Andean bear (*Tremarctos ornatus*), biodiversity, and puma (*Puma concolor*) conservation on private lands in the Ecuadorian Andes: implications for conservation in a human-dominated landscape

By

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Dissertation Abstract

Protected areas have long been seen as the primary method for conservation of wildlife. Throughout the tropics, lack of enforcement or inappropriate coverage of the protected area system have demonstrated that they alone might not be sufficient to conserve healthy populations of wildlife, particularly those with large ranges or species that are seen as a threat to human livelihood. Private lands near protected areas could help to protect wildlife when levels of human-wildlife conflict are low and suitable habitat is available. In three chapters, we explore the potential for Andean bear (*Tremarctos ornatus*), biodiversity, and puma (*Puma concolor*) conservation on private lands in the Ecuadorian Andes. In Chapter 1, "The role of private lands in Andean bear conservation in the southern sector of Sangay National Park, Ecuador," we looked at factors associated with Andean bear presence to determine if bears on private lands could complement populations in protected areas, or if proximity to humans was a deterrent and private lands along park borders further isolated bear populations. We found that bears were only somewhat disturbed by human activities but habitat and access to annual changes in resources might be more important when planning for bear conservation on private lands. In Chapter 2, "Assessing the utility of Andean bears as conservation surrogates for Andean mammals on private lands in Ecuador," we used empirical data to evaluate how effective Andean bears are as conservation surrogates for other species. Our results suggest that for Andean bears to be a strong proxy for the conservation of Andean mammals, conservation strategies that include private lands must also conserve forested habitat. In Chapter 3, "How camera trap data can help us understand puma-livestock conflict in the Ecuadorian Andes," we used camera trap data to better understand depredation events on alpacas. We discuss non-lethal methods to mitigate conflict in this area and next steps for future research on pumas.

Resumen

Las areas protegidas han sido consideradas por largo tiempo como el mecanismo principal para la conservación de la vida silvestre. A lo largo de la zona tropical la falta de control y/o monitoreo en las áreas protegidas nos han demostrado que solas pueden resultar insuficientes para lograr conservar poblaciones sanas de vida silvestre, sobre todo en aquellas especies que requieren de amplios territorios o las que presentan una amenaza a la presencia humana. Las tierras privadas, aledañas a tierras protegidas, pueden ayudar a proteger a la vida silvestre cuando los niveles de conflicto entre humanos y vida silvestre son bajos, y hay un habitat adecuado disponible. En tres capítulos, exploramos el potencial para la conservación del oso andino (*Tremarctos ornatus*), la biodiversidad, y el puma (*Puma concolor*) en tierras privadas en los Andes ecuatorianos. En el Capítulo 1, "El papel de las tierras privadas en la conservación del oso Andino en el sector sur del Parque Nacional Sangay, Ecuador" analizamos los factores asociados con la presencia del oso andino para determinar si los osos que habitan tierras privadas complementan poblaciones en áreas protegidas, o si la proximidad a humanos es un factor de disuasión y que las tierras privadas cerca de áreas protegidas aislaban aún más a las poblaciones del oso. Encontramos que aunque los osos Andinos son levemente afectados por actividades humanas, la disponibilidad de habitat y el acceso a cambios anuales de los recursos naturales tienen un papel más importante en el diseño de proyectos de conservación del oso en tierras privadas. El Capitulo 2, "Evaluando la utilidad del oso Andino como especie de sustitución para mamíferos andinos en tierras privadas en Ecuador", utilizamos datos empíricos para evaluar cuán efectivos son los osos Andinos como sustitutos de conservación para otras especies. Nuestros resultados sugieren que para que el oso sea considerado un fuerte sustituto de la conservación de los mamíferos Andinos, las estrategias de conservacion que incluyen tierras privadas también deben conserver el hábitat boscoso. En el Capítulo 3, “Como los datos de cámeras trampas pueden ayudarnos a entender el conflicto entre pumas y ganado en los Andes ecuatorianos”, usamos datos de foto-captura para comprender mejor los eventos de depredación a alpacas. Discutimos mecanismos no-letales para reducer conflicto entre estas especies en esta área y proponemos los próximos pasos para futuras investigaciónes sobre pumas.

To JP

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Chapter 1: The role of private lands in Andean bear conservation in the southern sector of Sangay National Park, Ecuador

Abstract

Protected areas may not provide sufficient protection for wildlife that have some part of their range outside of park boundaries. Private lands next to protected areas may play an important role in the conservation of large carnivores when they provide an extension of habitat and other resources. Andean bears (*Tremarctos ornatus*) are the only bear species in South America, are globally threatened, and are endangered in Ecuador. They are the largest carnivore in the Andes and their presence on private lands is well-documented. The objective of our study was to determine if private lands with relatively low levels of human-bear conflict and suitable habitat could complement Andean bear populations in protected areas or if proximity to humans was a deterrent and private lands along park borders further isolated bear populations. From 2012-2014 we used camera traps to survey bear presence in the Nudo del Azuay region of Ecuador, where privately owned land is inside the southern border of Sangay National Park. Our study area (40 km^2) was a matrix of primary and secondary forests, shrublands, páramo (high-altitude grasslands), and pastures. We collected landowner information and extracted landcover and topographic data from a digital elevation model (DEM) and a RapidEye image to build four models to test human influence and habitat features against bear presence. We used a negative binomial regression with integrated nested Laplace approximation (INLA) to test our models. We detected Andean bears at 35 (45%) of camera traps sites on 11 (69%) participating properties. Andean bear presence was positively associated with an increase in distance from areas of high human use and low-quality bear habitat. Their presence was also positively associated with study year two, potentially indicating an annual shift in resource use in our study area. Presence of Andean bears was negatively associated with distance from rivers. Our results indicate that Andean bears are somewhat disturbed by human activities but that habitat and access to annual changes in resources might be more important when planning for bear conservation on private lands.

Introduction

Habitat loss and degradation are the primary threat to 40% of global mammal species (Schipper et al. 2008; Crooks et al. 2011). Only 15% of global wildlife habitat is inside protected areas (Gray et al. 2016) and many protected areas exist only on paper, not providing adequate protection for wildlife (Langholz & Krug 2004). Climate change is likely to make the protected area system insufficient, altering the distribution of some habitats and the species dependent on those habitats (Iturralde-Pólit et al. 2017). The majority of carnivore populations are outside of protected areas in low-quality habitat (Crooks et al. 2011). Therefore, lands managed by private individuals without strictly enforced legal protections for wildlife (private lands hereafter) could play an important role in the long-term survival of the species.

Large carnivore populations are declining and the majority of large carnivore species have experienced a substantial reduction in their ranges (Wolf & Ripple 2017). Carnivores are particularly vulnerable to anthropogenic threats due to their ecology (e.g. slow to reproduce), human perception of threat, and retaliatory killing after conflicts with humans. As apex predators, carnivores play an important role in the maintenance of ecosystem health, and the loss of key species (e.g. wolves *Canus lupus*) can trigger trophic cascades (Estes et al. 2011).

