

Habitat preferences of the Andean bear (*Tremarctos ornatus*) in the Bolivian Andes

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Abstract

Habitat preferences of the Andean bear *Tremarctos ornatus* were studied within two adjacent protected areas in the north-western Bolivian Andes. Standard transects measuring habitat variables and bear sign frequency were used spanning seven different vegetation types. Andean bears were present at 28 of 33 sampled sites and actively preferred high-elevation elfin forest and upper montane humid forests, and used high-elevation humid 'páramo' grasslands and middle montane humid forests according to their availability. Bears were absent from dry montane and Andean foothill forests and relative abundance was low in lower montane humid forests. Elevation and basal area of food items were the variables most closely related to the relative abundance.

Introduction

The first step in determining the relationship between the distribution and abundance of a species and the characteristics of its habitat is to document whether it exhibits preferential habitat use and to establish the different scales of selection. Subsequently, associated geographical or ecological variables can be used to help predict the presence or abundance of this species in other sites (Guisan & Zimmermann, 2000). This multiscale and nested approach acknowledges the influence of spatial variation of habitat-related variables on species behavior, recognizes that there is no such thing as an 'appropriate scale' (Luck, 2002) and allows the modeling of species distributions across wide ranges (Gómez, 2004). In this light, the selection of different scales of analysis might help us make more rigorous decisions regarding the conservation of key elements of a given landscape.

The Andean or spectacled bear *Tremarctos ornatus* is an endemic species of the tropical Andes, and the only representative of the Ursidae family in South America. The Andean bear range occupies around 26 000 km² spanning five countries, Venezuela, Colombia, Ecuador, Peru and Bolivia, with the latter two countries representing over 60% of their range (Peyton, 1999). In Bolivia, the Andean bear inhabits a broad altitudinal range (450–4000 m a.s.l.) to the east of the eastern mountain range of the Andes, mainly in montane humid grasslands, montane forests and Andean

foothill forests (Rumiz & Salazar, 1999). Nevertheless, field data regarding *Tremarctos* are scarce in Bolivia and even theoretical distribution maps are in need of revision (Salazar & Anderson, 1990; Eulert, 1995; PAHS, 1995; Rumiz & Salazar, 1999; Rivadeneira, 2000; Velez & Azurduy, 2000; Paisley, 2001; Rechberger, Wallace & Ticona, 2001).

Andean bears are considered to be principally vegetarian (Peyton, 1980; Suárez, 1985; Rivadeneira, 2000; Velez & Azurduy, 2000; Paisley, 2001). They are known to move significant straight-line distances in this challenging topography (Rechberger *et al.*, 2001) and are thought to move altitudinally across several types of vegetation in search of terrestrial bromeliads, shrub-borne fruits and forest fruits (Peyton, 1980, 1999; Suárez, 1985; Rodríguez & Cadena, 1992; Yarena & Torres, 1994; Paisley, 2001; Rodríguez *et al.*, 2003).

Andean bears are considered to be a flagship species for the conservation of the Tropical Andes (Cuesta, Peralvo & Sanchez, 2001; Rodríguez *et al.*, 2003). Across their range, they are the subject of considerable conflicts with farmers and ranchers in rural human communities, because of crop- or livestock-associated losses (Goldstein, 1991; Morales, 2003; Goldstein *et al.*, in press). Using the landscape species selection criteria (Coppolillo *et al.*, 2004), Andean bears were chosen as a 'landscape species' (Sanderson *et al.*, 2002) for the humid tropical Andes and were subsequently used to determine areas and actions for biodiversity conservation

in the Apolobamba protected area (Gómez, 2004) in the Greater Madidi Conservation Landscape.

There have been several attempts to describe Andean bear habitat (Peyton, 1980, 1986; Suárez, 1985; Eulert, 1995; Velez & Azurduy, 2000; Cuesta *et al.*, 2001); however, only Peyton (1980, 1984), Rumiz, Eulert & Arispe (1999) and Cuesta *et al.* (2001) linked *Tremarctos* presence or relative abundance to clearly defined habitat and vegetation variables.

In this article we present an evaluation of habitat use across the north-western Bolivian Andes, using the relationship between some ecological and physical variables and the relative abundance of Andean bear signs.

Methods

Study area

We conducted the study across two adjacent Bolivian protected areas: Madidi National Park and Natural Area of Integrated Management and Apolobamba Natural Area of Integrated Management. These protected areas are found in the northern portions of the Department of La Paz in Bolivia ($69^{\circ}02' - 69^{\circ}50'W$ and $14^{\circ}12' - 15^{\circ}10'S$), and the altitude of the study area ranged between 500 and 3700 m a.s.l. (Fig. 1) and covered 9068 km².

