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Original Investigation

The effect of anthropic pressures and elevation on the large and medium-sized terrestrial mammals of the subtropical mountain forests (Yungas) of NW Argentina

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ABSTRACT

We conducted a 55-day long camera-trap survey in the Yungas subtropical forest in NW Argentina, to assess the effect of human accessibility, conservation status of the area, domestic animals and elevation on the diversity and composition of the large and medium-sized native terrestrial mammal assemblage. We deployed 24 camera-trap stations at distances of \sim 2 km from each other. The study area is covered by continuous forest and has its center in the small community of Acambuco, in the Acambuco Provincial Reserve. The main economic activity in the area is oil/gas exploitation. Local residents raise cattle, hunt and use timber and non-timber forest products. The human impact was indirectly measured with an accessibility cost model. We used a multiple regression ANCOVA to assess the effect of elevation (range: 628-1170 masl), accessibility, protection status (reserve vs not) and frequency of records of domestic animals on the native mammal species richness and on a nonmetric multidimensional scaling (NMDS) ordination based on the frequency of records of the native mammals recorded at >3 camera-trap stations. We recorded 15 species of native mammals. Native mammal species richness decreased with elevation. Elevation was correlated with NMDS axes. Other predictive variables had no effect on species richness or the NMDS ordination, probably as a result of the relatively narrow range of conditions assessed in this study. The effect of elevation on mammal assemblages should be considered in landscape planning processes aimed at promoting biodiversity conservation.

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Introduction

Nearly one-quarter of the 5488 mammal species assessed in the 2008 IUCN Red List are currently threatened or extinct (www.iucnredlist.org). The greatest threat to mammals is habitat destruction (Schipper et al., 2008), but overexploitation, invasive species, and other human disturbances are also important threatening sources (Sodhi and Ehrlich, 2010). Hunting by humans is pervasive in tropical and subtropical forests of the World and may affect the abundance, diversity and behavior of large and mediumsized mammals (Bodmer et al., 1997; Peres, 2000, 2010; Di Bitetti et al., 2008). Intense hunting may eventually produce the local

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extinction of mammal species (Bodmer et al., 1997) and result in the "empty forest syndrome" (Redford, 1992). The domestic animals associated with people, can also have a negative effect on the populations of native mammals (Hibert et al., 2010).

Although the creation of protected areas could be an effective solution to ensure the protection of ecosystems and biodiversity (Bruner et al., 2001), in developing countries protected areas do not always achieve that goal (Hayes, 2006; Bonham et al., 2008). Assessing the impact of human interventions on the natural communities will help prioritize conservation actions and mitigate their negative effects, particularly within multiple use protected areas, aimed at achieving both sustainable use of natural resources and biodiversity conservation.

Besides anthropic pressures, natural environmental variables (e.g., soil conditions, topography) can also affect the diversity and composition of native mammal assemblages. Along elevation gradients there is usually a turnover of species and the ecological communities change along them (Morin, 1999; Lomolino, 2001).

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Some mammal groups show a complete replacement of species along an elevation gradient (Patterson et al., 1998). Small mammal richness usually shows a mid-elevation peak along altitudinal gradients in cross study comparisons (Brown, 2001; McCain, 2005, 2007). In NW Argentina, mammal diversity is higher in the Yungas (at low-intermediate altitudes) and lower in the highest elevations of the Puna (Ojeda et al., 2003). Within the Yungas ecoregion, mammal diversity is higher in the lower montane forests than in the upper montane forests (Ojeda and Mares, 1989). Thus, we expect elevation to have an effect on the alpha diversity and composition of the mammal assemblage of the Yungas of Argentina, a region characterized by high levels of diversity for some mammal groups (bats: Barquez and Díaz, 2001; felids: Di Bitetti et al., 2011; other mammal groups: Jayat and Ortiz 2010).