Consequently, private lands near protected areas may play an important role in conserving global carnivore populations. Living with and conserving carnivores often involves costs to human residents, including economic losses due to crop damage and predation on livestock, and possible human injury or loss of life (Löe & Röskaft 2004). People who live near protected areas that restrict their ability to respond to problems with wildlife may come to see them as an encroachment on their rights and wildlife presence as a burden (Wilson 1997; Neumann 1998; Knight 2000; Goldstein et al. 2006).

Andean bears (*Tremarctos ornatus*) are the largest carnivore in the Andes and often have ranges that overlap human settled lands (Flores et al. 2005; Goldstein et al. 2006; Zug 2009; Jones 2010). Throughout their distribution only an estimated 18% of potential bear habitat is within protected areas (Peyton 1999), resulting in Andean bears leaving protected areas in search of resources found on adjacent private lands where they will inevitably encounter people, livestock, and crops.

However, human-bear conflicts often result in bears being killed by landowners attempting to protect their crops and livestock. Thus, the survival of wild populations of Andean bears may depend on human tolerance but there has been little research on how bears are using private lands beyond reports of conflict. In Ecuador, the *Estrategia Nacional de Conservación del Oso Andino* (National Strategy for the Conservation of the Andean Bear; Castellanos et al. (2010) mentions the need for inclusion of private landowners in conservation planning but does not directly address the issue of bear presence and management on private lands. Deforestation in Ecuador is increasing, and only an estimated 60% of the original natural vegetation cover remains in the Ecuadorian Andes (Cuesta et al. 2017). This combination of factors and Ecuador's high population density (58 people/km^2) (The World Bank 2012) put Andean bears and rural people in relatively close contact.

Andean bear ecology and conservation status

The Andean bear is the only species of bear in South America and is threatened throughout its range. The species is listed as vulnerable on the International Union for the Conservation of Nature (IUCN) Red List, and the Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES) lists the Andean bear as an Appendix I species, prohibiting international trade except under exceptional circumstances (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2017; Velez-Liendo & García-Rangel 2017). Their current population trend is decreasing , and in Ecuador, the species is endangered (Tirira 2011; Velez-Liendo & García-Rangel 2017). They are taxonomically unique and youngest of the bear species (García-Rangel 2012). Also called the spectacled bear, Andean bears are perhaps most well-known for the beige-colored patterning around their eyes, muzzle and chest. This ornate patterning is unique to each individual and can be used to identify individuals (Rios-Uzeda et al. 2007; Zug 2009; Jones 2010; Van Horn et al. 2014).

The Andean bear is distributed throughout five Andean nations- Venezuela, Colombia, Ecuador, Peru and Bolivia (Velez-Liendo & García-Rangel 2017). There is some debate about whether Andean bears exist in Argentina and Panama (Goldstein et al. 2008; García-Rangel 2012; Cosse et al. 2014). A population estimate for Andean bears is widely speculative and based on extrapolation from other bear species, genetic diversity across Andean bear range, or small sample sizes (Garshelis 2011). Two commonly cited population estimates are 5,000 - 30,000 bears, based on a genetic study conducted by Ruiz-Garcia (2003), and <20,000, based on minimum density estimates of American black bear (Ursus americanus) (Peyton et al. 1998). A recent study estimated density in an Andean bear population northwest of Quito to be 7.45 bears/100 km^2 (Molina et al. 2017), similar to the low-density estimate for American black bears. Human activities throughout Andean bear habitat are thought to isolate populations and lack of information on population and distribution make conservation planning difficult (Kattan et al. 2004; Garshelis 2011).

Andean bears use a variety of habitats including cloud forests, montane evergreen and deciduous forest, dry forests, steppe lands, and páramo (high altitude grasslands and scrublands)

(Velez-Liendo & García-Rangel 2017). Andean bear habitat typically ranges in elevation from 1,000 to 4,750 m but a resident population of bears is known to live as low as 250 m in dry forest in Peru (Cuesta et al. 2003; García-Rangel 2012). Their current distribution stretches across a mosaic of protected and private lands, highlighting the importance of private lands in the success of current and future Andean bear conservation efforts. Information on individual home ranges is limited and based on other bear species or a few radio collared individuals. Females are thought to have smaller ranges than males with extensive overlap with other females and males (García-Rangel 2012). Two estimates of mean day range based radio collar data of wild and reintroduced bears are 800 m (Paisley 2001) and 3-4 km (pers. comm. Castellanos in García-Rangel 2012).

Andean bears are mostly herbivorous with diets consisting primarily of bromeliads (*Bromeliaceae*), epiphytes, and *Moraceae* and *Lauraceae* fruiting species (Flores et al. 2005; García-Rangel 2012). But the species is also known to eat insects, rodents, birds, carrion and livestock (Servheen et al. 1999). Food selection, nest building, and claw markings on trees demonstrate that this is a highly arboreal species. They display some of the most extreme sexual dimorphism seen within all bear species- females weigh from 64-82 kilograms while males can weigh 100-150 kilograms. Individuals are known to be solitary, coming together only at times of great food abundance and to breed. Experiencing no long periods of food scarcity, these bears do not hibernate (Peyton 1999).

Andean bears are shy, elusive, and the least aggressive of the bear species (García-Rangel 2012). While few published accounts report aggressive behavior toward humans, negative interactions with humans are typically limited to crop raiding and livestock depredation (Peyton 1999; Can et al. 2014; Zukowski & Ormsby 2016).

Individual bears require large areas and a diversity of habitats, and the Andean bear is often used as a focal species for conservation and management of Andean habitats. The major threats to Andean bears are habitat loss, illegal killing, and climate change (Velez-Liendo & García-Rangel 2017). Andean bears may act as a conservation surrogate for other Andean mammals, whereby protecting the large areas required for viable populations will also protect other native species and habitats (see Chapter 2). Maintenance and conservation of ecosystems used by this species could also protect future sources of drinking water in range countries and ensure the provision of environmental services vital to human survival. Threats to Andean bears are increasing as the human population grows and as agriculture and livestock farming expand, fragmenting bear habitat and isolating populations.

Our research aimed to contribute to a wide-scale conservation strategy for Andean bears. Our objective was to empirically evaluate the potential for private lands to complement core protected areas. Can private lands increase available habitat and resources for individuals bears who live in protected areas? Or is proximity to humans a deterrent and are private lands along park borders unsuitable for bear populations? Our hypothesis was that private lands with almost no human-caused bear mortality, available natural food resources, and relative connectivity to protected areas could act as an extension to protected areas for bears.