In general, the study area belongs to the biogeographical province of the Bolivian Yungas (Mueller, Beck & Lara, 2002; Navarro & Maldonado, 2002). Vegetation types in the study area began at high elevations with Andean open grasslands (páramo yungueño; 9% of the study area) chan-

ging into elfin forest (6%) at the tree line, and then upper montane humid forest (10%), middle montane humid forest (26%), low montane humid forest (31%) and foothill humid forest (15%), with dry montane forest (3%) also present in one valley within the study area. Details regarding the structure and composition of these vegetation types are provided in Zenteno, Ríos-Uzeda & Gómez (in press).

Sample collection

First, a series of 1:100 000 scale maps of the study area were examined, and vegetation types were assigned to each of the 1000 m² quadrants. Subsequently, 60 points were selected using a stratified random system based on the proportion of each vegetation type within the study area. We then chose a sub-sample of 33 points based on logistical accessibility, where points that were considered more than 2 days from the nearest access route (road or established trail) were excluded from the sample.

Under this arrangement, we sampled six sites in páramo yungueño (18% of samples sites), four sites in elfin forest (12%), four sites in upper montane humid forest (12%), nine sites in middle montane humid forest (27%), five sites in lower montane humid forest (15%), three sites in foothill humid forest (9%) and two sites in dry montane forest (7%). Thus, páramo yungueño, elfin forest and dry montane forest were slightly oversampled according to their importance in the study area, and lower montane forest was undersampled. We then conducted evaluations between December 2000 and October 2003, with the majority of

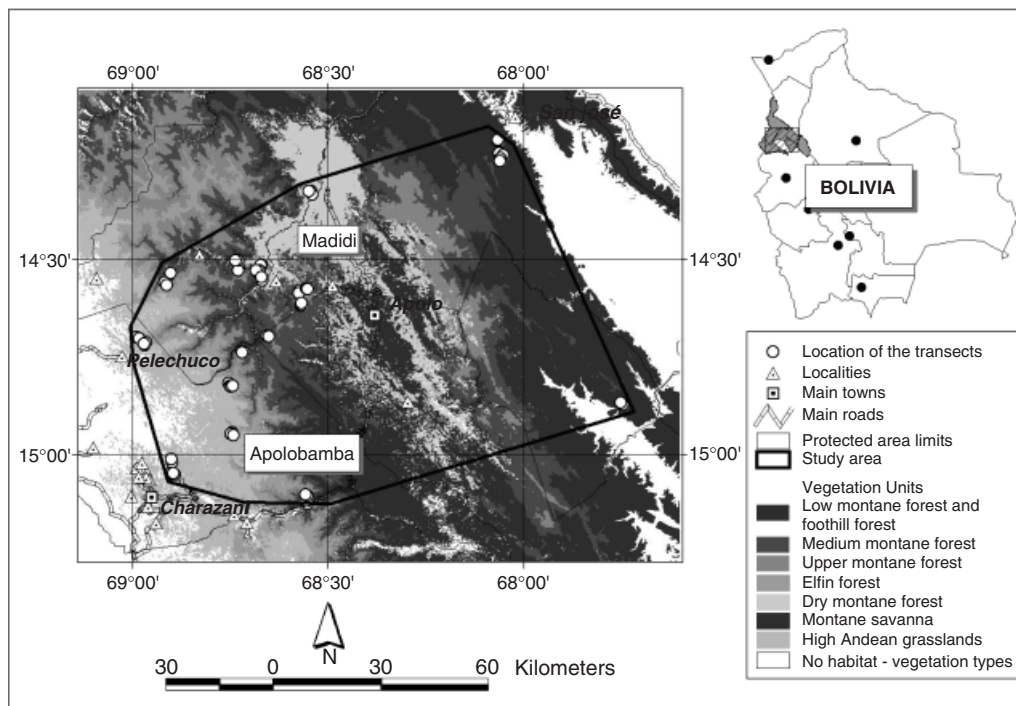


Figure 1 Study area and sample sites within the Madidi and Apolobamba protected areas of northern La Paz Department, Bolivia.

transects (28) evaluated during the dry season (May to October).

Evaluations at each selected point consisted of a straight 1 km transect that was 3 m wide (1.5 m either side of the trail). Additionally, from this transect five randomly selected 300 m perpendicular lines were sampled in the same manner for a total sample of 2.5 km. Each transect was exclusively situated in one of the recognized vegetation units. Along transects we recorded the number of different types of Andean bear sign; scat, tree nests, hairs, scratch marks, feeding sites, beds and Andean bear paths. These paths were clear travel routes used by the bears and were always associated with footprints or another type of Andean bear sign. In order to reflect the relative abundance of Andean bears by vegetation type, we used sign encounter rates, expressed as the number of signs km^{-1} of transect.