In this paper we studied the potential effects of accessibility (a surrogate of hunting and other anthropic impacts), frequency of domestic animals, protection status, and elevation, on the diversity and composition of the large and medium-sized terrestrial mammal assemblage in an area of the Yungas ecoregion in NW Argentina. We predicted that the diversity of native mammals and the probability of recording ungulates and large carnivores will increase with protection and will decrease with accessibility and the frequency of domestic animals. The opposite pattern

was predicted for the small-medium sized carnivores. We predicted changes in the mammal assemblage with elevation and a negative relationship between this predictive variable and native mammal species diversity.

Material and methods

Study area

We conducted this study in a sector of the Yungas ecoregion of southern Bolivia and NW Argentina (Grau and Brown, 2000). This ecoregion is characterized by subtropical montane forests that expand north to south and in an altitudinal gradient, along the eastern slopes of the Andes (Brown et al., 2001). The study area comprises portions of Premontane Forest (Selva Pedemontana) and Montane Humid Forest (Selva Montana) at elevations that range between 628 and 1170 masl (mean = 923 masl, SD = 136 m). The study site is located in a portion of the Yungas of the province of Salta, Argentina, centered in the small (70 families) rural community of Acambuco (22°09′51″ S and 63°54′40″ W), and the Acambuco Provincial Reserve (created in 1979, Fig. 1). Local people practice extractive activities (including hunting), practice agriculture, and raise cattle within the Acambuco Reserve. Thus, the

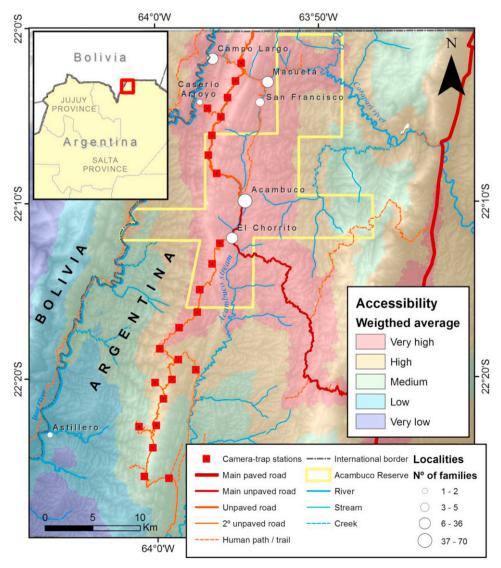


Fig. 1. Map of the study area in the province of Salta, NW Argentina, showing the arrangement of the camera-trap stations and the accessibility model.

reserve is not a strictly protected area and one of the questions we explore is its potential contribution to wildlife conservation. Six other small rural communities, represented by 1–36 scattered family units each, are located in the study area (Fig. 1). The whole area has been under oil and gas exploitation since the mid XX century. Other productive or extractive activities within these lands include selective logging of a few native tree species, cattle raising and small scale slash-and-burn agriculture (Fundación ProYungas, 2004).

The study area, with the exception of the large valley where the localities of Acambuco and El Chorrito are located (about 3000 ha) and a few other spots (mostly as a result of oil/gas operations), is covered by continuous native forest. Most of the local people living in the small rural communities raise domestic animals (cattle, pigs, horses and dogs). Cattle and other domestic animals roam freely in the forest during most of the year. Local people hunt for recreation and to complement their diets. Local people kill jaguars, pumas and, occasionally, small carnivores when they detect them in the proximity of their settlement or a domestic animal has been killed (Fundación ProYungas, 2004). The staff of the oil companies is not allowed to hunt.

Survey design

Camera-traps constitute an effective tool to conduct mammal surveys since this group includes many rare, nocturnal or elusive species, that are rarely observed in line transect census (Silveira et al., 2003; Tobler et al., 2008). We conducted a camera-trap survey between September 23 and November 18, 2010. We deployed 24 camera-trap stations, each with a digital camera-trap unit (Moultrie M-40), at elevations ranging from 628 to 1170 masl. Camera-trap stations were located along the main dirt road which extends north and south of the locality of Acambuco (Fig. 1). Camera-trap stations varied in relation to the independent variables: (1) access of people to the forest, indirectly measured with an accessibility model (see below), (2) abundance of domestic animals, indirectly measured as the frequency of camera-trap records of domestic animals, (3) legal protection status of the area and (4) elevation.

