19

Small Mammal Diversity in the Tropical Andes: An Overview

José Luis Mena, Sergio Solari, Juan Pablo Carrera, Luis Fernando Aguirre, and Humberto Gómez

The tropical Andes constitute one of the most important regions globally of mammal diversity and endemism (Ceballos and Ehrlich 2006; Mittermeier et al. 1998; Schipper et al. 2008). Nevertheless, taxonomy and distribution of most of mammals there remain inadequately known and revisions of most groups are needed (Gardner 2007). In South America, mammal species new to science are still being discovered at high rates and most species described in recent years are from the tropical Andes and Brazil (Patterson 2000; Reeder et al. 2007).

Small mammals (e.g., bats and rodents) are the most diverse group and account for more than half of the total mammal fauna in any given area. They affect the structure, composition, and dynamics of ecosystems through natural processes such as pollination, seed dispersal and depredation, mycorrhizal dispersal, insectivory, and as food for predators (DeMattia et al. 2004; Mangan and Adler 2002; Muchhala and Jarrín-V 2002; Napolitano et al. 2008; Naranjo et al. 2003; Steiner 1981; Vieira and de Moraes 2006; Walker et al. 2007; Williams-Guillén et al. 2008). Small mammals such as bats are good indicators of habitat disturbance (Castro-Luna et al. 2007; Medellín et al. 2000; Solari et al. 2002; Wilson et al. 1996). Likewise, small mammals have been particularly useful in the study of elevational gradients, mainly because they form well-defined assemblages (in contrast to medium-sized and large mammals) along such gradients (Lomolino 2001; Mena and Vázquez-Domínguez 2005; Patterson et al. 1998).

We here present an overview of the current knowledge about patterns of diversity and endemism for small mammals in the tropical Andes of Colombia, Ecuador, Peru, and Bolivia: marsupials (Didelphimorphia: Didelphidae and Paucituberculata: Caenolestidae), lagomorphs (Lagomorpha: Leporidae), rodents (Rodentia: Abrocomidae, Caviidae, Cricetidae, Ctenomyidae, Echimyidae, Heteromyidae, and Sciuridae), shrews (Soricomorpha: Soricidae), and bats (Chiroptera: Emballonuridae, Furipteridae, Molossidae, Mormoopidae, Natalidae, Noctilionidae, Phyllostomidae, Thyropteridae, and Vespertilionidae). Peru is the fifth most diverse country for mammals in the World (Pacheco et al. 2009) and Ecuador is listed as the ninth most diverse country despite its considerably small area compared to other megadiverse countries such as Brazil or Mexico (Tirira 2007). In order to assess and characterize small mammal diversity in the region, we conducted a survey of the literature (with special attention to elevational gradient studies), plus specimen records from US museum collections in the Mammal Networked Information System (MaNIS) data portals (http://manisnet.org/portals.html) and unpublished reports whenever these were available to us. Elevational gradient studies included here had to cover at least 70 % of the available elevational gradient and were grouped as local or regional (McCain 2007b), representing alpha or gamma diversity, respectively. They were evaluated based on the study group (bats or nonvolant small mammals), proportion of the entire elevational gradient that was sampled, species richness, and general geographic location (see Table 19.1). We follow Wilson and Reeder (2005) as a taxonomic reference.

Diversity and Distribution

At least 411 small mammal species inhabit the tropical Andes above 800 m. Marsupials are represented by 39 species, shrews by 7, bats by 166, rodents by 198, and lagomorphs by 1. Only 28 mammal species (6.2%) are endemic to Colombia, the majority of them are rodents and shrews (Alberico and Rojas-Díaz 2002), but a recent biogeographic analysis on bats added 5 endemic species, some of them restricted to the Andes (Mantilla-Meluk et al. 2009). In Ecuador, 38 species are recognized as endemic (Tirira 2007), although this number is decreasing due to extensive fieldwork and taxonomic revisions in neighboring Colombia and Peru (Mantilla-Meluk and Baker 2008; Pacheco et al. 2009). Most of the small nonvolant endemic species (1 shrew opossum, 2 shrews and 26 rodents) were collected on Andean slopes and highlands (1500 – 4000 m) (Voss 2003; Tirira 2007). Most of the Peruvian endemics (five genera and 65 species) are restricted to the Yungas of the east Andean slope (39 species), followed by the tropical lowland rainforest (14 species) (Pacheco et al. 2009). In Bolivia, one genus and 17 species are endemic, where the Altiplano has the highest degree of regional endemism (followed by the Yungas), and rodents contribute most to the endemism (Salazar-Bravo et al. 2002).

Highland Species Distributions

Among marsupials of the family Caenolestidae, shrew opossums (shrew equivalents or ecomorphs) of the genus *Caenolestes* are restricted to the northern Andes above 2000 m (Lunde and Pacheco 2003), whereas the genus *Lestoros* is restricted to the highlands of southern Peru and northwest Bolivia (Brown 2004). Short eared shrews (genus *Cryptotis*) are restricted to the Andes from Colombia to northern Peru above 1000 m (Eisenberg 1989; Eisenberg and Redford 1999; Gardner 2007), but knowledge about their taxonomy, distribution, and ecology is the most incomplete among Neotropical small mammals (Gardner 2007).

Two groups of rodents are associated with higher elevations in the tropical Andes. In the northern Andes, Ichthyomyini diversity reaches its peak on Andean slopes with nine species in four genera (Voss 1988): *Chibchanomys* (above 2400 m), *Anotomys* (2900 – 4000 m), *Ichthyomys* (300 – 2700 m), and *Neusticomys* (up to 3700 m). By contrast, the Phyllotine genus *Galenomys*, the Akodontine genus *Necromys*, and the genera *Chinchillula, Neotomys*, and *Punomys* are restricted to the puna of the Altiplano in southern Peru and western Bolivia (Pearson 1951; Reig 1986). The genus *Thomasomys* is a smaller but still species-rich taxon that is endemic to tropical Andean cloud forests from Venezuela to Bolivia (Nowak 1999; Voss

Table 19.1. Elevational data sets of small mammal diversity in the tropical Andes. Elevational sample coverage is the percentage of the available gradient sampled (NVSM = nonvolant small mammals).