We also recorded information on certain habitat parameters along each transect, including the height and diameter at breast height (DBH) of all the trees greater than 5 cm DBH. A detailed analysis of different tree communities across vegetation types was conducted (Zenteno *et al.*, in press). This analysis also allowed the calculation of basal areas of potential food resources for each transect. A list of potential bear resources (food or shelter) was first drawn from our own field information and a thorough literature review (Peyton, 1980; Suárez, 1988; Mondolfi, 1989; Goldstein, 1991; Rodríguez & Cadena, 1992; Herrera *et al.*, 1994; Eulert, 1995; Rivadeneira, 2000; Sandoval, 2000; Velez & Azurduy, 2000; Paisley, 2001). Subsequently, tree species found on the transects that had not been linked but that fit the characteristics of known bear resources, for example, fleshy fruits and palms, were also included in the list.

We recorded additional environmental variables in plots of 9 m² at 50 m intervals along the transects; including elevation, aspect, slope, canopy cover, visibility at ground level, tree density, palm density, shrub density, bromeliad density, density of potential resource trees for bears, leaf litter depth, mean tree height, mean height of emergent trees and distance to water and human influence (modified from Sandoval, 2000 and Gentry, 2001).

Minor human activity in the form of remote trails in forested areas and extensive livestock management in open

grasslands was recorded at all sites; however, no human presence was detected along transects at 31 of the 33 sample sites.

Statistical analysis

We tested normality assumptions for all habitat variables and encounter rates using the Shapiro–Wilks test. When variables were not normally distributed, we transformed them accordingly (Sokal & Rohlf, 1995). In order to select the most appropriate relative abundance index, we used a Spearman's coefficient $\text{tg}(\text{correlation matrix})$ using the different types of bear sign and their respective encounter rates. We then examined Andean bear sign encounter rate variation between vegetation types using the Kruskal–Wallis (KW) test. We evaluated vegetation type selection using a χ^2 test and the Bonferroni confidence intervals on bear sign frequencies. To examine possible relationships between Andean bear relative abundance and habitat variables we used stepwise regression. We analyzed the multicollinearity between variables using the Pearson correlation coefficient, and $r \geq 0.80$ was considered a suitable criterion for omitting a variable from the multivariate analysis (Luck, 2002).

Results

Of the 33 sampled sites, we found Andean bear sign at 28 sites (representing 84% of the total). Andean bear sign was absent at both dry montane forest sample sites, and all three foothill forest sample sites. In total, we recorded 487 Andean bear paths, 121 feeding signs, 10 beds, 23 scratch marks, nine scats, one tree nest and seven hairs.

Correlation among indices

Andean bear sign encounter rates were highly variable between different vegetation types (Table 1). Andean bear path encounter rate (PER = number of paths km^{-1} of transect) was significantly related to encounter rates of all other types of bear sign ($r = 0.49$, $P = 0.004$ with feeding sites; $r = 0.389$, $P = 0.025$ with scats; $r = 0.407$, $P = 0.019$ with scratch marks; $r = 0.405$, $P = 0.02$ with hairs and $r = 0.347$, $P = 0.048$ with beds). A test was not possible for

Table 1 Mean (sd) of Andean bear *Tremarctos ornatus* sign ERs by vegetation type

Vegetation type	Sign ER (number of signs km^{-1} transect evaluated)							
	Feeding sites	Paths	Beds	Scratch marks	Scats	Tree nests	Hairs	Total
FHHF	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
LMHF	1.5 (1.3)	5.8 (1.7)	0.0 (0.0)	0.2 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	7.6 (2.6)
MMHF	0.8 (1.3)	6.3 (4.0)	0.1 (0.1)	0.7 (0.9)	0.0 (0.1)	0.0 (0.0)	0.1 (0.1)	7.8 (5.0)
UMHF	0.7 (1.1)	8.4 (6.0)	0.2 (0.4)	0.1 (0.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	9.4 (6.1)
EF	4.0 (1.6)	16.7 (11.7)	0.7 (0.8)	0.5 (0.5)	0.8 (1.0)	0.1 (0.2)	0.7 (0.6)	23.5 (14.3)
DMF	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
OHG	3.0 (6.0)	3.4 (5.2)	0.1 (0.3)	0.0 (0.0)	0.1 (0.3)	0.0 (0.0)	0.1 (0.2)	6.7 (9.0)

ER, encounter rate; FHHF, foothill humid forest; LMHF, lower montane humid forest; MMHF, middle montane humid forest; UMHF, upper montane humid forest; EF, elfin forest; DMF, dry montane forest; OHG, open highland grasslands.

tree nests due to the extremely small sample size ($n = 1$). We therefore decided to use PER as an indicator of Andean bear use to compare relative abundance across different vegetation types in the landscape. No significant differences in PER were found between sample years (KW test, $X^2_1 = 1.730$, $P = 0.421$), and so years were combined for posterior evaluations.