Our study area comprised private lands titled to individual owners or community cooperatives. The extended southern border of Sangay National Park contains many of these private lands and passes directly through several others. As such, our study area is not a buffer zone because park management does not oversee landowners nor does it restrict their actions in any way (Shafer 2015). Protected areas are often public lands that prohibit hunting. In the case of our study area the land is privately owned inside and outside of the park, making this sector of

Sangay National Park similar to a park more in name, with no negotiated protected area rules. Landowners inside park boundaries are not under different imposed management strategies than those outside of the park. There is no difference in land management and little recognition of the park's existence on a day-to-day basis. For these reasons, we look at these private lands as a complement to the protected area, not as a buffer zone.

Materials and Methods

Study Area

Sangay National Park (SNP) is Ecuador's largest protected area on the *cordillera real*, or eastern Andes, and is one of only seven protected areas in Ecuador large enough to sustain a population of Andean bears (Peyton 1999). The study area is within the southern sector of SNP, on private lands in the Nudo del Azuay (NdA) mountain range of Cañar Province, Ecuador (2°33'S, 78°43'W). An estimated 85% of the NdA is located within the southern portion of SNP. This area is recognized globally for its biological diversity, forming part of the Tropical Andes biodiversity hotspot, the most diverse hotspot in the world for species richness and endemism (Myers et al. 2000; Critical Ecosystem Partnership Fund 2015). Previous studies in the Nudo del Azuay have recorded >18 species of mammals, including endemic species such as little red brocket deer (*Mazama rufina*), mountain coati (*Nasuella olivacea*), mountain tapir (*Tapirus pinchaque*), Andean white-eared opossum (*Didelphis pernigra*), and mountain paca (*Cuniculus taczanowskii*). Other notable species are the Andean bear (>20 individuals) and the puma (*Puma concolor*) (Fundación Cordillera Tropical 2012). Birds (>150 spp.), reptiles, and amphibians are also abundant in the area. In 2013 a new species of frog (Strabomantidae: *Pristimantis*) was discovered here (Guayasamin & Arteaga 2013).

In addition to its biological richness, the NdA forms part of the lower watershed of the Paute river. During the study period, the Paute river generated 35% of Ecuador's hydroelectric energy. Its six sub-watersheds (Dudas, Mazar, Llavircay, Juval, Púlpito, and Cardenillo) cover more than 96,000 hectares (Figure 1.1). The NdA has steep and rugged topography with slopes of 60° or steeper and elevations from 1200-4500 meters above sea level (Fundación Cordillera Tropical 2008; Anderson 2010). Approximately 79% percent of land cover consists of combinations of subpáramo (a mosaic of shrubs and grasslands), grass páramo, and montane evergreen forests (native and secondary). An additional 20% is in pastures and <1% in agricultural land (Sierra 1999). FCT estimated that ~5% of the area was covered in non-native pine plantations. Average annual temperatures range from 1ºC to 18ºC, and average precipitation ranges from 1,200 mm to 1,600 mm per year (Fundación Cordillera Tropical 2010). This area has two distinct seasons, cool and wet from May-August, and dry and warm from October-January/February (Fundación Cordillera Tropical 2008).

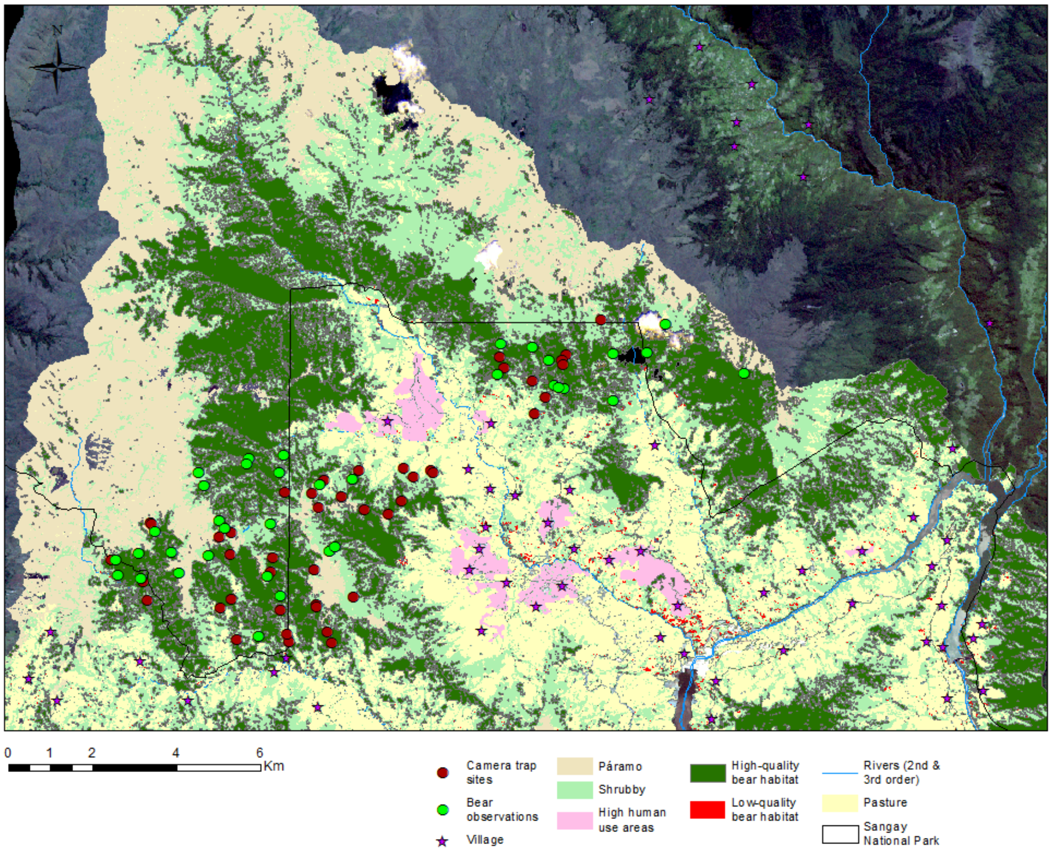

Figure 1. 1 Land cover and land use in the Nudo del Azuay region of Ecuador based on data extracted from 2010 multispectral sensor RapidEye image with spatial resolution of 5 meters.

FCT estimated 47% of the NdA that is within SNP park boundaries is privately held by individuals and indigenous communities, with land titles predating the southern expansion of the park (Gobierno del Ecuador 1992). Despite the designation as a protected area, development still occurs within the park, including government sanctioned roads, illegal colonization, and expansion of ranching. Lack of demarcation, signage, or park presence on the ground makes it difficult for even landowners to determine the boundaries of SNP.

During our study, agricultural practices in the NdA were primarily small-scale. Milk, for example, was produced and sold locally or consumed in the home. Agricultural activities included cattle production (milk and beef), alpaca farming (wool), crop production (e.g. potatoes, peas, corn), and some production of timber (charcoal) and non-timber (*dudas* cane) forest products (Fundación Cordillera Tropical 2008). In general, landholdings ranged from 1 to 3500 ha, including large haciendas (>150 ha), medium-sized properties (50-150 ha), and small properties (<50 ha).

