant for the rest of the year, including a period of about eight months of arrested development of the implanted embryo. This means that they are pregnant for 95% of their lives. *Ptenochirus* has a similar pattern, but gives birth twice each year (Heideman and Powell, 1998). Reproduction by other species in the country is known only by the number of embryos and time of year when they give birth, or by no data at all. There is great opportunity and need for many more studies of reproductive biology.

Population ecology of fruit bats has been studied in detail by Heideman and Heaney (1989), Ingle (1992, 1993) and Utzurrum (1995), who found them to be characterized by a low rate of reproduction, long lives, and high density. In general, these bats have either small home range size (the endemic genera) or very large home ranges (the widespread Southeast Asian genera). The widespread Southeast Asian fruit bats (and many insectivores) tend to live in disturbed habitats, whereas the endemic species of fruit bats (and many endemic insectivorous bats) live in old-growth or high-quality secondary forest (references above and Heaney et al, 1991, 1999; Rickart et al., 1993). An unpublished PhD dissertation on the foraging ecology of insectivorous bats (Sedlock, 2001) provides a first glimpse of how this diverse part of the mammal fauna uses habitats and food resources. One initially startling discovery is that many murid rodents feed heavily on earthworms, and that density of these specialist vermivore rodents is highly correlated with that of their earthworm prey (Rickart et al., 1991). The single study of forest rodent population ecology (Balete and Heaney, 1997) demonstrated high density of both omnivorous and vermivorous/insectivorous species in mossy forest, and home range size for most species of one-fourth to one-half hectare, which is moderately large. There is great need for many more studies of population ecology, undertaken on single species and complete communities, at all elevations, and of all groups of species, if we are to understand how these animals have evolved in response to their island environment, and, on the basis of that information, how to effectively conserve them.

Conservation Research

While conservation of Philippine mammals has received attention for many decades (reviewed by Rabor 1966; Gonzales and Alcala, 1969; Tabaranza, 1979), some fundamental changes have taken place recently, especially in the last decade. Previously, most attention regarding mammals was given to a few large species (e.g., tamaraw and Calamianes spotted deer) and unusual species (e.g., tarsier and flying lemur), and to a semi-captive population of non-native African large mammals on Calauit Island. For these few species, nearly all effort went to captive breeding; the bulk of Philippine endemic mammals were not considered. Within the last decade, the emphasis has shifted strongly to a much broader concern for the entire mammal fauna, regardless of body size or popular appeal. This has been associated with the growing body of information about the natural history of the mammal fauna as a whole that was described above, but has also been associ-

ated with a recognition that habitat conservation needs to play a much greater role in preservation of the Philippine biota. Awareness that Philippine old-growth rain forest has declined from about 70% in 1900 to about 6% currently has reached the public in part due to the educational efforts of members of the Wildlife Conservation Society of the Philippines (WCSP). Further, the recognition that at least 111 endemic mammals species are present and depend on good-quality rain forest is due largely to the efforts of members of the Wildlife Conservation Society of the Philippines. Some of the key issues and new perspectives concerning conservation of Philippine mammals that have been documented during the past decade, especially those resulting from new research, are the following.

Patterns of diversity and endemism. The Philippine system of parks and protected areas initially was not based on biological criteria, but rather on political criteria. Beginning in about 1988, biologists began to advise governmental, non-governmental, and international agencies (including the Department of Environment and Natural Resources, World Bank, European Union, IUCN, World Wildlife Fund, and Conservation International) on patterns of biotic diversity in the archipelago. In particular, the seemingly complex patterns of endemism within the archipelago were clarified by biogeographic studies that showed the extent of islands during the late Pleistocene period of low sea level; each late Pleistocene island that has been inventoried is a unique center of endemism, with 50 - 80% of the terrestrial mammals being unique (Hauge et al., 1986; Heaney, 1986, 1991b; Heaney and Regalado, 1998). This approach to understanding biodiversity patterns in the archipelago was used recently as the primary baseline for structuring all data and analysis in the National Conservation Priority-Setting Workshop organized by the Department of Environment and Natural Resources and Conservation International in 2000-2001 (Ong et al., in press). This research has also allowed documentation of gaps in the current protected areas system and assessment of priorities for development of protected areas (e.g., Heaney and Mallari, in press; Heaney et al., in press).