Habitat preferences

Andean bear relative abundance was significantly different across vegetation types (KW test, $X^2_1 = 15.336$, $P = 0.018$), with PER highest in elfin forest, upper montane humid forest and middle montane humid forest; lower in lower montane humid forest and high Andean humid grasslands; and absent during the study in dry montane forest and foothill humid forest.

In all, 487 paths were recorded at 27 of the 33 sample sites. Andean bear path sign frequency differed significantly across vegetation types from the expected frequency according to availability across the landscape ($X^2_7 = 471.08$, g.l. = 6; $P < 0.001$). Bonferroni confidence limits revealed that elfin and upper montane forests are clearly preferred by Andean bears, while lower montane humid forest is not actively selected by bears, and foothill forest and dry montane forest do not appear to be viable habitat for Andean bears. High Andean humid grasslands and middle montane humid forest were used according to their availability.

Ecological and physical variables related to the Andean bear relative abundance in the landscape

Table 2 summarizes the mean values for each habitat variable at sample sites where Andean bears were present. The majority of these variables were significantly correlated with elevation (mean emergent tree height: $R = -0.929$, $P < 0.001$; mean tree height: $R = -0.892$, $P < 0.001$; density of potential bear resource trees: $R = -0.475$, $P = 0.005$; shrub density: $R = -0.693$, $P < 0.001$; canopy cover: $R = -0.477$, $P = 0.005$; visibility at ground level: $P = -0.465$, $P = 0.006$; slope: $R = -0.418$, $P = 0.016$; palm density: $R = -0.475$, $P = 0.005$; basal area: $R = -0.574$, $P < 0.001$; distance to water: $R = -0.255$, $P = 0.151$; bromeliad density: $R = -0.113$, $P = 0.532$; leaf litter depth: $R = -0.063$, $P = 0.729$; and aspect: $R = -0.067$, $P = 0.713$). Thus, the mean emergent tree height and the mean tree height were excluded from the analysis, and a total of 10 variables were used in the stepwise regression to determine the most parsimonious model. The final model (Table 3) was highly significant ($F_{4,28} = 4.2411$, $P < 0.008$), and explained 61% of PER variance (coefficient of regression R). Habitat selection by Andean bears was positively related to elevation and basal area of potential food items, and to a lesser degree, slope and distance to water, but only the first two variables had a significant ($P < 0.05$) β coefficient.

Discussion

Andean bear habitat use

Andean bears in the north-western Bolivian Andes showed clear preferences for higher elevation forest vegetation types (elfin and upper montane humid forests) up to 3700 m. However, it is important to emphasize the relative scarcity of these vegetation types in the landscape (see Fig. 1). Middle montane forest was also an important habitat and was used in proportion to its availability. Previous multiple sign-type studies of Andean bear habitat use also identified higher elevation forests as the preferred habitat (Peyton, 1980), mainly related to food resources within these forest types. Rumiz *et al.* (1999) found that Andean bears in the Amboró Protected Area preferred forests above 2000 m and they avoid forests below 1000 m, while the majority of the signs were found between 1000 and 1500 m in Carrasco National Park. The latter has more human pressure in higher elevations because of the presence of human settlements and the Cochabamba–Santa Cruz road, a heavy traffic road.

Several studies have suggested that high-elevation Andean humid grasslands and immediately adjacent montane forests are preferred habitats for Andean bears (Peyton, 1980, 1986, 1987; Suárez, 1988; Yarena & Torres, 1994). In this study, Andean bears used 'páramo' grasslands according to their availability. Páramo grasslands offer a limited diversity of food types such as large bromeliad plants (*Puya* spp.), and some Ericaceae fruits near the forest border. Local people report bears more frequently from open habitats precisely because they are more visible and because livestock conflicts with Andean bears are almost entirely confined to this habitat (Goldstein *et al.*, in press).

Lower mountain humid forest was also registered as bear habitat, but bears were not recorded in the immediately adjacent vegetation types of dry montane forest (ranging between 700 and 1200 m elevation) and foothill forests at the base of the Andes (ranging between 700 and 1500 m elevation). Additional information from interviews with park guards and several local community members suggests that true dry forest is not a suitable habitat for the Andean bear, although occasional records in transitional areas with lower montane humid forest exist (Ríos *et al.*, 2001). It is also worth mentioning that occasional records from foothill forest occur across the region, for example, a photograph of an adult on a beach of the river Tuichi at 450 m a.s.l. (Chalalan Ecolodge, pers. comm. to B. Ríos-Uzeda), but so far we have been unable to demonstrate that foothill forest is a viable habitat for the Andean bear in the north-western Bolivian Andes landscape. Nevertheless, in other regions of Bolivia, Andean bears have been shown to prefer low-elevation forests (Rumiz *et al.*, 1999).