Our study focused on the Mazar (16,577 ha) and Dudas (8,452 ha) sub-watersheds with only a few camera trap locations in Llavircay (2,513 ha). This area consisted of montane forest at lower elevations that transitioned to shrubby and grass páramo between 3000 and 3200 meters. Typically, lower elevations were a matrix of shrubs, forest remnants, and grass pastures.

Data Collection: Site Selection and landowner participation

To gain a representative sample of our entire study area, we used a map to divide it into 1 km^2 grid cells (100 total), and excluded grid cells containing >80% páramo (36% of grid cells). Past attempts to camera trap in the páramo failed because the grassland vegetation and shadows caused numerous false triggers, draining the camera traps of batteries while also filling the memory card within days of deploying the traps. Previous studies and evidence of bear sign do indicate that Andean bears use the páramo to feed on *Puya* spp. (Kattan et al. 2004; Troya et al. 2004) and as a travel route between forested areas (Zug 2009; Jones 2010; García-Rangel 2012). However, for technical reasons we focused on bear use of shrub and forested habitats.

Our site selection for camera trap locations was restricted by landowner participation. We began talking to landowners and asking for permission three months in advance of the start of the project (June 2012) but landowners were slow to agree. As a result, property entry into the project was staggered. We asked 21 landowners to participate in the project but only 16 agreed. Lack of participation from the landowners of three large properties resulted in access to only approximately 33% (33) of the remaining grid cells within the original 100 km^2 study area. However, we were able to add seven new grid cells to the east in Monay, slightly expanding the original target area. The resulting layout of the study area was access to 40 grid cells, a large southern portion (28 ha) and a smaller portion in the northeast (12 ha).

Camera Trapping

We conducted the study from September 12, 2012 - September 3, 2014, using one, Reconyx® PC800 (Holmen, WI, USA) rapid-fire, digital camera trap per site (40 camera traps). The PC800 used infra-red technology to trigger the camera when an animal passed in front and had a semi-covert infra-red flash with a range of up to 70 feet for black and white nighttime photos. Daytime photos were in color. When necessary we used an older model of camera trap, PC85 (Reconyx® PC85, Holmen, WI, USA) as replacement equipment (6 camera traps). This model had the same specifications and was programmed with the same settings as the PC800. We set the camera traps on high sensitivity to take 5 photos per trigger, rapid fire, with no time delay between triggers. Camera start-up speed was 1/5 second. We set the photo resolution to "high" (3.1 megapixels). Cameras were powered by 12 AA batteries. Camera traps also collected data on date and time of hit, temperature (C°), and moon phase. We attached the camera traps to a tree at shoulder height of an average adult Andean bear (~80 cm above ground level) and facing up or down a trail. To prevent the bears from interfering with the equipment, in December 2012 we installed metal security housing (custom-made and constructed in Cuenca, Ecuador) for each camera trap. We checked the camera traps every other month (~60 days) in groups based on site location and access points. We did not use a scent lure for this study because we did not want to attract bears to our camera trap sites but rather to observe their natural movement throughout the study area.

The effective detection area for camera traps varied due to the density of the surrounding forest but no site radius was larger than the distance of the nighttime covert flash (~21m), and most sites occupied a much smaller area (~5m^2). We selected sites within the 1 km^2 grid cells based on the presence of a wildlife trail and, when possible, bear sign. Traps sites were as close to the center of each grid cell as possible. This site selection method was developed to optimally sample dense forests in the study area. Camera traps were deployed for the duration of the project but were moved at least once to a new site after 1) we determined that no bears were present at a location based on lack of photos and lack of bear sign and/or 2) at the beginning of Study Year 2.

At the start of Year 2 of the project (September 2013) we noticed increasing failure and malfunction rates with our camera traps, especially those that had been in the field the longest and in the wettest locations. Consequently, we removed all the camera traps from the field in December 2013 for repair and maintenance. We cleaned each trap, reinforced silicon seals, removed oxidation, and dried them in the sun and with a fan for two weeks. In January 2014, we returned all camera traps to the field. In the analysis, we accounted for the differences in camera trap days for each site.

Data Analysis

We used RStudio (RStudio Team 2015) for analysis and model selection. We performed a negative binomial regression where our response variable was bear hits at camera trap sites. We began by building a covariate database using five covariate groups (predictor variables): (1)

landowner characteristics, (2) microsite features, (3) distance to landscape features, (4) land cover value, and (5) topographical features (Table 1.1). We used the program ArcMap® 10.2.2 (ESRI, Redlands, CA) to extract distances and land cover value in 1 km circular buffers around trap sites (group 3, group 4) from a 2010 multispectral sensor RapidEye image (the most current image available) with a spatial resolution of five meters (PROMAS, Universidad de Cuenca, Ing. Bastiaan Stoop) and slope, aspect, and elevation (group 5) from a 5 x 5 m digital elevation model (DEM) (U.S. Geological Survey (USGS) et al. 2014). To make the classifications relevant to our study of bears, we combined and reinterpreted several land cover classes (Appendix 1.1). Most notably, we defined the land cover class "land with forest, trees" as high-quality habitat for bears and "land with natural forest in the process of degradation" as low-quality habitat for bears. High-quality habitat was more mature, relatively connected forest while low-quality bear habitat was degraded forest, typically occurring far from high-quality bear habitat.

Table 1. 1 Covariate groups selected for testing in negative binomial models fit with INLA in analysis of 2012-14 Andean bear data from in the Nudo del Azuay, Ecuador.

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(1) Landowner Characteristics

- Participation in a formal conservation program
- Landowner location
- Land size

(2) Microsite Features

- Ground cover type

(3) Macrosite Features

- Inside Sangay National Park (yes/no)

Euclidean distance to:

- Páramo
- Low-quality bear habitat
- High-quality bear habitat
- Shrubby forest
- Rivers (2nd & 3rd order)

Land cover value:

- Páramo
- High-quality bear habitat

(4) Human Influence

Euclidean distance to:

- Pastures
- Small towns/settlements
- Primary roads
- Burned areas
- Rural areas with high levels of human use

Land cover value:

- Pastures

(5) Physical Features

- Altitude
- Slope
- Aspect

Covariate reduction and model selection process

We conducted Shapiro-Wilk tests for normality on all continuous data using the alpha value of 0.05. We removed all covariates with values of 0. We examined quartile plots for each variable and visually checked normality. Most variables appeared reasonably normal on the plot even if they did not meet the criteria for the Shapiro-Wilk test. If they failed both tests we removed them from the analysis. We tested for collinearity using a Spearman rank-order correlation matrix because we were using both continuous and categorical variables. We considered variables highly correlated if they had correlations >0.70. We then selected the variable more relevant to the analysis and removed the other. We converted *altitude* into a categorical variable, (250 m classes: low, medium, and high) to help avoid overfitting the model. We wanted to explore a seasonal effect (wet/dry) on bear hits so we reformatted the dataset to a panel format, using the new observational unit “site-season-study year”.