Location	Country	Diversity	Lower elevational limit	Upper elevational limit	Elevational sample coverage (%)	Taxa	Spp	Richness peak	Reference
La Libertad (Western slope)	Peru	Gamma	8	3962	99	NVSM	19	2800-3100	Osgood (1914)
South western Peru	Peru	Alpha	0	4500	98	NVSM	20	4000	Pearson and Ralph (1978)
Manu (Eastern slope)	Peru	Gamma	340	3450	95	NVSM	65	< 400	Solari et al (2006)
Manu (Eastern slope)	Peru	Gamma	340	3450	95	Bats	92	< 400	Solari et al (2006)
Eastern slope (8° to 17°S)	Peru	Gamma	0	3200	91	Bats	101	< 400	Graham (1983)
Eastern Cordillera	Colombia	Gamma	350	4000	90	Bats	42	1600-1900	Bejarano-Bonilla et al. (2007)
SW Choco	Colombia	Gamma	500	3500	85	Bats	36	1400	Fawcett (unpubl - 1994)
Central Cordillera	Colombia	Gamma	120	3160	75	Bats	39	500-600	Muñoz (1990, 1993)
Carrasco (Eastern slope)	Bolivia	Gamma	500	3500	70	Both	54	300-600	Vargas & Patterson (2007)
Yanachaga (Eastern slope)	Peru	Gamma	300	2800	68	Both	98	300-600	Vivar (2006)
Eastern Slopes	Ecuador	Gamma	600	3000	67	Bats	67	600 -1200	Carrera (unpubl - 2003)
Lima (Western slope)	Peru	Gamma	0	4400	67	NVSM	21	2400-2800	Unpublished data
Vilcabamba, (Eastern slope)	Peru	Gamma	850	3350	66	NVSM	22	?	Emmons et al. (2001) and Solari et al. (2001)
Eastern Cordillera	Colombia	Gamma	326	2640	55	Bats	29	600-1500	Tamsitt (1965)
Apurimac, (Eastern slope)*	Peru	Alpha	805	3500	53	Both	60	805	Pacheco et al. (2007)
Abiseo, (Eastern slope)	Peru	Gamma	2100	3850	45	NVSM	14	2100-3200	Leo & Romo (1992)
Central Cordillera	Colombia	Gamma	2200	3750	45	Both	42	?	Sanchez et al. (2004)
Sabana, Eastern Cordillera	Colombia	Gamma	2500	3600	31	Bats	10	2600	Tamsitt et al. (1964)
SW Choco	Colombia	Gamma	870	1950	30	Bats	28	900-1100	Alberico & Orejuela (1982) and Cadena et al. (1998)
Central Cordillera	Colombia	Gamma	2500	3500	25	NVSM	15	constant richness	Gomez-Valencia (unpublished - 2006)
Eastern Cordillera	Colombia	Gamma	2300	3100	22	NVSM	13	?	Lopez-A. & Montenegro-D. (1993)
Eastern Cordillera	Colombia	Gamma	1900	2600	17	NVSM	15	?	Gomez-Laverde (1994)

2003). Apparently, the center of diversity for this genus with at least seven species includes eastern Ecuador, where several species may occur sympatrically (Voss 2003).

Rodents are the only small mammals that inhabit elevations above 4000 m: Abrocomidae (1 species), Caviidae (2), Cricetidae (14), and Ctenomyidae (3). The rodent genus *Punomys* has records exclusively in localities above 4000 m (Eisenberg and Redford 1999; Pacheco and Patton 1995). The low partial pressure of oxygen and low ambient temperatures of high-elevation environments present a number of physiological challenges for endothermic animals. Camelids and some rodents (*Chinchilla* spp. and *Cavia porcellus*) of the high Andes are adapted to high-elevation hypoxia with hemoglobin that has high oxygen affinity (Ostojic et al. 2002; Storz 2007). Preliminary observations indicate that high-Andean rodents tolerate very low atmospheric oxygen concentrations, but the available data do not permit an analysis of the altitudinal limits of their distribution (McNab 2002; Morrison 1964). Lowland species may be limited by low barometric pressure at higher elevations, but highland species may face lower elevational limits to their distribution, which are unlikely to be related to high barometric pressures (McNab 2002).

There are few montane species among bats, including nectarivores (*Anoura aequatoris, A. fistulata, A. latidens, A. luismanueli*), frugivores (*Carollia manu, Stunira aratathomasi, S. bogotensis, S. nana,Platyrrhinus ismaeli*), and insectivores (*Eptesicus andinus, Histiotus humboldti, Mimon koepckeae, Mormopterus phrudus*). Reduced species richness and poorly developed endemism in Andean bat communities contrast with patterns shown by sympatric rodent faunas, which are diverse and strongly endemic on the Altiplano (see Figure 19.1) and markedly zoned along the eastern versant (Patterson et al. 1998). There are few records of bat species above 3500 m, with the probable exception of *Histiotus montanus* (up to 4000 m; Graham 1983, Gardner 2007). Koopman (1978) pointed out that Stenodermatinae bats have not been found at elevations higher than 3800 m. One of the species with records at higher elevations is the common vampire bat *Desmodus rotundus* (up to 3680 m) (Quintana and Pacheco 2007). In Costa Rica, LaVal (2004) found evidence of an upslope movement of *D. rotundus* as an apparent result of global warming; this has not been corroborated in the tropical Andes.

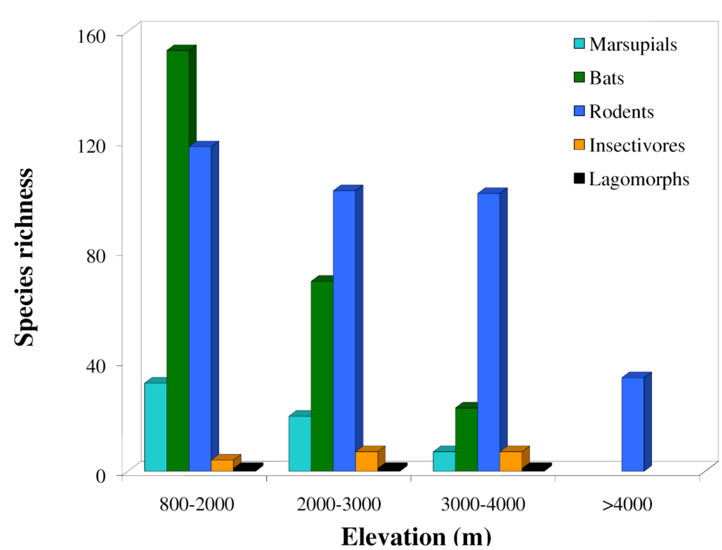

Figure 19.1. Species richness of mammals in elevational intervals along Tropical Andes (Colombia, Ecuador, Peru and Bolivia), including both eastern and western versants.

Biogeographic Role of the Andes

The high Andes have played a major role as "islands" where sigmodontine rodents (Cricetidae) experienced long periods of isolation and as a consequence evolved into several species, whereas lowland biomes contributed only secondarily to the process of diversification (Reig 1986). The number of rodent species endemic to the Andes supports the hypothesis that geographic isolation has been the most important cause of diversification among these mammals (Patton and Smith 1992). Although Koopman (1978) did not find evidence for any biogeographic role of the Andes for bats, concluding that bat distributions offer little support for a vicariance hypothesis, more recently, patterns similar to those of sigmodontines have been reported for the genera *Sturnira, Platyrrhinus* and *Carollia* (Ditchfield 2000; Mantilla-Meluk et al. 2009; Pacheco et al. 2004; Patterson et al. 1992; Velazco and Patterson 2008).