Discovery of new species and the need for new national parks. As biogeographic and systematic research has progressed, it has become apparent that certain areas were likely to be centers of endemism, but were nearly or entirely unknown in 1990. For example, the previously unknown mammals of Sibuyan Island, an isolated oceanic island surrounded by deep water, were inventoried in 1989 and 1992. Five new species of mammals were discovered, all endemic to the island (Goodman and Ingle, 1993; Heaney et al., 1997, 1998), resulting in much of the island being declared a national park, and the park being included in the list of eight national parks funded by the European Union through the National Integrated Protected Areas Program. Similarly, Camiguin Island had been surveyed briefly (reported in Heaney, 1984), and no endemic mammals were known, but later analyses indicated that endemic species should be present. Surveys in 1994 and 1995 discovered two distinctive species of rodents (Heaney and Tabaranza, 1997), and resulted in declaration of the mountainous core as a national protected area. Discoveries of new species on Mt. Isarog (southern Luzon) and on Mt. Kitanglad (northern Mindanao) had similar impact on areas that had been given little attention. The discovery of a new species of cloud rat on Panay Island (Gonzalez and Kennedy, 1996) has heightened focus on that island and has led to proposals for designation of a "Panay Mountains National Park", and attention is now being drawn to Balbalan-Balbalasang National Park, an area of unusually high biodiversity in the northern Central Cordillera of Luzon (Heaney et al., 2000). Rediscovery of "extinct" birds and bats on Cebu Island is having a markedly positive effect (Oliver and Pedregosa, unpubl.).

Documentation of the conservation status of mammals. As noted above, previous listing of the conservation status of mammals in the Philippines included only a few large and taxonomically distinctive species. Field studies during the last decade have allowed us to make reasoned judgements of the status of most species, based on actual distributions, habitat requirements, status of the habitat, relative abundance, and assessment of the impact of hunting; for all but a very few species, these had been virtually or entirely unknown. These assessments (e.g., Cox, 1987; Garcia and Deocampo, 1997; Heaney and Heideman, 1987; Heaney and Utzurrum, 1992; Oliver, 1992, 1994, 1999; Oliver et al., 1992, 1993a, 1993b); Heaney et al., 1997, 1998; Utzurrum, 1992; Wildlife Conservation Society of the Philippines, 1997) form the basis for the IUCN Red Data Books (Baillie and Groombridge, 1996) and other similar listings. As a result, some species, including the wood-shrew (*Podogymnura truei*) and tarsier (*Tarsius syrichta*), have been delisted (both are abundant in widespread suitable habitat), but 52 others have been added to the official lists.

Demonstration that mature forest is essential for most species of Philippine endemic mammals. Recent field work has nearly always compared the mammals present in forest of varying degrees of disturbance and agricultural areas, and has produced clear evidence that most of the endemic species, especially those that are threatened, require forested areas with only limited disturbance due to logging (e.g., Heaney et al., 1989, 1991, 1999; Heideman and Heaney, 1989; Ingle, 1992, 1993; Lepiten, 1997; Mallari and Jensen, 1993; Rickart et al, 1991, 1993). These data are often utilized in discussions about the desirability of continued commercial logging in the country. Reforestation with exotic species such as *Gmelina* and *Eucalyptus* is unlikely to promote biodiversity conservation because these species produce tree plantations that are virtually biologically sterile; "re-rain-forestation" in nature is promoted by seed dispersal from remnant forest by birds and bats (Utzurrum, 1995; Ingle, unpubl.) While the debate about logging and reforestation is likely to continue for some years, there is no doubt that biological data, including data about the magnificent endemic mammalian fauna, will play a meaningful role in the future, as the public and government officials recognize that all aspects of the ecosystem, both natural and human-dominated, are interconnected, and that stability of human economic, social, and political systems require stable biological systems.

Some thoughts on the future of research on Philippine mammals

Realistically, it is unlikely that we can anticipate many of the needs for research of the coming decade, much less the conceptual/ theoretical issues that will develop unexpectedly. However, it may still be worthwhile to emphasize some of the current large gaps in our knowledge, and some of the conceptual issues that seem likely to be especially productive.