We then explored the data using a Poisson regression because we had count data that fit a Poisson distribution. We detected more variability in the data than expected (overdispersion) so we analyzed a test sample of the data using a quasi-Poisson regression and a negative binomial regression, both of which are suitable for overdispersed data. The negative binomial regression better fit the data.

Difficult terrain, dense vegetation, and access issues forced us to place some of the camera trap stations close together, potentially violating the assumption of independence. To account for spatial autocorrelation, we analyzed the data using a negative binomial regression fit with INLA (integrated nested Laplace approximation) (www.r-inla.org). INLA is a Bayesian approach designed as a faster alternative to simulation-based schemes for latent Gaussian models. It accounts for spatial dependency through a grid structure, which we built using GPS coordinates for each camera trap site. In both analyses we included an offset (natural log of active days) to control for the differences in the days each camera trap site was active due to equipment failure, staggered entry of camera trap stations, and the December 2013 camera trap repair and staggered replacement times. We tested for the overall effects of season, study year, slope, aspect, and altitude but did not have any significant results. We then controlled for them to reduce the variability in the data. We assigned groups of covariates to four different models (Table 1.2) and tested each model for significance.

We tested three models to determine the influence of human activity and landscape features on Andean bear presence in the study area: *human influence*, *human influence without landowner effects*, and *habitat*. The negative binomial model with INLA reports a 95% credible region rather than a confidence interval. For our purposes, the two are analogous. Each model included groupings of related covariates. We were unable to test a global model including all covariates because there were too many covariates relative to the number of observations.

Table 1. 2 Models tested in analysis of 2012-14 Andean bear data from in the Nudo del Azuay, Ecuador.

Model Name	**Covariate groups:**				
Global*	landowner characteristics	microsite features	macrosite features	human influence	physical features
Human Influence	landowner characteristics			human influence	
Human Influence w/o landowner effects				human influence	
Habitat		microsite features	macrosite features		physical features

*Unable to run a Global model because the number of covariates exceeded the number of observations

Results

We conducted the study for a total of 17,407 trap days (Year 1= 9,136; Year 2= 8,271) on 16 different privately-owned properties. The total number of sites used in the analysis was 80, within 40 grid cells (Figure 1.2). We photo-captured bears on 124 occasions at 36 (45%) camera trap sites within 26 (65%) grid cells on 11 (69%) properties. We considered bears photo-captured at the same site within 24-hours as a single observation (n=2), unless we could identify different individuals (n=4). Twenty-four percent of total observations came from one site (C13-1). Bears were active from approximately 06:00 to 18:30 with two outliers at 19:11 and 20:29, roughly coinciding with daylight hours in the study area (Figure 1.3). Although this study was not designed to recognize individual bears, we were able to use facial patterning to recognize at least three individual bears from previous studies (Zug 2009; Jones 2010; Fundación Cordillera Tropical 2012) indicating these bears are long-term residents. Notably, a bear first seen in 2008 was photo-captured again in 2014 with a small cub. Using these photos, we can estimate this female bear is at least 6 years old (Appendix 1.3).

Data Analysis

We used negative binomial regression fit with the INLA package to test three models to determine which features affect bear presence: human influence, human influence without landowner effects, and habitat (Table 1.3).

Human Influence model: The human influence model included the covariate categories *landowner characteristics* and *human influence*. This model had no significant results.

Human Influence without Landowner Characteristics model: The human influence without landowner characteristics model included only the covariate group *human influence*. The results indicated only "distance to rural areas with high human use" was important (mean= 1.004, 95% credible region= 1.000, 1.0008). For this covariate, the mean estimate is a 4% increase in bear hits for every 100 m increase in distance from rural areas of high human use.

Habitat model: The habitat model included the covariate groups *microsite features, macrosite features,* and *physical features*. The results indicated three important covariates: study year (mean= 3.14, 95% credible region = 1.18, 8.80), distance to low-quality bear habitat (mean= 1.00, 95% credible region = 0.99, 1.0024), and distance to river (2nd & 3rd order) (mean= 0.99, 95% credible region = 0.99, 1.000). The mean estimate is a 213% increase in bear hits from study year 1 to study year 2, an 11.6% increase in bear hits for every 100 m increase in distance to low-quality bear habitat, and a 2.5% decrease in bear hits for every 100 m increase in distance to river (2nd & 3rd order).