The camera-trap stations were spaced >1.4 km between each other to avoid sampling the same individuals for most species. The mean distance from a camera-trap station to its nearest one was 2.09 (SD=0.35, range=1.44–2.61) km. Camera-trap stations were located inside the forest 30–100 m away from a dirt road and were active for 54–56 consecutive days, totaling 1316 camera-trap days of effort. Camera-traps were placed at the base of a tree trunk, 40–50 cm above the ground and were baited with a perforated tuna fish can located on the forest floor at approximately 2.5 m away from the camera-trap. Baits were replaced periodically. Camera-traps were programmed to take pictures during a 24 h cycle, with a 5 min delay between successive shots.

Human impacts on the ecological communities may vary spatially according to the accessibility of the area (Naves et al., 2003; Peres and Lake, 2003; Nielsen, 2006). To summarize the human impacts on the mammal assemblage we used the "accessibility modeling" tool for ArcView 3.x developed by Farrow and Nelson (2001). We built a GIS of the study area and used the accessibility modeling tool to estimate the relative cost of access from each cell to a human settlement for the whole study area (see De Angelo et al., 2011). The cost of access is measured as the time it takes to access a certain point in the landscape from a certain locality, which depends on the speed of movement on different landscape features (e.g., presence and quality of roads, land use, etc.). The GIS and the accessibility cost model incorporated information on road quality (five categories ranging from main pave roads to trails), rivers (three categories ranging from main river to creek), land use

Table 1Variables and categories used and values assigned to each of them in the accessibility cost model (see text for details). Values are based on guidelines provided by Nelson (2000, 2008) and Somma (2006) but adjusted to local conditions based on our knowledge on how local people navigate this landscape.

Variable	Speed (seconds to transverse 30 m)
Access type	
Main paved road	1
Main unpaved road	2
Unpaved road	3
Secondary unpaved road	4
Human path/trail	7
Water flow type	4.4
River	14
Stream	18
Creek	36
Land use	
Forest	27
Degraded/secondary forest	18
Agriculture	7
Bare soil	9
Anthropic pastures	8
Urban areas	2
Wetland	11
Slope	
0-7.5%	No effect on speed
7.5–15%	Reduces speed by half
>15%	Reduces speed to one third

(forest, degraded or secondary forest, agriculture, pastures, bare soil, wetland and rural areas), and slope (Table 1). We built one such accessibility model for each of the seven small localities that may have an impact in the study area. We finally built an average accessibility model by weighting the accessibility cost value of each cell by the number of families living in each of the seven settlements (range 1–70 families, Fundación ProYungas, 2004; Fig. 1).

Data analysis

To evaluate if camera-trap stations were spatially independent we conducted a Mantel test (Quinn and Keough, 2002) with program R (R Development Core Team, 2012). We tested for the existence of a correlation between two matrices, one based on the linear distance among stations and the other based on the Bray-Curtis dissimilarity index among them. We estimated Pearson's product–moment correlation statistic and its associated P-value based on 999 permutations of the matrices.

To evaluate the effect of the predictive variables on the native mammal species richness we performed an ANCOVA-like multiple regression analysis. We used a backward elimination procedure (Sokal and Rohlf, 1995) to decide which predictive variables to retain in the final model. The dependent variable in this analysis was the native mammal species richness recorded in each camera-trap station (N=24 stations). Predictive variables were: (1) accessibility (access time to the location), (2) the natural logarithm of the frequency of records +1 of domestic animals (cows, horses, donkey, domestic pigs and dogs) at the camera-trap stations, (3) protection status of the area (whether a camera-trap station was located within the limits of the Acambuco Reserve or not) and (4) elevation (meters above sea level). Of these predictive variables, only accessibility and legal protection status were statistically correlated (Spearman Rho = -0.55, P = 0.005) and may have been redundant. This analysis was performed with JMP (version 3.2.2; SAS Institute Inc., Cary, NC) statistical software.