A recent compilation has demonstrated that most of the provinces on Luzon and Mindanao, and many of the medium and small islands around the country, have not yet been the subject of even the most basic and superficial biological survey (Heaney et al., in press). Obtaining information on the distribution and status of species is the most fundamental issue for both conceptual understanding and for well-planned and successful conservation. In the course of such research, it is virtually certain that new species will be discovered, and these should be described and their basic biology documented. The voucher specimens that are produced will also allow other taxonomic studies that will certainly enlighten us about Philippine biodiversity.

One exciting new area for investigation is the historical development of patterns of biological diversity - the investigation of how the biological diversity of the archipelago was generated, in the context of our greatly increased understanding of the geological history of the islands. Molecular techniques (especially DNA sequencing) hold great promise for helping us to define the evolutionary relationships of species, to determine their place of origin outside of the Philippines, and to document their means of diversification within the archipelago.

Ecological studies need to focus on at least two major issues: first, how the communities of organisms manage to co-exist at a single locality (the ecology of communities); and second, how species respond to various levels of habitat disturbance and destruction (population ecology). These data will be crucial for developing management plans that minimize the impact of humans on the natural biodiversity of the nation, as well as for understanding the natural functioning of this remarkable center of biodiversity. The ecology of special habitats, especially caves, is badly in need of attention.

Conservation research studies need to continue to work hand-in-hand with basic ecological and systematic biodiversity research; I hope that, if nothing else, this review has demonstrated that there can be no real progress on conservation without being a part of on-going basic biodiversity research programs. Moreover, all of the research programs and issues discussed above depend heavily not only on high-quality field work, but also on consistent and timely scholarship - the frequent and careful publication of the results of research and conservation programs, so that the information becomes a matter of public record. Without publication, all of our work could ultimately be little more than an expensive and unproductive hobby.

Finally, during the last decade, we have learned that successful research and conservation depends on the full recognition by regulatory agencies—especially the Department of Environment and Natural Resources and the Protected Areas and Wildlife Bureau—that research on the biota of the Philippines, including mammals, is needed for the welfare of the nation and its natural patrimony, since conservation is fundamentally dependent on good and current data based on carefully conducted, thorough field research. The recent experience with the unintended will work to the benefit of the nation by promoting the most active, high-quality national research program possible on the amazing biodiversity of the nation.

Acknowledgments

I thank the Department of Environment and Natural Resources, especially the Protected Areas and Wildlife Bureau, for encouragement, assistance, and permits for field studies during the last decade. Funding for this research has been provided by the National Science Foundation (BSR-8514223), the Smithsonian Institution Office of Fellowships and Grants, the Barbara Brown, Marshal Field, and Ellen Thorne Smith Funds of The Field Museum, and the John D. and Catherine T. MacArthur Foundation (90-09272A). I thank Nina R. Ingle and Eric A. Rickart for their comments on an earlier draft.

Literature Cited

Baille, J., and B. Groombridge, 1996. 1996 IUCN Red List of Threatened Animals. International Union for the Conservation of Nature, Gland, 368 pp.

Balete, D. S., and L. R. Heaney. 1997. Density, biomass, and movement estimates for murid rodents in mossy forest on Mount Isarog, southern Luzon, Philippines. Ecotropica, 3:91-100.

Cox, R. 1987. The Philippine spotted deer and the Visayan warty pig. Oryx, 21:37-42.

Danielsen, F., D. S. Balete, T. D. Christensen, M. Heegaard, O. F. Jakobsen, A. Jensen, T. Lund, and M. K. Poulsen. 1994. Conservation of Biological Diversity in the Sierra Madre Mountains of Isabela and southern Cagayan Province, the Philippines. BirdLife International, pp. 1-146.

Fooden, J. 1991a. Eastern limit of distribution of the slow loris, *Nycticebus coucang*.International Journal of Primatology, 12:287-290.

Fooden, 1991b. Systematic review of Philippine macaques (Primates: Cercopithecidae: *Macaca fascicularis* subspp.). Fieldiana: Zoology, new series, 64:1-44.

Garcia, M. G. and A. H. Deocampo. 1997. Wild pig meat trading in Iligan City, Mindanao. Sylvatrop 5 (1995):29-34.

Goodman, S. M., and N. R. Ingle. 1993. Sibuyan Island in the Philippines -- threatened and in need of conservation. Oryx, 27:174-180.

Gonzales, P. C. and R. S. Kennedy. 1996. A new species of *Crateromys* (Rodentia: Muridae) from Panay, Philippines. Journal of Mammalogy 77:25-40.