Puna and Paramo

The puna rodent fauna of Bolivia and Peru has more genera (at least 16) and species (at least 34) than the paramo rodent fauna of Colombia, Ecuador, and Peru (at least 8 genera and 16 species). This difference is probably the result of three main factors that have favored diversification in the puna (Reig 1986): the puna is older than the paramo biome (historical effect), it has greater environmental heterogeneity (ecological effect), and it has a larger and more continuous extension, especially on the extensive Altiplano (spatial effect).

Some studies suggest a biogeographical subdivision along the eastern border of the Lake Titicaca basin, with dry puna to the west and humid puna to the east. The dry highland zone of the Titicaca basin itself is characterized by the presence of *Phyllotis osilae osilae, Auliscomys boliviensis, Punomys lemminus, Akodon andinus, A. berlepschii, A. boliviensis, A. subfuscus arequipae, Necromys amoenus, Chroeomys jelskii pulcherrimus*, and *Galea musteloides* (Pacheco and Patton 1995; Ramirez et al. 2007). The humid puna of the Cordillera Oriental, on the other hand, is characterized by *Phyllotis osilae phaeus, Punomys kofordi, Chreomys jelskii cruceri, Auliscomys pictus, Oxymicterus paramensis, Akodon puer*, and *Akodon subfuscus subfuscus* (Pacheco and Patton 1995). A recent analysis by Ramirez et al.(2007) suggests that small mammal assemblages in the humid puna have greater similarity with those of the paramo than those of the dry puna.

The Elevational Gradient of Small Mammal Diversity

The Tropical Andes Scale

Available data on the elevational range size for species above 800 m shows that small mammal richness generally decreases with elevation for the tropical Andes as a whole (Figure 19.1; nonvolant small mammals: $R^2 = 0.84$, $P < 0.0001$; bats: $R^2 = 0.99$, $P < 0.0001$). Lomolino (2001) predicted that gamma diversity, the total richness of an entire elevational zone, should vary directly with the total area of each elevational zone, peaking in those zones that cover the largest area (e.g., the Amazon lowlands). Therefore, and because area decrease with elevation in the tropical Andes, the influence of area on this relationship should be considered (see Rahbek

1997). However, McCain (2007b) found evidence that area and spatial constraints (mid-domain effect) represent sources of error rather than mechanisms underlying mammalian diversity patterns. Indeed, the Amazonian lowlands have more species than the puna or paramo, which has been explained as a consequence of climatic, edaphic, spatial (area), and historical factors (Patton et al. 2000; Patton et al. 1997; Voss and Emmons 1996). However, especially at middle and higher elevations (puna, paramo, and yungas) the tropical Andes are richer in higher taxonomic levels such as tribes and genera (see previous sections).

The rodent tribes Akodontini, Phyllotini, and Thomasomyini (Cricetidae: Sigmodontinae) show highest species richness at mid elevations (Figure 19.2), a pattern not seen in marsupials and bats. A recent analysis of regional mammal endemism (mainly rodents) on the eastern versant of Bolivia and Peru showed a narrow elevational band with high numbers of endemic species (with ranges entirely confined to the area under consideration) occurring just below the treeline in upper Yungas forest (Pacheco et al. 2007). Nevertheless, it is important to highlight that these levels of endemism at middle elevations should be corroborated, especially because of our deficient knowledge about distribution, potentially misidentified specimens (see below), and lack of taxonomic syntheses.

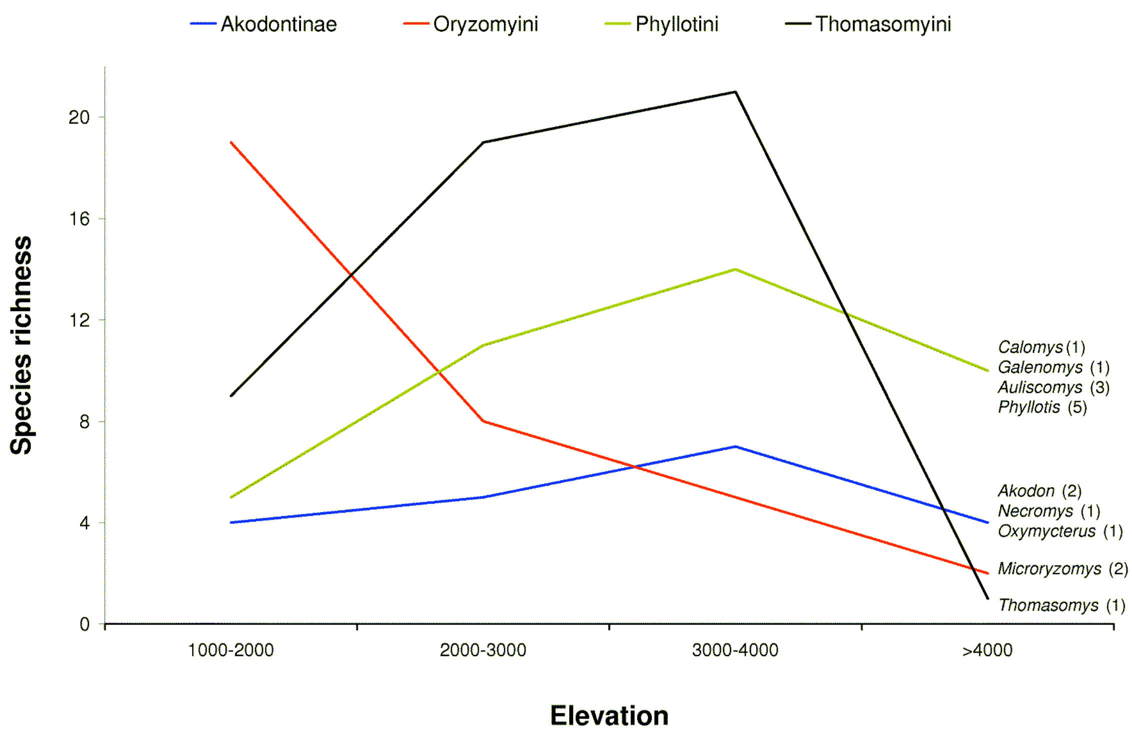

Figure 19.2. Species richness of Sigmodontinae tribes along elevation on the western versant of the Tropical Andes (species number in parentheses). The same pattern was recorded along the eastern slope (data not shown).