To assess if the predictive variables affect the structure and composition of the native mammal assemblage we performed a Nonmetric Multidimensional Scaling (NMDS) ordination based on the Bray–Curtis dissimilarity index. We did this analysis with

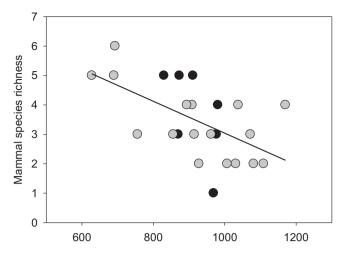


Fig. 2. The richness of mammals decreased with the elevation of the cameratrap station. The line represents the least-squared regression line. Black symbols = stations located within the Acambuco Provincial Reserve, gray symbols = stations located outside this reserve.

the frequencies of records of the six species of native mammals recorded in at least four camera-trap stations. We used the criterion that >12 h had to pass between successive photographs of the same species to be considered independent records. We used a scree plot and Kruskal's stress value to determine how many axes to include in the ordination and to assess if the results are ecologically interpretable (stress values should be ideally lower than 0.1, Quinn and Keough, 2002). NMDS, as most ordination methods, is a graphic approach to detect patterns in community structure. This is usually accomplished by fitting environmental vectors onto ordination. These vectors (arrows) point in the direction of more rapid environmental change and their relative lengths indicate the correlation between the environmental variables and the ordination. These correlations can be assessed using the squared correlation coefficient (r^2) and the statistical probability estimated using random permutations (N = 9999) of the data (Oksanen, 2011). The loadings of the species on the axes can also be plotted on the ordination to evaluate how they correlate with the environmental vectors. The NMDS was performed with program R (R Development Core Team, 2012), using library vegan (Oksanen et al., 2012).

Results

We found no correlation between the linear distance among camera-trap stations and their ecological similarity (Mantel test, r = -0.018, P = 0.59). Thus, camera-trap stations can be considered spatially independent.

We recorded 15 species of native mammals and five species of domestic ones (Table 2). The most frequently recorded species were the tapeti *Sylvilagus brasiliensis*, the tayra *Eira barbara* and the crabeating fox *Cerdocyon thous*. The domestic species most frequently recorded was the cattle.

The mean number of native species recorded per camera-trap station was 3.46 (SEM=0.26, range=1-6 species). Accessibility, the natural logarithm of the frequency of records of domestic animals and the location of the camera-trap stations inside or outside the Acambuco Reserve had no statistical effect on native mammal species richness (P > 0.30). Elevation was the only predictive variable retained in the final regression model. Mammal species richness per camera-trap station decreased with elevation ($F_{1.22} = 10.83$, P = 0.003, Fig. 2).

The scree plot suggested the use of three NMDS axes rendering a relatively low stress value of 0.077. Only elevation had a statistically

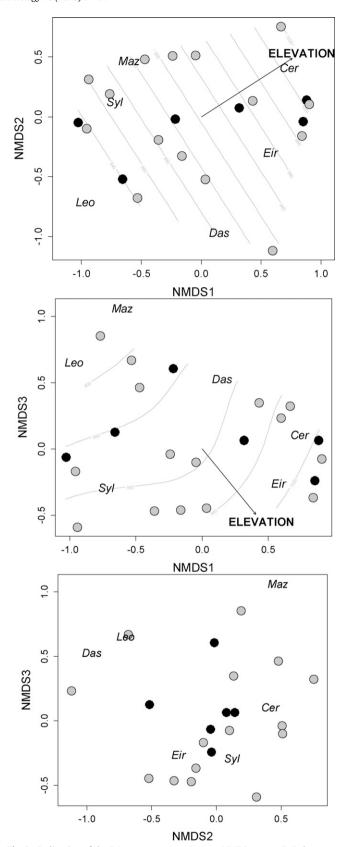


Fig. 3. Ordination of the 24 camera trap stations on NMDS axes 1–3. Only vectors of variables with significant correlations with the ordination axes (elevation, P < 0.10, Table 3) are depicted. Gray lines indicate elevation gradients. Black symbols = stations located within the Acambuco Provincial Reserve (N = 7), gray symbols = stations located outside this reserve (N = 17). The number of symbols in the graph (N = 21) does not match the number of stations (N = 24) because two groups of 2 and 3 stations respectively achieved same values in the ordination space. Cer = Crab - eating fox, Das = agouti, Eir = tayra, Leo = ocelot, Maz = gray brocket deer, Syl = tapeti.