Gonzales, R. B., and A. C. Alcala. 1969. Rare and threatened Philippine vertebrates. Philippine Biota, 4:6-13.

Gonzalez, J. C. T. and A. T. Dans. 1999. Birds and mammals of the fragmented forests along the Anahawin River, Mt. Iglit-Baco National Park, Mindoro Island, Philippines. Sylvatrop 8 (1998):43-61.

Groombridge, B. (ed.) 1992. Global biodiversity: status of the Earth's living resources. Chapman and Hall, London. 585 pp.

Groves, C. P. 1997a. Taxonomy of wild pigs (*Sus*) of the Philippines. Zoological Journal of the Linnean Society 120:163-191.

Groves, C. P. 1997b. Leopard-cats, *Prionailurus bengalensis* (Carnivora: Felidae) from Indonesia and the Philippines, with the description of two new subspecies. Zeitschrift fur Saugetierkunde 62:330-338.

Grubb, P. 1993. Order Artiodactyla, pp. 377-414. *In* Wilson, D. E., and D. M. Reeder, eds., Mammal Species of the World, a Taxonomic and Geographic Reference, 2nd ed. Smithsonian Institution Press, Washington, 1206 pp.

Hauge, P., J. Terborgh, B. Winter, and J. Parkinson. 1986. Conservation priorities in the Philippines. Forktail, 2: 83-. 91.

Heaney, L. R. 1984. Mammals from Camiguin Island, Philippines. Proceedings of the Biological Society of Washington, Washington D. C., 97:119-125.

Heaney, L. R. 1986. Biogeography of mammals in Southeast Asia: estimates of rates of colonization, extinction, and speciation. Biological Journal of the Linnean Society, 28:127-165.

Heaney, L. R. 1991a. A synopsis of climatic and vegetational change in

Southeast Asia. Climatic Change, 19:53-61.
Heaney, L. R. 1991b. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). Bulletin of the American Museum of Natural History, 206:145-167.
Heaney, L. R. 1993. Biodiversity patterns and the conservation of mammals in the Philippines. Asia Life Sciences, 2:261-274.
Heaney, L. R. 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Global Ecology and Biogeography 9:59-74.
Heaney, L. R. 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. Global Ecology and Biogeography, 10:15-39.
Heaney, L. R., D. S. Balete, and A. T. L. Dans. 1997. Terrestrial Mammals. Pp. 116-144. In Wildlife Conservation Society of the Philippines, Philippine Red Data Book. Bookmark, Manila, Philippines. 240 pp.
Heaney, L. R., D. S. Balete, L. Dolar, A. C. Alcala, A. Dans, P. C. Gonzales, N. Ingle, M. Lepiten, W. Oliver, E. A. Rickart, B. R. Tabaranza, Jr., and R. C. B. Utzurrum. 1998. A synopsis of the mammalian fauna of the Philippine Islands. Fieldiana Zoology new series, 88:1-61.
Heaney, L. R., D. S. Balete, E. A. Rickart, R. C. B. Utzurrum, and P. C. Gonzales. 1999. Mammalian diversity on Mt. Isarog, a threatened center of endemism on southern Luzon Island, Philippines. Fieldiana Zoology new series, 95:1-62.
Heaney, L. R., A. Diesmos, B. R. Tabaranza Jr., N. A. Mallari, and R. Brown. 2000. Beacon of Hope - a first report from Kalinga Province, in the Northern Central Cordillera. Haring Ibon (Manila), 2:14-18.
Heaney. L. R., P. C. Gonzales, and A. C. Alcala. 1988. An annotated checklist of the taxonomic and conservation status of land mammals in the Philippines. Silliman Journal (Philippines), 34 (1987):32-66.
Heaney, L. R., P. C. Gonzales, R. C. B. Utzurrum, and E. A. Rickart. 1991. The mammals of Catanduanes Island: implications for the biogeography of small land-bridge islands in the Philippines. Proceedings of the Biological Society of Washington, 104:399-415.
Heaney, L. R., and P. D. Heideman. 1987. Philippine fruit bats, endangered and extinct. Bats, 5:3-5.
Heaney, L. R., P. D. Heideman, E. A. Rickart, R. B. Utzurrum, and J. S. H. Klompen. 1989. Elevational zonation of mammals in the central Philippines. Journal of Tropical Ecology, 5:259-280.
Heaney, L. R., N. R. Ingle, J. L. Sedlock, and B. R. Tabaranza, Jr. 1999.