Regional and local scale

Our literature review shows that gradients along the eastern versant of the Andes have received the most attention: 14 out of 22 studies/localities (Table 19.1). Most studies from the tropical Andes suffer from incomplete elevational sampling (either covering only the mid-range or the upper part of the gradient), and most are characterized by insufficient sampling effort at each local survey site. Studies that sample only part of an elevational gradient often provide spurious results by excluding the lower (lowlands) or upper (highlands) end of the mountain from the analysis, so that they are impractical to identify elevational patterns. McCain (2007b) illustrated how difficult it is to obtain data from complete elevational gradients extending from lowlands to mountain peaks. As for insufficient sampling effort, most bat surveys, for example, depend on mist nets that are set at ground-level (despite the availability of other methods such as searching roost sites or identifying echolocation calls), and results thus are biased towards understory species, whereas canopy and open-area species remain underrepresented. We recognize that misidentifications of specimens represent a potential bias, especially in older literature (but we included only one "older" gradient study). Indeed, an update of these datasets based on current taxonomy is necessary.

Nonvolant Small Mammals

In general, there are few elevationally complete studies on both eastern and western slopes. We recorded only three studies with > 70% of the gradient sampled (Table 19.1). A study along the Peruvian eastern versant in Manu National Park shows a decrease of species richness with elevation (Figure 19.3; $R^2 = 0.82$, $P = 0.0001$). This result contrasts markedly with the pattern of a mid-elevation peak in nonvolant small mammal richness (McCain 2005). Manu has particular rodent assemblages restricted to elevational zones with replacements at species, genus, and even tribal levels (Patterson et al. 1998). A similar pattern of decreasing species richness with elevation occurs in both Yanachaga (Figure 19.3), Peru, with the 68% of gradient sampled ($R^2 = 0.48$, $P = 0.0001$), and Carrasco National Park in Bolivia (Vargas and Patterson 2007; original data not available). Peru's Manu National Park (340 – 3675 m) has become the most intensively studied protected area in the tropical Andes with more than 20 years of mammalogical research (Pacheco et al. 1993; Patterson et al. 1998; Solari et al. 2006), but no similar efforts have occurred in other tropical countries (see below). There are no studies of complete elevational gradients in Bolivia, Ecuador, or Colombia. We did not consider the data of Osgood (1914) from Libertad, Peru, because they would require reanalysis based on reidentification of specimens using current taxonomy.

On the western slope of the Peruvian Andes (Pearson and Ralph 1978), diversity increases with elevation ($R^2 = 0.44$, $P = 0.0001$), probably as a result of increased precipitation (and vegetation) with elevation, and more speciation events in the puna than in coastal deserts (Marquet 1994; Pearson and Ralph 1978). No studies appear to have been conducted on the more humid and diverse Pacific slope of Colombia, Ecuador (the Chocó), and northern Peru (Pacific tropical forest). Detailed studies testing both historical and environmental hypotheses should be conducted to improve our knowledge of the relationship between nonvolant small mammal richness and elevation along the latitudinal extension of the western slope of the tropical Andes, which presents contrasting lowlands such as the Pacific desert and Pacific tropical rainforests, and highlands such as dry puna and humid páramo, and even inter-Andean valleys. For example, the Peruvian eastern versant is more species rich in small mammals than the western versant (Pacheco et al. 2009), whereas the western and eastern versants of the Colombian Andes have similarly high diversity (Kattan et al. 2004). In general, there are very few studies on elevational gradients in nonvolant small mammals. Published general inventories of nonvolant mammals at elevations above 800 m are scarce (Gómez-Valencia 2006; Mena and Medellín 2010; Ramirez et al. 2007; Sánchez et al. 2004; Vivar 2006).

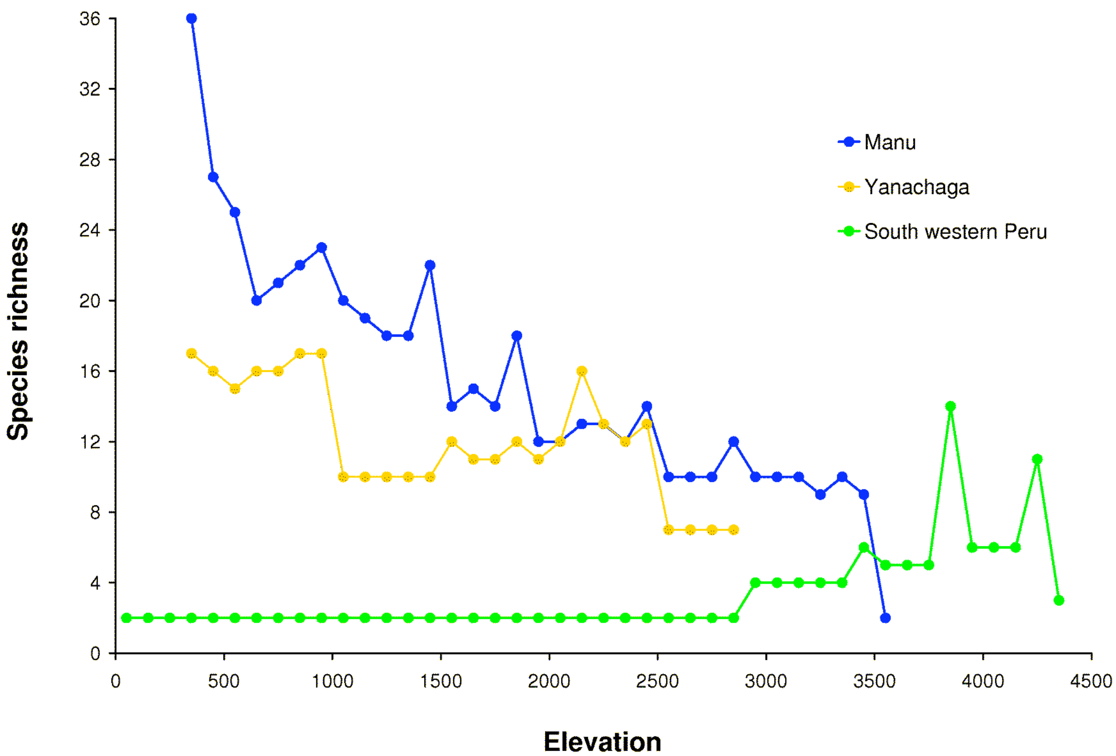

Figure 19.3. Elevational gradients in both western (WS) and eastern slopes (ES) of the Peruvian Andes: Manu (Solari et al. 2006), Yanachaga (Vivar 2006) and South western Peru (Pearson and Ralph 1978). See Table 19.1 for sources and details.