The results of the stepwise regression confirm that existing habitat preferences are related to high densities of potential resource trees, as well as shrub stems in general. This result points to a tapering increase in resource availability, both in terms of food and shelter, and as such

Table 2 Mean, median and range values for habitat parameters in vegetation types where Andean bear *Tremarctos ornatus* signs occurred (*mean and **median)

Variable	Units	Vegetation			LMHF			MMHF			UMHF			EF			OHG			Total		
		Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean	Mode	Range
Aspect ^{a++}		4		2–8	4		2–8	4		2–8	6.5		5	4–8		1–8	5		1–8	5		1–8
Basal area ⁺	m ²	3.5 (1.7)		2.3–6.5	2.7 (1.1)		1.3–4.8	1.3 (0.7)		0.4–2.2	1.3 (0.7)		2.9 (0.8)	1.8–3.7		0–0	0		0–0			0–4.1
Bromeliad density ⁺	n9 m ⁻²	22.2 (4.8)		16–28	38.3 (29.7)		10–111	27 (13.1)		15–45	6 (3.5)		6 (3.5)	3–11		0–56	14.2 (21.4)		0–56	23.9 (23)		0–111
Canopy cover ^{b++}		3		2–5	4		3–5	3.5		2–5	2		1–5	0		0–0	0		0–0	3		0–5
Distance to water ^{c++}		6		6–6	6		5–6	6		6–6	5.5		4–6	6		5–6	6		5–6	6		4–6
Elevation ⁺	m a.s.l.	1151.4 (238.4)		908–1497.5	1829.6 (218.2)		1343–2086.5	2426.9 (227.4)		2222.9–2737.9	3302.1 (171.7)		3045.8–3405.7	3515.1 (156.6)		3309.5–3699.6	2419.4 (880.9)		3309.5–3699.6	2419.4		958.1–3699.6
Emergent tree height ⁺	m	27.3 (3.7)		22.2–31.3	21.3 (2.9)		17.4–26.3	12.7 (3.6)		8.7–17.3	7.45 (1.8)		5.3–9.7	0.04 (0.1)		0–0.2	13.9 (10.1)		0–0.2			0–30
Leaf litter depth ⁺	cm	6.6 (3.7)		2.4–11.3	30.2 (8.4)		19.1–41.1	49.4 (14.2)		36.6–64.7	23.9 (10.2)		13.1–34.2	0.4 (0.8)		0–2.1	18.9 (18.1)		0–2.1			0–64.7
Human influence ⁺⁺		0–0		0–0	0		0–0	0		0–0	0		0–0	0		0–3	0		0–3	0		0–3
Mean tree height ⁺	m	16.9 (5.7)		10.8–23.6	12.9 (3.3)		10.3–0.1	8.7 (2.9)		5.5–12.3	4.5 (1.2)		3.1–6.1	0.02 (0.1)		0–0.2	8.5 (6.1)		0–0.2			0–22.5
Orchids ⁺	n9 m ⁻²	1.8 (4.1)		0–9	10.7 (16.7)		0–51	40 (44.4)		4–100	1 (1.4)		0–3	0		0–0	8.1 (20.5)		0–0			0–100
Palm density ⁺	Ind km ⁻²	13.8 (12.5)		1–30	21.6 (20.5)		4–69	1.75 (2.2)		0–5	0		0–0	0		0–0	27.3 (47.1)		0–0			0–69
Slope ⁺	Degrees	17.1 (3.2)		13.8–21.1	15.6 (5.4)		7.5–25.9	18.5 (5.1)		12.5–24.1	24.1 (7.2)		14.1–30.2	25.3 (9.3)		8.8–33.9	19.7 (7.2)		8.8–33.9			7.5–33.9
Visibility ^{d++}		2		2–3	3		2–3	3.5		3–4	2		2–4	0		0–0	2		0–0	2		0–4

^a1 = N, 2 = NE, 3 = E, 4 = SE, 5 = S, 6 = SW, 7 = W, 8 = NW.^b and ^cSix quadrants of same proportion.^d1 = < 5 m, 2 = 5–15 m, 3 = 15–30 m, 4 = 30–60 m, 5 = 60–120 m, 6 = > 120 m.

LMHF, lower montane humid forest; MMHF, middle montane humid forest; UMHF, upper montane humid forest; EF, elfin forest; OHG, open highland grasslands.