Non-flying mammals of Mindanao Island, Philippines. Laminated color field guide, 2pp. The Field Museum, Chicago.
Heaney, L. R. and N. A. D. Mallari. 2001. A preliminary analysis of current gaps in the protection of threatened Philippine terrestrial mammals. Sylvatrop, 9: in press.
Heaney, L. R. and J. C. Regalado, Jr. 1998. Vanishing Treasures of the Philippine Rain Forest. The Field Museum, Chicago. 88 pp.
Heaney, L. R., and E. A. Rickart. 1990. Correlations of clades and clines: geographic, elevational,and phylogenetic distribution patterns among Philippine mammals. pp. 321-332. In G. Peters and R. Hutterer (eds.), Vertebrates in the Tropics. Museum Alexander Koenig, Bonn. 424 pp.
Heaney, L. R. and M. Ruedi. 1994. A preliminary analysis of biogeography and phylogeny of shrews (Mammalia: Soricidae) from the Philippine Islands. pp 357-377. The biology of shrews; J. Merritt, G. Kirkland, and R. Rose, eds. Special Publications, Carnegie Museum.
Heaney, L. R., and B. R. Tabaranza, Jr. 1997. A preliminary report on mammalian diversity and conservation status of Camiguin Island, Philippines. Sylvatrop 5 (1995):57-64.
Heaney, L. R., and R. C. B. Utzurrum. 1992. A review of the conservation status of Philippine land mammals. Association of Systematic Biologists of the Philippines Communications, 3 (1991):1-13.
Heaney, L. R., E. K. Walker, B. R. Tabaranza, Jr., and N. R. Ingle. 2001. Mammalian diversity in the Philippines: an assessment of the adequacy of current data. Sylvatrop, 9: in press.
Heideman, P. D. 1989. Delayed development in Fischer's pygmy fruit bat, *Haplonycteris fischeri*, in the Philippines. Journal of Reproduction and Fertility, 85:363-382.
Heideman, P. D., J. A. Cummings, and L. R. Heaney. 1993. Observations on reproductive timing and early embryonic development in an Old World fruit bat, *Otopteropus cartilagonodus* (Megachiroptera). Journal of Mammalogy, 74:621-630.
Heideman, P. D., and L. R. Heaney. 1989. Population biology of fruit bats (Pteropodidae) in Philippine submontane rainforest. Journal of Zoology (London), 218:565-586.
Heideman, P. D., L. R. Heaney, R. L. Thomas, and K. R. Erickson. 1987. Patterns of faunal diversity and species abundance on non-volant mammals on Negros Island, Philippines. Journal of Mammalogy, 68:884-888.
Heideman, P. D. and K. S. Powell. 1998. Age-specific reproductive strategies and delayed embryonic development in an Old-World fruit

bat, *Ptenochirus jagori*. Journal of Mammalogy 79:295-311.
Ingle, N. R. 1992. The natural history of bats on Mt. Makiling, Luzon Island, Philippines. Silliman Journal, 36:1-26.
Ingle, N. R. 1993. Vertical stratification of bats in a Philippine rainforest. Asia Life Sciences, 2:215-222.
Ingle, N. R. and L. R. Heaney. 1992. A key to the bats of the Philippine Islands. Fieldiana Zoology (new series), 69:1-44.
Ingle, N. R., J. L. Sedlock, and L. R. Heaney. 1999. Bats of Mindanao Island, Philippines. Laminated color field guide, 2pp. The Field Museum, Chicago.
Lepiten, M. V. 1997. The Mammals of Siquijor Island, central Philippines. Sylvatrop, 5(1995): 1-17.
Mallari, N. A. D., and Arne Jensen. 1993. Biological diversity in Northern Sierra Madre, Philippines: its implication for conservation and management. Asia Life Sciences, 2:101-112.
Mittermeier, R. A., P.Robles Gil and C.G. Mittermeier (Eds.). 1997. Megadiversity. Earth's Biologically Wealthiest Nations. CEMEX, Monterrey, Mexico. 501 pp.
Mittermeier, R. A., N. Myers, P. Robles G., and C. G. Mittermeier (eds.). 1999. Hotspots, earth's biologically richest and most endangered terrestrial ecosystems. CEMEX, Mexico City. 431 pp.
Musser, G. G., and L. R. Heaney. 1992. Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). Bulletin of the American Museum of Natural History, 211:1-138.
Musser, G. G., L. R. Heaney, and B. R. Tabaranza, Jr. 1998. Philippine rodents: redefinition of known species of *Batomys* (Muridae, Murinae) and description of a new species from Dinagat Island, Philippines. American Museum Novitates, 3237:1-51.
Myers, N. et al. 2000. Hotspots: Earth's biologically richest and most endangered terrestrial ecoregions. Nature 403:
Ocampo, C. C., A. T. L. Dans, J. C. T. Gonzalez, P. A. Alviola, and A. B. Dimapilis. 1999. Mammalian fauna of Mt. Malasimbo, Puerto Galera, Oriental Mindoro, Mindoro Island, Philippines. Sylvatrop 8 (1998):79-85.
Oliver, W. L. R. 1992. The taxonomy, distribution, and status of Philippine wild pigs. Silliman Journal, 36:55-64.
Oliver, W. L. R. 1994. Threatened endemic mammals of the Philippines: an integrated approach to the management of wild and captive populations. pp. 467-477. In P. J. S. Olney, G. M. Mace, and A. T. C. Feistner (eds.), Creative Conservation: Interactive management