Bats

We recorded five studies on elevational gradients with > 70 % of the gradient sampled (Table 19.1). Along the Peruvian eastern versant, bat faunas tend to show a monotonic decrease of diversity with elevation both for the region as a whole (Graham 1983; $R^2 = 0.92$, $P = 0.0001$) and for Manu (Solari et al. 2006; $R^2 = 0.83$, $P = 0.0001$). The decrease of bat diversity with increasing elevation has been linked to an inefficient thermoregulation of species with Neotropical origin (especially for Phyllostominae species) (Graham 1983, 1990; Soriano 2000; Soriano et al. 1999). Highland faunas generally are attenuated versions of those found in the lowlands (Patterson et al. 1996; Patterson et al. 1998). For example, species richness of bat assemblages in Manu decreases monotonically, from 77 species between 300-500 m to only seven above 3000 m.

In Colombia, two studies on the eastern slope of the Cordillera Central (Muñoz 1990, 1993) and in the Chocó (Fawcett 1994) showed higher bat species richness at mid-elevations (Table 19.1). This was explained by the presence of secondary forests at middle elevations, providing support for the intermediate disturbance hypothesis (Bejarano-Bonilla et al. 2007). Similarly, Carrera (2003) analyzed the effect of elevation on species richness of bats on the central eastern slopes of the Ecuadorian Andes and found evidence of a mid-elevation peak between 1000 - 1100 m, which may be mainly due to the presence of a complex system of caves located in this gradient and a considerable collecting effort performed in the area since the 1980's (Rageot and Albuja 1994).

In a global analysis, McCain (2007a) suggested that elevational patterns of bat richness are related to local climatic gradients (temperature and water availability), habitat complexity, and species composition. Thus, decreasing species richness with elevation will occur on mountains with wet and warm lowlands (e.g., Manu, Yanachaga), but mid-elevation peaks will occur on mountains with arid lowlands (e.g., western Peru). Whereas some studies along the eastern slope corroborate the first prediction, studies on alpha diversity along the dry western slope of Peru are necessary to test the second prediction. In general, despite an increasing number of studies on bat species assemblages in Colombia, Ecuador, Peru, and Bolivia (Aguirre 2002; Aguirre et al. 2003; Ascorra et al. 1993; Ascorra et al. 1996; Bejarano-Bonilla et al. 2007; Espinoza et al. 2008; Hice et al. 2004; Numa et al. 2005; Pacheco et al. 2007; Pérez-Torres and Ahumada 2004; Rex et al. 2008; Sánchez et al. 2007; Vargas and Patterson 2007), there are few studies on elevational gradients for bat faunas. For example, in Bolivia the only attempt to study patterns of bat distribution along an elevational gradient was conducted by Vargas and Patterson (2007) in a gradient from 400 to 3600 m in Carrasco National Park (Cochabamba).

Directions for future research

In general, the current knowledge of distributional limits (both ecological and geographic), population demography, basic life history parameters, and natural history is still inadequate for most species inhabiting the tropical Andes. This incomplete understanding does not allow for a realistic or objective analysis and comparison of alpha, beta, or gamma diversity patterns. It also is the main obstacle to understanding elevational gradients of diversity in the tropical Andes. For example, in the first assessment of elevational richness patterns in Manu, Patterson et al. (1998) determined that rodent richness was high both in the lowlands and in the highlands, with an apparent minimum at intermediate elevations. However, additional inventories in Manu (Solari et al. 2006) revealed a steady decline in rodent richness with elevation (Figure 19.3). This highlights the importance of complete and standardized inventories along elevational gradients to improve our knowledge about diversity patterns. In addition, the integration of databases of natural history collections and museums are a high-priority for investigators and future collaborations between institutions in the area.

The limited availability of information on elevational and latitudinal gradients from the tropical Andes impede a thorough understanding of how global warming and land use change are stressing mammal assemblages at local to regional scales. Undoubtedly, it is necessary to increase basic information, which can be obtained through standardized surveys along elevation gradients on eastern and western slopes, which will also allow for monitoring of potential upslope movements of species due to global warming. For example, the study of population dynamics of the common vampire bat can provide valuable information about global warming, spread of diseases, and destruction of natural environments.

In summary, detailed and accurate information about patterns of diversity in Andean mammals is needed to advance conceptual understanding in biogeography and ecology, as well as for the development of effective conservation strategies. This is a critical issue because recent climate change has already begun to affect species' geographic ranges around the world.

Literature Cited

Aguirre, L. F. 2002. Structure of a Neotropical savanna bat community. *Journal of Mammalogy* 83:775-784.

Aguirre, L. F., X. Velez-Liendo, A. Muñoz, and A. Selaya. 2003. Patrones de distribución y zoogeografía de los murciélagos de Bolivia. *Revista Boliviana de Ecología y Conservación Ambiental* 14:3-17.

Alberico, M., and V. Rojas-Díaz. 2002. Mamíferos de Colombia. Pp. 185-226 in *Diversidad y conservación de los mamíferos neotropicales*, edited by G. Ceballos and J. A. Simonetti. México City: CONABIO-UNAM.

Alberico, M., and J. Orejuela. 1982. Diversidad específica de dos comunidades de murciélagos en Nariño, Colombia. *Cespedesia* 11 Sup. 3:31-40.

Ascorra, C. F., D. Gorchov, and F. Cornejo. 1993. The bats from Jenaro Herrera, Loreto, Peru. *Mammalia* 57:533-552.

Ascorra, C. F., S. Solari, and D. E. Wilson. 1996. Diversidad y ecología de los quirópteros en Pakitza. Pp. 593-612 in *Manu: the biodiversity of southeastern Peru*, edited by D. E. Wilson and A. Sandoval. Lima: Smithsonian Institution Press.

Bejarano-Bonilla, D. A., A. Yate-Rivas, and M. H. Bernal-Bautista. 2007. Diversidad y distribución de la fauna quiroptera en un transecto altitudinal en el departamento del Tolima, Colombia. *Caldasia* 29:297-308.

Brown, B. E. 2004. Atlas of the New World marsupials. *Fieldiana Zoology, New Series* 102:1-308.

Cadena, A., R. P. Anderson, and P. Rivas-Pava. 1998. Colombian mammals from the Chocoan slopes of Nariño. *Occasional Papers, Museum of Texas Tech University* 180:1-15.

Carrera, J. P. 2003. *Distribución de murciélagos (Chiroptera) a través de un gradiente altitudinal en las estribaciones orientales de los Andes ecuatorianos.* Licenciatura thesis. Quito: Pontificia Universidad Católica del Ecuador.

Castro-Luna, A. A., I. J. Sosa, and G. Castillo-Campos. 2007. Quantifying phyllostomid bats at different taxonomic levels as ecological indicators in a disturbed tropical forest. *Acta Chiropterologica* 9:219-228.

Ceballos, G., and P. R. Ehrlich. 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences* 103:19374-19379.

DeMattia, E. A., L. M. Curran, and B. J. Rathcke. 2004. Effects of small rodents and large mammals on Neotropical seeds. *Ecology* 85:2161-2170.