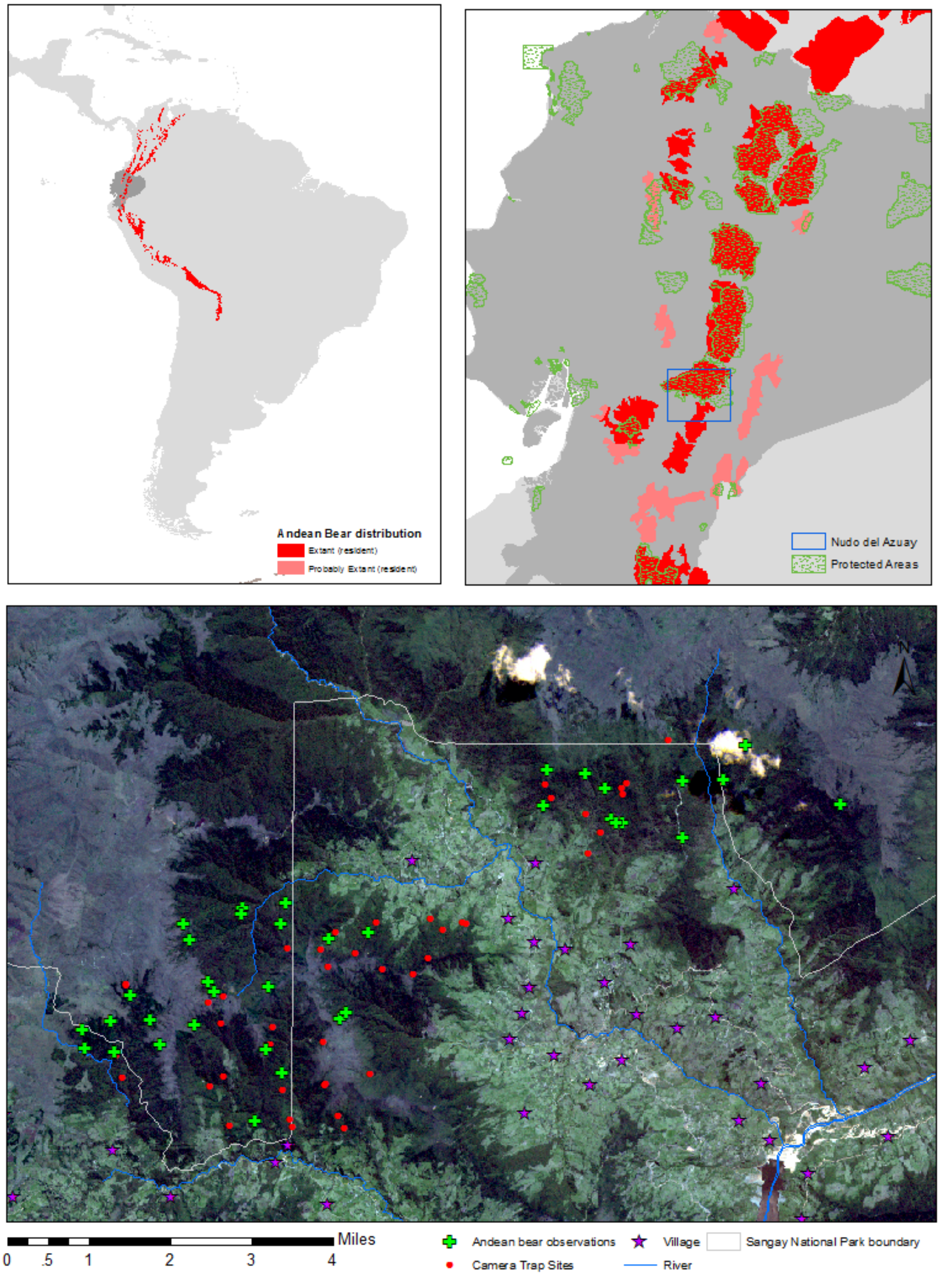

Figure 1. 2 Global distribution of *Tremarctos ornatus*, distribution in Ecuador with overlay of Ecuador's protected areas, and map of 2012-14 study area with camera trap locations and bear observations in the Nudo del Azuay, Ecuador.

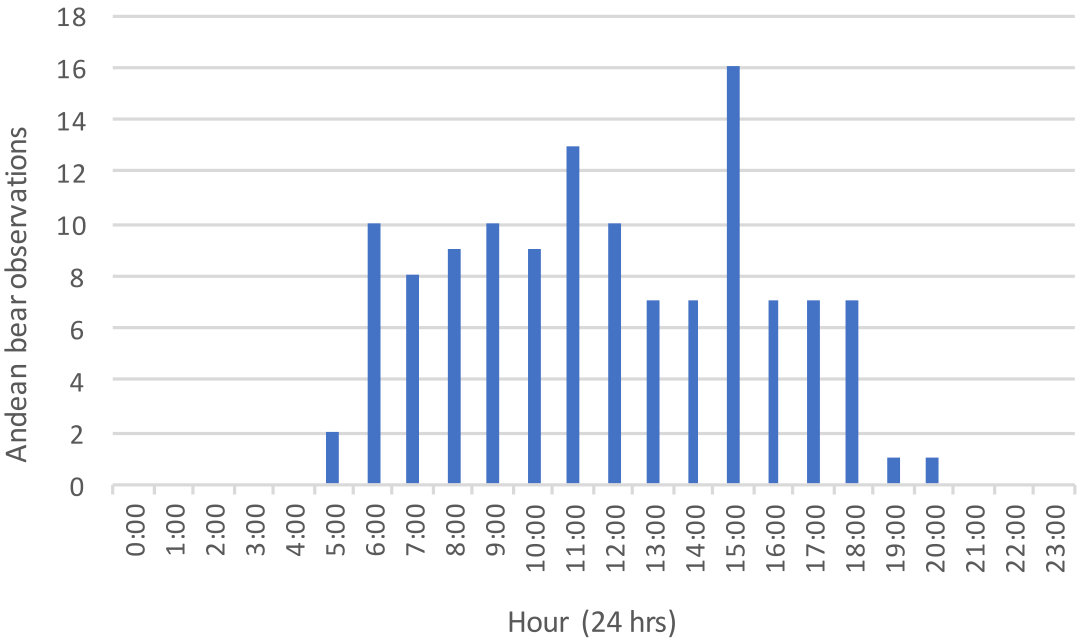

Figure 1. 3 Frequency distribution of Andean bear observations by camera traps in the Nudo del Azuay, Ecuador from 2012-14 (n=124).

Table 1. 3 Significant results from negative binomial model with INLA analysis of 2012-14 Andean bear data from in the Nudo del Azuay, Ecuador.

Model	Significant Covariate(s)	Mean*	Lower 95% CR*	Upper 95% CR*	% change in bear observations**	Average bear observations per site^
Human Influence w/o landowner characteristics	distance from rural areas with high levels of human use	1.00038	1.00002	1.00076	4%	1.81
Habitat	study year	3.14	1.180	8.8	213%	-
	distance to low-quality bear habitat	1.00	1.000	1.002	11.6%	1.94
	distance to river (2nd & 3rd order)	0.999	0.998	1	-2.5%	1.70

* Exponentiated results
** Percent change is based on per 100 m increase in distance
CR = Credible region
^ Based on the study average of bear hits per site (1.74)

Discussion

Our results indicate that the private lands in our study area could complement the bear population in Sangay National Park if human activity and deforestation of mature forests is controlled and bears have access to annual resources. Landowner characteristics had no effect on bear observations. Annual variation in the study area and habitat seem to be more important indicators of bear presence.

The habitat model showed a marked difference in bear presence between year 1 and year 2 of the study, with an increase in bear observations in year 2. We did not alter our methods between study years and saw an increase in humidity-related camera trap failures in year 2 (but accounted for this in the analysis). FCT was present in the field during our study and did not observe other sources of development or disturbance. Our results indicate that bears may be moving through the study area, potentially using different resources in different years. Similar to other species of bears, Andean bears following food availability (Cuesta et al. 2003). Camera trap data from previous studies in the area showed that Andean bears used these private lands with frequency but not evenly (Zug 2009; Jones 2010; Fundación Cordillera Tropical 2012). Bears migrated up and down topographical gradients using a wide variety of habitats throughout the year, relying in equal parts on the high-elevation páramo (3,200 to 3,700 m) as well as montane cloud forests (2,400 to 3,199 m; (Fundación Cordillera Tropical 2012). Andean bears feed on giant terrestrial bromeliads (Genera: *Puya*) which occur in patches in the grass páramo, the dominant páramo type in our area (Troya et al. 2004). In this region, we have observed that bears feed on these plants more when they flower, which occurs asynchronously across years (Pers. comm. Teresa Clare). We did not survey these plants during our study period but could be observing bears using the study area to access this páramo plant species, supporting the importance of conserving both forested and páramo habitats for bears (Peralvo et al. 2005).