Table 3 Habitat variables included in the final regression model showing the values of beta (β) coefficients

Variables	β coefficients	SD	Sig. <i>P</i>	<i>R</i>
Constant	-38.138	16.327	0.027	
Elevation	0.005	0.001	<0.001	0.296
Basal area ^a	5.879	1.692	0.001	0.544
Distance to water	3.832	2.227	0.096	0.587
Slope ^b	46.961	38.639	0.234	0.614

Standard deviation (SD), levels of significance (Sig. *P*) and cumulative proportion of the variance explained (*R*).

^aTransformed into square root.

^bTransformed into its inverse.

bear greater importance. Literature reviews confirm that most identified Andean bear food species are concentrated in these two habitats (Zenteno *et al.*, in press). Available dietary information suggests that Andean bears primarily consume bromeliad hearts, berries, palm hearts and fleshy fruits (Cabrera & Yepes, 1960; Peyton, 1980; Suárez, 1985; Lozada, 1989; Rivadeneira, 2000; Velez & Azurduy, 2000; Paisley, 2001). However, very little information on Andean bear diet has been collected at lower elevations, and given that these dietary items remain abundant in lower elevation forests (Flores, Batte & Dapara, 2002; Zenteno *et al.*, in press), we suggest that greater Andean bear abundance in higher elevation forests might also be partially due to a relative dearth of potential vegetarian competitors. In the lower elevation montane forests of northern La Paz, several Amazonian taxa are present in significant numbers: *Tapirus*, *Tayassu*, *Pecari*, *Mazama*, *Lagothrix*, *Ateles*, *Alouatta*, *Cebus*, *Cuniculus*, *Dasyprocta*, *Nasua*, *Eira*, *Mutu*, *Penelope* and *Pipile*. Many of these taxa begin to disappear in middle montane humid forests and are entirely absent from the highest elevation forest types (Ríos, 2001; Ríos *et al.*, 2001), leaving the Andean bear as the main mammalian fruit and berry consumer in these forests.

Altitude is obviously strongly related to vegetation type and is a major factor in differentiating the various habitat forms across the north-western Bolivian Andes (Zenteno *et al.*, in press). Slope was not expected to be a major factor as Andean bears are known to be excellent climbers, although vegetation type and tree size might be expected to be stunted on extreme inclines. Distance to water is also of limited use given that most of the Andean landscape is relatively close to streams; however, vegetation immediately adjacent to streams and rivers is specific and this might influence bear presence. This might be most relevant in elfin forests that climb further in fingers alongside highland streams.

Encounter rate as a relative abundance index

Given that any Andean bear sign is related to bear movements, it is not surprising that Andean bear path encounter rates were significantly related to encounter rates for all other sign types. The PER represents a promising measure of Andean bear relative abundance given the ease with which bear paths are identified and their overall frequency compared to other types of bear sign. Indeed, we recom-

mend that future studies use path encounter rates as a standard measure of Andean bear relative abundance, particularly as scat, bed and nest decomposition rates are unknown and are likely to vary more considerably across habitats than the detectability of bear paths. Feeding sign encounter rates may also be problematic if bear diet varies significantly across vegetation types, implying variation in feeding sign type and as a result decomposition rates. Studies assessing variations in detectability over time for all types of bear sign across different types of habitat should be a priority for further evaluating the robustness of relative abundance measures.

Previous studies that have used Andean bear sign as a measure of relative abundance have suggested that, due to independence concerns, signs within 100 m of each other (Peyton, 1980) or 5 m of each other (Cuesta, Peralvo & van Manen, 2003) should be considered as one record. Unfortunately, there is no biological justification for either of the distances used as independence criteria, and given what little is known about Andean bear daily, monthly, seasonal, annual and lifetime-ranging behavior (Paisley, 2001), it would be difficult to justify a measure of sign independence biologically. Nevertheless, we reran our analyses using Peyton's (1980) 100 m independence criteria, and the results for habitat preference analyses and order of importance of sample sites were extremely similar to those reported here.

A possible criticism of PER as a relative abundance measure is that the detectability of Andean bear paths may be related to ground-level vegetation density, a variable that varied across vegetation types. However, this situation was recognized at the beginning of the study and care was taken in the field to reduce this potential bias, for example, the same field team implemented all 33 transects and were trained by experienced Andean bear researchers prior to the campaign. Additionally, large mammal communities diversify as altitude decreases, and future studies should be aware that the possibility of misidentifying bear paths and feeding signs increases as other large mammals begin to appear.

Reliable estimates of Andean bear relative abundance are critical in order to evaluate the overall conservation potential of different regions across the Tropical Andes for this threatened species. The operational budget for the surveys presented in the paper was *c.* 200 US dollars per sample site, and the results have allowed the construction of reliable distributional and biological models for Andean bears.

These models, in combination with information concerning human activities across the landscape, have permitted the development of a landscape scale action plan for the conservation of Andean bear and the biodiversity they represent in the northwestern Bolivian Andes (Gómez, 2004).