of wild and captive animals. Chapman & Hall, London.
Oliver, W. L. R. 1999. Taxonomy and conservation of Philippine wild pigs: an update. Sylvatrop 8 (1998):27-41.
Oliver, W. L. R., C. R. Cox, P. C. Gonzales, and L. R. Heaney. 1993a. Cloud rats in the Philippines - preliminary report on distribution and status. Oryx, 27:41-48.
Oliver, W. L. R., C. R. Cox, and C. P. Groves. 1993b. The Philippine warty pigs (*Sus philippensis* and *Sus cebifrons*. *In* Oliver, W. L. R., ed., Pigs, Peccaries, and Hippos: Status survey and conservation action plan. IUCN, Gland, 202 pp.
Oliver, W. L. R., L. L. Dolar, and E. Alcala. 1992. The Philippine spotted deer, *Cervus alfredi* Sclater, conservation program. Silliman Journal, Dumaguete City, Philippines, 36:47-54.
Peterson, A. T., and L. R. Heaney. 1993. Genetic differentiation in Philippine bats of the genera *Cynopterus* and *Haplonycteris*. Biological Journal of the Linnean Society, 49: 203-218.
Rabor, D. S. 1966. Conservation in the Philippines. Silliman Journal, 13:594-604.
Rickart, E. A. 1993. Diversity patterns of mammals along elevational and disturbance gradients in the Philippines: implications for conservation. Asia Life Sciences, 2:251-260.
Rickart, E. A., and L. R. Heaney. 1991. A new species of *Chrotomys* (Muridae) from Luzon Island, Philippines. Proceedings of the Biological Society of Washington, 104:387-398.
Rickart, E. A., L. R. Heaney, D. S. Balete, and B. R. Tabaranza, Jr. 1998. A review of the genera *Crunomys* and *Archboldomys* (Rodentia, Muridae, Murinae) with descriptions of two new species from the Philippines. Fieldiana Zoology new series, 89:1-24.
Rickart, E. A., L. R. Heaney, P. D. Heideman, and R. C. B. Utzurrum. 1993. The distribution and ecology of mammals on Leyte, Biliran, and Maripipi islands, Philippines. Fieldiana Zoology (new series), 72:1-62.
Rickart, E. A., L. R. Heaney, and M. J. Rosenfeld. 1989. Chromosomes of ten species of Philippine fruit bats (Chiroptera: Pteropodidae). Proceedings of the Biological Society of Washington, 102:520-531.
Rickart, E. A., L. R. Heaney, and R. B. Utzurrum. 1991. Distribution and ecology of small mammals along an elevational transect in southeastern Luzon, Philippines. Journal of Mammalogy, 72:458-469.
Rickart E. A., J. A. Mercier, and L. R. Heaney. 1999. Cytogeography of Philippine bats. Proceedings of the Biological Society of Washington, 112:453-469.
Rickart, E. A., and G. G. Musser. 1993. Philippine rodents: chromosomal characteristics and their significance for phylogenetic inference