Table 2
Species of mammals recorded during the camera-trap survey conducted at Acambuco, Salta, Argentina. The last two columns represent the frequency of records (number of pictures of same species obtained with a time lapse between successive photographs of >12 h) and the number of stations where each species was recorded.

Order	Family	Common name	Species	Native or domestic	Frequency of records	Number of stations with presence
Didelphimorphia	Didelphidae	Mouse oposum	Thylamys sp.a	N	1	1
Cingulata	Dasypodidae	Six-banded armadillo	Euphractus sexcinctus	N	3	1
Rodentia	Cricetidae	Big-headed rice rat	Euryoryzomys legatus ^b	N	2	2
	Dasyproctidae	Agouti	Dasyprocta punctata	N	12	4
Lagomorpha	Leporidae	Tapeti	Sylvilagus brasiliensis	N	72	17
Perissodactyla	Equidae	Donkey	Equus asinus	D	4	2
-	-	Horse	Equus caballus	D	3	3
	Tapiridae	Lowland tapir	Tapirus terrestris	N	2	2
Cetartiodactyla	Bovidae	Cattle	Bos taurus	D	62	14
J	Cervidae	Gray brocket deer	Mazama gouazoubira	N	22	6
	Tayassuidae	Collared pecari	Pecari tajacu	N	5	3
	Suidae	Domestic pig	Sus scrofa	D	14	2
Carnivora	Felidae	Puma	Puma concolor	N	1	1
		Jaguarundi	Puma yagouaroundi	N	4	3
		Ocelot	Leopardus pardalis	N	9	4
		Margay	Leopardus wiedii	N	5	3
	Canidae	Domestig dog	Canis lupus	D	7	3
		Crab-eating fox	Cerdocyon thous	N	57	15
	Procyonidae	Coati	Nasua nasua	N	2	2
	Mustelidae	Tayra	Eira barbara	N	63	19

^a Either Thylamys sponsorius or T. venustus (David Flores, pers. comm.).

significant correlation with the ordinations that combined axes 1–2 and 1–3 (Fig. 3, Table 3). Accessibility, the natural logarithm of the frequency of records of domestic animals and the conservation status of the area had no correlation with the ordination. The gray brocket deer (*Mazama gouazoubira*), the ocelot (*Leopardus pardalis*), the agouti (*Dasyprocta punctata*) and the tapeti were generally associated with stations located at low altitudes while the crab eating fox and the tayra showed an opposite pattern (Fig. 3).

Discussion

The number of native species recorded was not very high (N=15). A comparison with a list of potential species present in the study area (Jayat et al., 2009; Jayat and Ortiz, 2010) suggests that the completeness of our species record was ~46% of the species potentially recorded during our survey. Some of the species not recorded during this survey (red brocket deer Mazama americana, white lipped peccary Tayassu pecari, jaguar Panthera onca) may be locally rare as a result of hunting or as a result of the widespread presence of domestic animals. However, some other species (armadillum Dasypus sp., common opossum Didelphis albiventris, tamandua Tamandua tetradactyla, oncilla Leopardus tigrinus) have been frequently recorded in similarly designed surveys conducted in other localities of the Yungas (Di Bitetti et al., unpublished results). The lack of records of these species may represent a relatively low local abundance as a result of ecological or historical reasons. Further studies conducted at a larger spatial scale may provide a clear picture of the degree of variation in the composition of the mammal assemblage of the Yungas in relation to natural vs anthropic factors.