Ditchfield, A. D. 2000. The comparative phylogeography of Neotropical mammals: patterns of intraspecific mitochondrial DNA variation among bats contrasted to nonvolant small mammals. *Molecular Ecology* 9:1307-1318.

Eisenberg, J. F. 1989. *Mammals of the Neotropics: the northern Neotropics. Panama, Colombia, Venezuela, Guyana, Suriname, French Guiana*. Chicago: University of Chicago Press.

Eisenberg, J. F., and K. H. Redford, eds. 1999. *Mammals of the Neotropics: the central Neotropics. Ecuador, Peru, Bolivia, Brazil*. Chicago: University of Chicago Press.

Emmons, L. H., L. Luna, and M. Romo. 2001. Mammals of the northern Vilcabamba mountain range, Peru. Pages 105-109 in *Biological and social assessments of the Cordillera de Vilcabamba, Peru. RAP Working Papers 12 and SI/MAB Series 6*, edited by L. E. Alonso, A. Alonso, T. S. Schulenberg, and F. Dallmeier. Washington, DC: Conservation International.

Espinoza, A., L. F. Aguirre, M. I. Galarza, and E. Gareca. 2008. Ensamble de murciélagos en sitios con diferente grado de perturbación en un bosque montano del Parque Nacional Carrasco, Bolivia. *Mastozoología Neotropical* 15:297-308.

Fawcett, D. 1994. Bats. Pp. 60-67 in *Surveys and conservation of biodiversity in the Chocó, south-west Colombia*, edited by P. G. W. Salaman. Cambridge: BirdLife International.

Gardner, A. L. (ed.). 2007. *Mammals of South America, volume 1*. Chicago: University of Chicago Press.

Gómez-Laverde, M. 1994. Los pequeños mamíferos no voladores del Parque Regional Ucumari. Pages 377-396 in J. O. Rangel-Churrio, editor. *Ucumari: un caso típico de la diversidad biótica andina*. Bogotá: CARDER-Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

Gómez-Valencia, B. 2006. *Estructura de la comunidad de pequeños mamíferos en un gradiente altitudinal, reserva Rio Blanco, Manizales, Caldas.* Tesis de pregrado. Bogotá: Departamento de Biologia, Universidad Nacional de Colombia.

Graham, G. L. 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of Mammalogy* 64:559-571.

Graham, G. L. 1990. Bats versus birds: comparisons among Peruvian volant vertebrate faunas along an elevational gradient. *Journal of Biogeography* 17:657-668.

Hice, C. L., P. M. Velazco, and M. R. Willig. 2004. Bats of the Reserva Nacional Allpahuayo-Mishana, northeastern Peru, with notes on community structure. *Acta Chiropterologica* 6:319-334.

Kattan, G. H., P. Franco, V. Rojas, and G. Morales. 2004. Biological diversification in a complex region: a spatial analysis of faunistic diversity and biogeography of the Andes of Colombia. *Journal of Biogeography* 31:1829-1839.

Koopman, K. F. 1978. Zoogeography of Peruvian bats with special emphasis on the role of the Andes. *American Museum Novitates* 2651:1-33.

LaVal, R. K. 2004. Impact of global warming and locally changing climate on tropical cloud forest bats. *Journal of Mammalogy* 85:237-244.

Leo, M., and M. Romo. 1992. Distribución altitudinal de roedores sigmodontinos (Cricetidae) en el Parque Nacional río Abiseo, San Martin, Perú. *Memorias del Museo de Historia Natural UNMSM* 21:105-118

Lomolino, M. V. 2001. Elevational gradients of species-density: historical and prospective views. *Global Ecology and Biogeography* 10:3-13.

López-Arévalo, H. F., and O. L. Montenegro-Díaz. 1993. Mamíferos no voladores de Carpanta. Pp. 165-187 in *Carpanta: selva nublada y páramo*, edited by G. I. Andrade. Fundación Natura, Bogotá.

Lunde, D. P., and V. Pacheco. 2003. Shrew opossums (Paucituberculata: *Caenolestes*) from the Huancabamba region of east Andean Peru. *Mammal Study* 28:145-146.

Mangan, S., and G. Adler. 2002. Seasonal dispersal of arbuscular mycorrhizal fungi by spiny rats in a Neotropical forest. *Oecologia* 131:587-597.

Mantilla-Meluk, H., and R. J. Baker. 2008. Mammalia, Chiroptera, Phyllostomidae, *Anoura fistulata*: distribution extension. *Check List* 4:427-430.

Mantilla-Meluk, H., A. M. Jiménez-Ortega, and R. J. Baker. 2009. Phyllostomid bats of Colombia: annotated checklist, distribution, and biogeography. *Special Publications, Museum of Texas Tech University* 56.

Marquet, P. A. 1994. Diversity of small mammals in the Pacific coastal desert of Peru and Chile and in the adjacent area: biogeography and community structure. *Australian Journal of Zoology* 42:527-542.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. *Ecology* 86:366-372.

McCain, C. M. 2007a. Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography* 16:1-13.

McCain, C. M. 2007b. Area and mammalian elevational diversity. *Ecology* 88:76-86.

McNab, B. K. 2002. *The physiological ecology of vertebrates: a view from energetics*. Ithaca, NY: Cornell University Press.

Medellín, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology* 14:1666-1675.

Mena, J. L., and E. Vázquez-Domínguez. 2005. Species turnover on elevational gradients in small rodents. *Global Ecology and Biogeography* 14:539-547.

Mena, J. L., and R. A. Medellín. 2010. Small mammal assemblages in a disturbed tropical landscape at Pozuzo, Peru. *Mammalian Biology* 75:83-91.

Mittermeier, R. A., N. Myers, J. B. Thomsen, G. A. B. Da Fonseca, and S. Olivieri. 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. *Conservation Biology* 12:516-520.

Morrison, P. R. 1964. Wild animals at high altitudes. *Symposia of the Zoological Society of London* 13:49-57.

Muchhala, N., and P. Jarrín-V. 2002. Flower visitation by bats in cloud forests of western Ecuador. *Biotropica* 34:387-395.

Muñoz, J. 1993. Murciélagos del norte de Antioquia (Colombia). *Studies on Neotropical Fauna and Environment* 28:83-93.

Muñoz, J. 1990. Diversidad y hábitos alimenticios de murciélagos en transectos altitudinales a través de la Cordillera Central de los Andes en Colombia. *Studies on Neotropical Fauna and Environment* 25:1-17.

Napolitano, C., M. Bennett, W. E. Johnson, S. J. O'Brien, P. A. Marquet, I. Barría, E. Poulin, and A. Iriarte. 2008. Ecological and biogeographical inferences on two sympatric and enigmatic Andean cat species using genetic identification of faecal samples. *Molecular Ecology* 17:678-690.