This result also highlights the importance of multi-year studies in large mammal research. A one-year study would have missed this annual effect on the movement pattern of bears. When used for conservation planning, short-term data may provide an incomplete view of target species and habitats. Future studies could monitor annual food availability in the páramo and forested habitat in this area.

In our habitat model, we also saw a slight signal that bear observations increased farther from low-quality habitat. Low-quality bear habitat is degraded forest, typically occurring far from high-quality habitat. Historically, there is little commercial logging in the region and most of the land cover class defined as low-quality is secondary forest (Pers. comm. Stuart White). Given the slower growth rates at high elevation in the Andes, the secondary forest may be as young as 15 years old or as old as 40 years old. Further botanical studies would augment our understanding of this dynamic.

A 2009 Andean bear habitat analysis in this area found that bears favored habitat where trees had greater DBH (diameter at breast height), indicating a preference for more mature forests (Achig 2009). The author suggested this could be linked to the increase in epiphytic bromeliads, a major food source for Andean bears found in older forests (Troya et al. 2004). Low-quality forest primarily occurred on forest edge, close to pastures, and areas of human presence. Indeed, our human influence model without the effects of landowners showed an increase in bear observations as distance increased from rural areas with high levels of human activity, supporting the theory that Andean bears are selecting more mature forests which, in this area, occur farther from human activity. This result is likely based on the effect of habitat conversion closer to areas of high human use, rather than physical presence of people. The conservation implications are that these properties are not likely to be successful at conserving bears unless clearing mature forest is controlled.

Less significant but worth noting is a slight decrease in bear observations farther from 2nd and 3rd order rivers. These are rivers that have one or more tributaries, and are considered headwater streams. Flow in the Mazar River (closest to our study area) can vary from as little as 1.25 m3/s to over 80 m3/s, like other mountain streams around the world (FCT, unpublished data). Although bears can swim across rivers, larger rivers can limit movement and dispersal of other bear species, notably American black bears (*Ursus americanus*) (White et al. 2000). The rivers in our study area are smaller and unlikely to block Andean bear movement. At other locations, Andean bears have been observed using river banks to travel through steep, forested areas (Pers. comm. Teresa Clare) but to our knowledge this behavior has never been studied.

Our study did not focus on individual identification of bears but we were able to recognize at least three bears from previous studies, where we have identified as many as 20 individual bears (Fundación Cordillera Tropical 2012). We have photo-captured several bears over multiple field seasons, suggesting they are residents. Nonetheless, many bears were not photo-captured again, indicating this area might also be a dispersal area or a seasonal food source.

We were unable to survey the middle portion of the study area because the landowners did not want to participate or requested financial compensation. Land cover data and satellite imagery indicated that this is a large expanse of forest that connects the western and eastern forests of the southern Nudo del Azuay to uninterrupted páramo to the north. A portion of the unsurveyed area (5000 ha) was owned by a community cooperative (Colepato) whose land we surveyed for bears in 2008 and 2009 (Zug 2009; Jones 2010). During both studies, we saw many bears and many of the same individuals we observed again in camera traps on wildlife reserve to the west. A bear survey has never been conducted on the other adjoining property but bears are likely to be present in this forest because it is an extension of similar habitat and provides access to páramo (Ríos-Uzeda et al. 2006; García-Rangel 2012). Future studies would benefit from surveying these two properties.

Our human influence model had no significant results. We selected three proxies to indicate the potential conservation value of each property based on property size, landowner location, and involvement in conservation (Appendix 1.2). Half of the properties in our study were from 50-150 hectares with a few smaller and a few larger properties. Nine (56%) of our landowners lived on their properties, meaning they were responsible for day-to -day decisions about land management. Only five (31%) of our landowners were actively involved in conservation on their property ("conservation allies"), including one privately designated wildlife reserve (Mazar Wildlife Reserve), two properties involved in the government sponsored Socio Bosque program, and two conservation-minded landowners who informally agreed to conserve wildlife and habitat on their land. Landowners in our study area engaged in small-scale cattle production (locally sold milk) and had some crops (e.g. corn, potatoes). Typically, properties in our study had some forested area (where we placed camera traps) and were narrow (e.g. 200-300 meters wide) and extended in long swathes (e.g. 4 km) from lower altitudes (e.g. 1800 m) to higher (e.g. 3600 m). Some larger properties included both forest and páramo habitat. Pastures were typically at lower altitudes with easy access to roads and close to homes but some landowners did have higher, more remote pastures.

None of these property characteristics predicted bear observations. We did observe that smaller properties (0-50 ha.) had zero bear observations except for one trap site that had 30. This trap site (C13-1) was on the edge of small property, had an extremely high-level of wildlife activity, and was within connected forest very close to the property boundary of the Mazar Wildlife Reserve, one of our largest properties (1800 ha). The Mazar Wildlife Reserve is managed for conservation (1500 ha) and for production of alpacas (300 ha). The reserve does not receive formal incentives to promote conservation (tax reduction, for example) but is nevertheless managed as a conservation parcel with the intention of no extraction of plants or animals, and the strict protection of habitat. On this property, we saw an abundance of bears and other wildlife species.

Consistent with the results from small properties was the lack of bear observations on both properties involved in the Socio Bosque program, which were also in the < 50-hectare land size category. Socio Bosque is a government designed conservation program, founded in 2008, with the aim to protect 3,600,000 hectares of native land cover on private lands in Ecuador (Ministry of Environment 2009). The Socio Bosque program selected property owners located in areas with the highest priority for conservation, using a nested set of criteria to define these geographic priorities (including level of threat, environmental service production, and poverty level). Given the uneven information available in Ecuador, the program employed a variety of proxies to complete the ranking. For example, the ranking for environmental service production is composed of three sub criteria: biodiversity, contribution to hydrological regulation, and carbon storage. Refuge for biodiversity is defined as habitat that is underrepresented in the national protected areas system (Ministry of Environment 2009). The Participation Manual defines the terms of agreement for the 20-year contract signed between the government and private landowners. For the duration of our study, the landowners received biannual payments based on the number of hectares protected (de Koning et al. 2011).

In the Nudo del Azuay, there were 12 landowners with 432 hectares participating in the Socio Bosque program, enrolled since October 2010. We placed camera traps on two participating properties, covering 110 hectares of forest and páramo in the Dudas and Mazar watersheds. In 2010, FCT assisted 33 landowners managing 53 properties with the application of 5,000 hectares to the Socio Bosque program. The Socio Bosque Program accepted only 12 of the 53 applications for participation but found that land tenure status, not conservation priority, determined who could participate (Schloegel 2012).