Nevertheless, for the conservation and management of Andean bear populations many critical data deficiencies remain, including robust estimates of population density. Similarly, little is known regarding Andean bear movements, either from a seasonal or life-history perspective (Paisley, 2001; Castellanos, 2003). For example, are bears found continually in lower montane forest or is this a seasonal use in times of relative resource scarcity in higher elevation montane forests?

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References

- Cabrera, A. & Yepes, J. (1960). *Mamíferos Sud Americanos*. Buenos Aires: Ediar.
- Castellanos, A.X. (2003). *Ecology of reintroduced Andean bears in the Maquipucuna biological reserve, Ecuador: conservation implications*. Quito: Espíritu del Bosque Foundation.
- Coppolillo, P., Gómez, H., Maisels, F. & Wallace, R. (2004). Selection criteria for suites of landscape species as a basis for site-based conservation. *Biol. Conserv.* **115**, 419–430.
- Cuesta, F., Peralvo, M. & van Manen, F.T. (2003). Andean bear habitat use in the Oyacachi River Basin, Ecuador. *Ursus* **14**, 198–209.
- Cuesta, F., Peralvo, M. & Sanchez, D. (2001). *Métodos para investigar la disponibilidad del hábitat del oso andino: El caso de la cuenca del río Oyachi, Ecuador*. Quito: Ecociencia.
- Eulert, C. (1995). *Evaluación del Estado Actual del Jukumari (Tremarctos ornatus), en el Parque Nacional Amboró, Santa Cruz – Bolivia*. Lic. thesis, Universidad Autónoma Gabriel Rene Moreno.
- Flores, J.G., Batte, C. & Dapara, J. (2002). Caracterización de la vegetación del río Undumo y su importancia para la conservación de la fauna silvestre. *Ecol. Bolivia* **37**, 23–48.
- Gentry, A.H. (2001). Patrones de diversidad y composición florística en los bosques de las montañas neotropicales. In *Bosques nublados del geotrópico*: 85–123. Kappelle, M. & Brown, A.D. (Eds). Costa Rica: Editorial INBio.
- Goldstein, I. (1991). Spectacled bear predation and feeding behavior on livestock in Venezuela. *Studi. Neotrop. Faun. Environ.* **26**, 231–235.
- Goldstein, I., Wallace, R., Paisley, S., Jorgenson, J., Torres, D., Castellanos, A., Galazo, L., Poveda, J., Cuesta, F. & Peyton, B. (in press). Andean bear-livestock conflicts: a regional perspective. *Ursus*.
- Gómez, H. (2004). *Usando el jukumari (Tremarctos ornatus) para determinar áreas prioritarias para la conservación en el Área Natural de Manejo Integrado Apolobamba (La Paz, Bolivia): el enfoque de las especies paisaje*. MSc thesis, Universidad Nacional de Costa Rica.
- Guisan, A. & Zimmermann, N. (2000). Predictive habitat distribution models in ecology. *Ecol. Model.* **135**, 147–186.
- Herrera, A.M., Nassar, J., Michelangeli, F., Rodriguez, J.P. & Torres, D. (1994). The spectacled bear in the Sierra Nevada national park of Venezuela. *Int. Conf. Bear Res. Mgmt.* **9**, 149–156.
- Lozada, R. (1989). Status of knowledge on the spectacled bear in Colombia: a preliminary report. In *Proceedings of the first international symposium on the spectacled bear*: 28–31. Rosenthal, M. (Ed.). Chicago: Lincoln Park Zoological Gardens.
- Luck, G.W. (2002). The habitat requirements of the rufus treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biol. Conserv.* **105**, 305–394.
- Mondolfi, E. (1989). Notes on the distribution, habitat, food habits, status and conservation of the spectacled bear (*Tremarctos ornatus*) in Venezuela. *Mammalia* **53**, 525–544.
- Morales, A. (2003). *Evaluación de Daños Causados por Vertebrados Silvestres en Maizales de Pajan, K'Apna y Wayrapata (ANMIN Apolobamba, La Paz – Bolivia)*. Lic. thesis, Universidad Mayor de San Andrés.
- Mueller, R., Beck, S.G. & Lara, R. (2002). Vegetación potencial de los bosques de Yungas en Bolivia, basado en datos climáticos. *Ecol. Bolivia* **37**, 5–14.
- Navarro, G. & Maldonado, M. (2002). *Geografía ecológica de Bolivia*. Cochabamba: Fundación Patiño.
- PAHS. (1995). *El Oso Jukumari en la Región de Lambate*. La Paz: Instituto Científico 'ALAX PACHA'.
- Paisley, S.L. (2001). *Andean bears and people in Apolobamba, Bolivia: culture, conflict and conservation*. PhD thesis, Durrell Institute of Conservation and Ecology, University of Kent.
- Peyton, B. (1980). Ecology, distribution, and food habits of spectacled bears, *Tremarctos ornatus*, in Peru. *J. Mammal.* **61**, 639–652.
- Peyton, B. (1986). A method for determining habitat components of the spectacled bear (*Tremarctos ornatus*). *Vida Silvestre Neotropical* **1**, 68–78.