Naranjo, M. E., C. Rengifo, and P. J. Soriano. 2003. Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae). *Journal of Tropical Ecology* 19:19-25.

Nowak, R. M. 1999. *Walker's mammals of the world*. Baltimore, MD: Johns Hopkins University Press.

Numa, C., J. R. Verdú, and P. Sánchez-Palomino. 2005. Phyllostomid bat diversity in a variegated coffee landscape. *Biological Conservation* 122:151-158.

Osgood, W. H. 1914. Mammals of an expedition across northern Peru. Fieldiana Zoology 10:143-185.

Ostojic, H., C. Veronica, and C. Monge. 2002. Hemoglobin affinity in Andean rodents. *Biological Research* 35:27-30.

Pacheco, V., and J. L. Patton. 1995. A new species of the Puna mouse, genus *Punomys* Osgood, 1943 (Muridae, Sigmodontinae), from the southeastern Andes of Peru. *Zeitschrift für Säugetierkunde* 60:85-96.

Pacheco, V., S. Solari, and P. M. Velazco. 2004. A new species of *Carollia* (Chiroptera: Phyllostomidae) from the Andes of Peru and Bolivia. *Occasional Papers, Museum of Texas Tech University* 235:1-15.

Pacheco, V., R. Cadenillas, S. Velazco, E. Salas, and U. Fajardo. 2007. Noteworthy bat records from the Pacific Tropical rainforest region and adjacent dry forest in northwestern Peru. *Acta Chiropterologica* 9:409-422.

Pacheco, V., R. Cadenillas, E. Salas, C. Tello, and H. Zeballos. 2009. Diversidad y endemismo de los mamíferos del Perú. *Revista Peruana de Biología* 16:5-32.

Pacheco, V., B. D. Patterson, J. L. Patton, L. H. Emmons, S. Solari, and C. F. Ascorra. 1993. List of mammal species known to occur in Manu Biosphere Reserve, Peru. *Publicaciones del Museo de Historia Natural "Javier Prado" UNMSM, Serie A, Zoología* 44:1-12.

Pacheco, V., H. L. Quintana, P. A. Hernandez, L. Paniagua, J. Vargas, and B. E. Young. 2007. Mamíferos. Pp. 40-45 in *Distribución de las especies endémicas en la vertiente oriental de los Andes en Perú y Bolivia*, edited by B. E. Young. Arlington, VA: NatureServe.

Patterson, B. D. 2000. Patterns and trends in the discovery of new Neotropical mammals. *Diversity and Distributions* 6:145-151.

Patterson, B. D., V. Pacheco, and M. V. Ashley. 1992. On the origins of the western slope region of endemism: systematics of fig-eating bats, genus *Artibeus*. *Memorias del Museo de Historia Natural UNMSM* 21:189-205.

Patterson, B. D., V. Pacheco, and S. Solari. 1996. Distributions of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology* 240:637-658.

Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography* 25:593-607.

Patton, J. L., and M. F. Smith. 1992. mtDNA Phylogeny of Andean mice: a test of diversification across ecological gradients. *Evolution* 46:174-183.

Patton, J. L., M. N. da Silva, and J. R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia. *Bulletin of the American Museum of Natural History* 244:1-306.

Patton, J. L., M. N. F. da Silva, M. C. Lara, and M. A. Mustrangi. 1997. Diversity, differentiation, and the historical biogeography of nonvolant small mammals of the Neotropical forests. Pp. 455-465 in *Tropical forest remnants: ecology, management, and* *conservation of fragmented communities*, edited by W. F. Laurance and R. O. Bierregaard. Chicago: University of Chicago Press.

Pearson, O. P. 1951. Mammals in the highlands of southern Peru. *Bulletin of the Museum of Comparative Zoology* 106:117-174.

Pearson, O. P., and C. P. Ralph. 1978. The diversity and abundance of vertebrates along an altitudinal gradient in Peru. *Memorias del Museo de Historia Natural "Javier Prado"* 18:1-97.

Pérez-Torres, J., and J. A. Ahumada. 2004. Murciélagos en bosques alto-andinos, fragmentados y continuos, en el sector occidental de la sabana de Bogotá (Colombia). *Universitas Scientiarum* 9:33-46.

Quintana, H., and V. Pacheco. 2007. Identificación y distribución de los murciélagos vampiros del Perú. *Revista Peruana de Medicina Experimental y Salud Publica* 24:81-88.

Rageot, R., and L. Albuja. 1994. Mamíferos de un sector de la alta Amazonía ecuatoriana: Mera, provincia de Pastaza. *Revista Politécnica* 19:165-208.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in Neotropical birds. *American Naturalist* 149:875-902.

Ramirez, O., M. Arana, E. Bazán, A. Ramirez, and A. Cano. 2007. Assemblages of bird and mammal communities in two major ecological units of the Andean highland plateau of southern Peru. *Ecologia Aplicada* 6:139-148.

Reeder, D. M., K. M. Helgen, and D. E. Wilson. 2007. Global trends and biases in new mammal species discoveries. *Occasional Papers, Museum of Texas Tech University* 269:1-35.

Reig, O. A. 1986. Diversity patterns and differentiation of high Andean rodents. Pp. 404-439 in *High altitude tropical biogeography*, edited by M. Monasterio and F. Vuilleumier. New York: Oxford University Press.

Rex, K., D. H. Kelm, K. Wiesner, T. H. Kunz, and C. C. Voigt. 2008. Species richness and structure of three Neotropical bat assemblages. *Biological Journal of the Linnean Society* 94:617-629.

Salazar-Bravo, J., T. L. Yates, and L. M. Zalles. 2002. Mamíferos de Bolivia. Pp. 65-113 in *Diversidad y conservación de los mamíferos neotropicales*, edited by G. Ceballos and J. A. Simonetti. México City: CONABIO-UNAM.

Sánchez, F., P. Sánchez-Palomino, and A. Cadena. 2004. Inventario de mamíferos en un bosque de los Andes centrales de Colombia. *Caldasia* 26:291-309.

Sánchez, F., J. Alvarez, C. Ariza, and A. Cadena. 2007. Bat assemblage structure in two dry forests of Colombia: composition, species richness, and relative abundance. *Mammalian Biology* 72:82-92.

Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A. S. L. Rodrigues, S. N. Stuart, H. J. Temple, J. Baillie, L. Boitani, T. E. Lacher Jr., R. A. Mittermeier, A. T. Smith, D. Absolon, J. M. Aguiar, G. Amori, N. Bakkour, R. Baldi, R. J. Berridge, J. Bielby, P. A. Black, J. J. Blanc, T. M. Brooks, J. A. Burton, T. M. Butynski, G. Catullo, R. Chapman, Z. Cokeliss, B. Collen, J. Conroy, J. G. Cooke, G. A. B. da Fonseca, A. E. Derocher, H. T. Dublin, J. W. Duckworth, L. Emmons, R. H. Emslie, M. Festa-Bianchet, M. Foster, S. Foster, D. L. Garshelis, C. Gates, M. Gimenez-Dixon, S. Gonzalez, J. F. Gonzalez-Maya, T. C. Good, G. Hammerson, P. S. Hammond, D. Happold, M. Happold, J. Hare, R. B. Harris, C. E. Hawkins, M. Haywood, L. R. Heaney, S. Hedges, K. M. Helgen, C. Hilton-Taylor, S. A. Hussain, N. Ishii, T. A. Jefferson, R. K. B. Jenkins, C. H. Johnston, M. Keith, J. Kingdon, D. H. Knox, K. M.

Kovacs, P. Langhammer, K. Leus, R. Lewison, G. Lichtenstein, L. F. Lowry, Z. Macavoy, G. M. Mace, D. P. Mallon, M. Masi, M. W. McKnight, R. A. Medellin, P. Medici, G. Mills, P. D. Moehlman, S. Molur, A. Mora, K. Nowell, J. F. Oates, W. Olech, W. R. L. Oliver, M. Oprea, B. D. Patterson, W. F. Perrin, B. A. Polidoro, C. Pollock, A. Powel, Y. Protas, P. Racey, J. Ragle, P. Ramani, G. Rathbun, R. R. Reeves, S. B. Reilly, J. E. Reynolds III, C. Rondinini, R. G. Rosell-Ambal, M. Rulli, A. B. Rylands, S. Savini, C. J. Schank, W. Sechrest, C. Self-Sullivan, A. Shoemaker, C. Sillero-Zubiri, N. De Silva, D. E. Smith, C. Srinivasulu, P. J. Stephenson, N. van Strien, B. K. Talukdar, B. L. Taylor, R. Timmins, D. G. Tirira, M. F. Tognelli, K. Tsytsulina, L. M. Veiga, J.-C. Vie, E. A. Williamson, S. A. Wyatt, Y. Xie, and B. E. Young. 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322:225-230

Solari, S., J. J. Rodríguez, E. Vivar, and P. M. Velazco. 2002. A framework for assessment and monitoring of small mammals in a lowland tropical forest. *Environmental Monitoring and Assessment* 76:89-104.

Solari, S., V. Pacheco, L. Luna, P. M. Velazco, and B. D. Patterson. 2006. Mammals of the Manu Biosphere Reserve. *Fieldiana: Zoology, n.s.* 110:13-22.

Solari, S., E. Vivar, P. M. Velazco, and J. J. Rodríguez. 2001. Small mammals of southern Vilcabamba region, Peru. Pp. 110-116 in *Biological and social assessments of the Cordillera de Vilcabamba, Peru. RAP Working Papers 12 and SI/MAB Series 6*, edited by L. Alonso, A. Alonso, T. Schulenberg, and F. Dallmeier. Washington, DC: Conservation International.

Soriano, P. J. 2000. Functional structure of bat communities in tropical rainforests and Andean cloud forests. *Ecotropicos* 13:1-20.

Soriano, P. J., A. Díaz de Pascual, J. Ochoa, and M. Aguilera. 1999. Biogeographic analysis of the mammal communities in the Venezuelan Andes. *Interciencia* 24:17-25.

Steiner, K. E. 1981. Nectarivory and potential pollination by a Neotropical marsupial. *Annals of the Missouri Botanical Garden* 68:505-513.

Storz, J. F. 2007. Hemoglobin function and physiological adaptation to hypoxia in high-altitude mammals. *Journal of Mammalogy* 88:24-31.

Tamsitt, J. R. 1965. Aspects of altitudinal distribution of chiropterans in the eastern Cordillera of Colombia. *American Zoology* 5:1-492.

Tamsitt, J. R., D. Valdivieso, and J. Hernandez-Camacho. 1964. Bats of the Bogota savanna, Colombia, with notes on the altitudinal distribution of Neotropical bats. *Revista Tropical de Biología* 12:107-115.

Tirira, D. 2007. *Guía de campo de los mamíferos del Ecuador. Publicación Especial 6.* Quito: Ediciones Murciélago Blanco.

Vargas, A., and B. D. Patterson. 2007. Comunidades de murciélagos montanos en Bolivia. Pp. 82-86 in *Historia natural, distribución y conservación de los murciélagos de Bolivia*, edited by L. F. Aguirre. Santa Cruz de la Sierra: Editorial Centro de Ecología y Difusión Simón I. Patiño.

Velazco, P. M., and B. D. Patterson. 2008. Phylogenetics and biogeography of the broad-nosed bats, genus *Platyrrhinus* (Chiroptera: Phyllostomidae). *Molecular Phylogenetics and Evolution* 49:749-759.

Vieira, E. M., and D. A. de Moraes. 2006. Carnivory and insectivory in Neotropical marsupials. Pp. 271-284 in *Predators with pouches: the biology of carnivorous marsupials*, edited by M. Jones, C. Dickman, and M. Archer. Collingwood, Australia: CSIRO Publishing.

Vivar, E. 2006. *Análisis de distribución altitudinal de mamíferos pequeños en el Parque Nacional Yanachaga-Chemillén, Pasco, Perú*. Tesis de maestria. Lima: Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos.

Voss, R. S. 1988. Systematics and ecology of ichthyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. *Bulletin of the American Museum of Natural History* 188:259-493.

Voss, R. S. 2003. A new species of *Thomasomys* (Rodentia: Muridae) from eastern Ecuador, with remarks on mammalian diversity and biogeography in the Cordillera Oriental. *American Museum Novitates* 3421:1-47.

Voss, R. S., and L. H. Emmons. 1996. Mammalian diversity in Neotropical lowland rainforests: a preliminary assessment. *Bulletin of the American Museum of Natural History* 230:1-115.

Walker, R. S., A. J. Novaro, P. Perovic, R. Palacios, E. Donadio, M. Lucherini, M. Pia, and M. S. Lopez. 2007. Diets of three specie of Andean carnivores in high-altitude deserts of Argentina. *Journal of Mammalogy* 88:519-525.

Wilson, D. E., C. F. Ascorra, S. Solari, D. E. Wilson, and A. Sandoval. 1996. Bats as indicators of habitat disturbance. Pp. 613-625 in *Manu: the biodiversity of southeastern Peru*. Lima: Smithsonian Institution Press.

Wilson, D. E., and D. M. Reeder (eds.). 2005. *Mammal species of the world*. Baltimore, MD: Johns Hopkins University Press.

Williams-Guillén, K., I. Perfecto, and J. Vandermeer. 2008. Bats limit insects in a Neotropical agroforestry system. *Science* 320:70-70.