Human activities usually have important direct (e.g. through hunting) and indirect (e.g., through domestic animals) effects on the mammal assemblages. Hunting usually reduces the relative abundance and total biomass of the larger species, occasionally increasing the absolute abundance of the smaller, less preferred ones (Peres, 2000, 2010; Peres and Dolman, 2000). Cascade effects through the ecological community can also follow the reduction in number of the large herbivores (Wright and Duber, 2001), and top predators (Crooks and Soulé, 1999; Berger et al., 2008). The abundance of both ungulates and top predators is usually higher in

the better-protected areas and increases with the distance to the more accessible areas frequented by poachers (e.g., Caro, 1999; Di Bitetti et al., 2008, 2010). Livestock grazing is an activity that usually has notorious effects on the structure and composition of natural communities (Cingolani et al., 2008; Blundo et al., 2012). Among the mammals, large herbivores may be negatively affected by cattle through competitive interactions (Madhusudan, 2004; Hibert et al., 2010). Large carnivores usually suffer the retaliation effect of cattle owners, which suffer predation on their livestock and see top predators as pests that should be eradicated (Loveridge et al., 2010).

These predictable changes in certain mammal guilds should translate into changes in species richness and in the composition of the mammal assemblage. However, we did not find any effect of accessibility, the protection status of the area or the presence of domestic animals on the composition of the native mammal assemblage or its richness. During this study we could not monitored the whole gradient of accessibility, protection or abundance of domestic animals present in the region, which may explain why we did not find an effect of these variables on the mammal assemblage. Future surveys should increase the range of situations considered in our study, something that could be accomplished by expanding the spatial scale of the surveyed area, including sites in the Bolivian side of the Yungas.

In the Yungas, tree species composition is mostly determined by elevation, with a secondary role for local effects such as presence of cattle (Blundo et al., 2012). Elevation in turn is highly correlated with other biotic (e.g. fraction of animal dispersed vs wind dispersed fruits) an abiotic (e.g. moisture stress) factors (Blundo et al., 2012; Malizia et al., unpublished results). In other tropical systems the diversity of mammals and the species composition of the mammal assemblage change along ecological gradients that vary is tree species composition and structural complexity (August, 1983; Williams et al., 2002; Tews et al., 2004) Thus, we expected to find the observed pattern of mean species richness per cameratrap station decreasing with elevation and the correlation between elevation and the NMDS ordination. These results suggest that elevation has an important effect on the medium size and large terrestrial mammal assemblages of the Yungas, somewhat previously suggested by Ojeda and Mares (1989) for the small mammals

^b At least one of the two Cricetine records could be assigned to this species. The other one is probably the same species but it is more difficult to be sure due to the quality of the picture (Pablo Jayat, pers. comm.).

Table 3Correlation of the predictive independent variables on the different combinations of the NMDS axes 1–3. r^2 = squared correlation coefficient, Pr (>r) = two tail statistical probability of obtaining such a coefficient by chance alone estimated using 9999 random permutations. Correlations with probability values < 0.10 are depicted in bold.

Variable	NMDS1 + NMDS2		NMDS1 + NM	NMDS1 + NMDS3		NMDS2 + NMDS3	
	r^2	Pr (>r)	r^2	Pr (>r)	r^2	Pr (>r)	
Accessibility	0.080	0.406	0.012	0.878	0.068	0.478	
Domestic animals	0.034	0.688	0.168	0.139	0.192	0.109	
Conservation status	0.009	0.807	0.009	0.794	0.000	0.995	
Elevation	0.211	0.084	0.274	0.035	0.115	0.282	

and bats. An effect of elevation on the native mammal assemblage was detected despite the relatively narrow altitudinal range studied (542 m) which comprises the transition zone between two previously described vegetation communities. These results highlight the importance of encompassing whole elevation gradients in landscape planning and conservation schemes aimed at biodiversity conservation in mountainous areas (Patterson et al., 1998). In the Yungas, it is critically important to preserve the last sectors of Premontane forests, which have suffered a higher conversion rate to agriculture than other vegetation types and are less represented within the protected areas of this region (Brown et al., 2002).

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