- Peyton, B. (1987). Habitat components of the spectacled bear in Machu Picchu, Peru. *Int. Conf. Bear Res. Mgmt.* **7**, 127–133.
- Peyton, B. (1999). Spectacled bear conservation action plan, status and conservation action plan. In *Bears: Status survey and conservation action plan*: 157–164. Servheen, C., Herrero, S. & Peyton, B. (Eds). Switzerland: IUCN.
- Rechberger, J., Wallace, R. & Ticona, H. (2001). Un movimiento de larga distancia de un oso andino (*Tremarctos ornatus*) en el norte del Departamento de La Paz, Bolivia. *Ecol. Bolivia* **36**, 73–74.
- Ríos, B. (2001). Presencia de mamíferos terrestres y medianos y grandes en el Parque Nacional y Área de Manejo integrado Cotapata a través del uso de métodos indirectos. *Ecol. Bolivia* **35**, 3–16.
- Ríos, B., Wallace, R., Aranibar, H. & Veitch, C. (2001). Evaluación de mamíferos medianos y grandes en el bosque semideciduo del Alto Tuichi (PN y ANMI, Depto. La Paz). *Ecol. Bolivia* **36**, 31–38.
- Rivadeneira, C. (2000). *Dispersión de semillas por el oso andino en Apolobamba, Bolivia*. Lic. thesis, Universidad Mayor de San Andrés.
- Rodríguez, D., Cuesta, F., Goldstein, I., Bracho, A.E., Naranjo, L.G. & Hernández, O.L. (2003). *Estrategia ecorregional para la conservación del oso andino en los Andes del Norte*. Colombia: WWF Colombia, Fundación Wii, Ecociencia, WCS.
- Rodríguez, R. & Cadena, G. (1992). *Evaluación y calidad del hábitat del Oso Andino tremarctos ornatus en el Parque Nacional Natural Las Orquídeas y zonas adyacentes*. Colombia: Instituto de Ciencias Naturales.
- Rumiz, D., Eulert, C. & Arispe, M.R. (1999). Situación del oso andino (*Tremarctos ornatus* cuvier), en los parques nacionales amboró y carrasco, Bolivia. In *Manejo y conservación de fauna silvestre en América latina*: 375–381.
- Fang, T.G., Montenegro, O.L. & Bodmer, R.E. (Eds). La Paz: Instituto de Ecología.
- Rumiz, D.I. & Salazar, J. (1999). Status and management of the spectacled bear in Bolivia. In *Bears: Status survey and conservation action plan*: 164–168. Servheen, C., Herrero, S. & Peyton, B. (Eds.) Switzerland: IUCN.
- Salazar, J. & Anderson, S. (1990). Informe sobre el estado actual del conocimiento del oso andino en Bolivia. *Ecol. Bolivia* **15**, 3–23.
- Sanderson, E., Redford, K.H., Vedder, A., Coppolillo, P.B. & Ward, S. (2002). A conceptual model for conservation planning based on landscape species requirements. *Landsc. Urb. Plan.* **58**, 41–56.
- Sandoval, S. (2000). *Dieta y Uso de Hábitat por parte del Oso Andino en la Reserva Natural La Planada, Nariño*. MSc thesis, Facultad de Ciencias, Departamento de Biología, Pontificia Universidad Javeriana, Bogotá.
- Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*. San Francisco: W. H. Freeman.
- Suárez, L. (1985). *Hábitos alimenticios y distribución del oso de anteojos, en el páramo suroriental del volcán Antisana, Ecuador*. MSc thesis, Pontificia Universidad Católica del Ecuador.
- Suárez, L. (1988). Seasonal distribution and food habits of spectacled bears (*Tremarctos ornatus*) in the highlands of Ecuador. *Studi. Neotrop. Faun. Environ.* **23**, 133–136.
- Velez, X. & Azurduy, C. (2000). Análisis de Hábitat y composición alimentaria estacional del Oso Andino en la cuenta Alta del Río Cañón Cochabamba, Bolivia. *UKUKU* **2**, 1–3.
- Yerena, E. & Torres, D. (1994). Spectacled bear conservation and dispersal corridors in Venezuela. *Int. Conf. Bear Res. Mgmt.* **9**, 169–172.
- Zenteno, F., Ríos-Uzeda, B. & Gómez, H. (in press). Composición, diversidad y estructura de bosques montanos del norte de La Paz, Bolivia. *Biotropica*.