Although we only had two Socio Bosque properties in our study it is notable that both were small properties, not close together, and lacked bears or other large mammals during our study. The other three properties we defined as conservation allies in our study also applied to the Socio Bosque program but were not accepted; none had a legal map in their land title which is not uncommon. All three properties were large, had forest and páramo habitat, and where our camera traps recorded both bears and pumas. Because many land titles in Ecuador do not comply with the norms for participation, participation in the Socio Bosque program is unequal and in many instances based on superficial technical differences, rather than conservation value. These findings urge future research examining wildlife presence and species richness on properties participating in the Socio Bosque program if the program aims to use biodiversity as a measure for environmental services.

We did not measure human-bear conflict during this study but we believe it is an important factor for bear conservation in this region. Other regions of Ecuador experience high levels of conflict, most notably the northern Cordillera, threatening the livelihoods of local people and the survival of bears in these areas (Zukowski & Ormsby 2016). Conflict between bears and humans in our study area is low, primarily related to livestock, and has been reported on average only 1-2 times per year since we began recording conflicts in 2007 (Pers. comm. Fundación Cordillera Tropical). We did not have any reports of bear killing in this area prior to or during our study. Further evidence of low human-caused bear mortality comes from camera trap data. Bears in our study area were active during daylight hours, coinciding with human activity.

It is difficult to determine exactly why conflict in our area seems to be low but it is worth noting that since 1999, our study area has experienced extremely high levels of emigration of working-aged men to urban areas in Ecuador, the United States, and Spain (Wunder 2000). Residents are predominantly women who remain to care for the family, property, and livestock. These responsibilities prevent them from walking long distances to graze cattle in the páramo or in distant pastures close to the forests where it is easy for bears to kill livestock. As such, cattle are kept closer to homes (pers. comm. FCT). Most rural livestock owners have few options other than to graze cattle in distant pastures despite the knowledge that it increases the risk of bear attacks (Goldstein et al. 2006; Zukowski & Ormsby 2016). In the Nudo del Azuay, this improvement in livestock husbandry is happening naturally and may partially contribute to low levels of human-bear conflict in this region. This is a critical factor in the contribution of private lands in bear conservation. Conservation of large mammals on land outside of protected areas is unlikely to be successful with unrestricted hunting because areas of high mortality can act can act as population sinks for bears (Knight et al. 1988; Naughton-Treves et al. 2003).

Our results indicate that Andean bears are only slightly disturbed by human activities and that habitat and access to annual changes in resources might be more important when planning for bear conservation on private lands. Private lands in our study area do not formally extend protection for wildlife in Sangay National Park because there is no enforcement of park rules; land use is the same both inside and outside of park boundaries. However, they do appear to provide a relatively safe human-wildlife interface for bears when human-wildlife conflict is low and habitat is not degraded. Landowners should be supported in their conservation efforts, especially when conservation planning includes adjacent protected areas. Larger properties where pastures are far from bear habitat and that have both connect forest and access to páramo, should be prioritized in conservation planning for Andean bears in Ecuador.

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Chapter 2: Assessing the utility of Andean bears as conservation surrogates for Andean mammals on private lands in Ecuador

Abstract

Andean bears (*Tremarctos ornatus*) frequently are cited as conservation surrogates for less charismatic but equally important Andean wildlife. They are attractive for a conservation surrogate because they are wide-ranging, use a variety of habitats, and are listed as vulnerable by the International Union for Conservation of Nature (IUCN), and are designated endangered in Ecuador. We used empirical data to evaluate the usefulness of using Andean bears as conservation surrogates on private lands. We predicted that detections of Andean bears would associate with increased species richness. From 2012-14 we placed camera traps on privately-owned lands in Ecuador's Sangay National Park. Our study region included páramo and forested habitat alongside an expanding agricultural and ranching frontier and rapid infrastructure development. Our camera traps detected bears at 46% of camera trap sites and other Andean mammals at 91% of trap sites. We performed a negative binomial regression using five categories of species richness (response variables) relevant to our site. Predictor variables included combinations of Andean bear observations, season (wet, dry), and habitat (forest, shrubland). Our results across all species richness categories indicated that Andean bears alone had a negative effect on species richness. However, the interaction between Andean bears and forested habitat had a strong, positive effect on species richness. Our results suggest that projects on private lands that use Andean bears as surrogates for biodiversity conservation must also consider forested habitat to provide a strong proxy for the

conservation of Andean mammals. Conservation projects must be multifaceted, addressing issues of deforestation as well as wildlife conservation.

Introduction

Charismatic, well-studied species often are used as surrogates, or proxies, for conservation of equally important but less charismatic or lesser known species (Lambeck 1997; Wiens et al. 2008). The study of individual species or taxonomic groups within a target area can be, among other limitations, logistically impossible, time consuming when conservation needs are urgent, or expensive (Wiens et al. 2008; Caro & Girling 2010). Conservation surrogate approaches may overcome these barriers because co-occurring species arguably benefit from conservation efforts focused on a surrogate. The needs of a surrogate species may encapsulate the needs of other species or represent important aspects of their shared environment (e.g. access to a variety of habitats, landscape-scale connectivity). Typically, a lot is already known about their ecology, they are relatively easy to detect, and are wide-ranging species who encompass the habitats of other species of interest (Lambeck 1997; Wiens et al. 2008; Caro & Girling 2010; Lindenmayer & Likens 2011). Conservation surrogates would ideally also have affordable, proven tools for detection (i.e. camera traps) and the potential for high capture rates. Alternate terms for surrogate approaches include those used to gain public support for conservation (flagship species), those used to indicate areas of conservation significance (umbrella or keystone species), and those used to detect and evaluate changes in environmental systems (indicator species) (Wiens et al. 2008; Caro & Girling 2010).

Criticisms of the conservation surrogate method focus primarily on lack of empirical support for this approach, the implicit rather than explicit value of a surrogate species, and varied and conflicting results from tests of effectiveness (Andelman & Fagan 2000; Roberge & Angelstam 2004; Favreau et al. 2006; Grantham et al. 2010; Branton &

Richardson 2011). Moreover, a single-species approach is relatively coarse and forfeits fine-scale ecosystem management, while abundance of the selected surrogate may or may not indicate abundance of other species (Wiens et al. 2008; Cushman et al. 2010). Despite criticism, conservation surrogates might be the best option for conservation in the short-term, particularly when data on one species are far more extensive than on co-occurring species (Rozylowicz et al. 2011; Ratnayeke & van Manen 2012). Nevertheless, many authors suggest a more complex approach to conservation surrogacy could provide a more accurate understanding of surrogates for conservation efforts, such as one that includes a suite of species or considers habitat factors along with species abundance (Lambeck 1997; Carroll et al. 2001; Roberge & Angelstam 2004). For example, a recent study in Montana, U.S.A., used both wolves (*Canis lupus*) and cougars (P*uma concolor*) as a "focal suite" for conservation of biodiversity, resulting in a more diverse landscape and higher quality habitat in their analysis (Kunkel et al. 2013).

A study in Sri Lanka found that the presence of sloth bears (*Melursus ursinus*) was positively associated with species richness of other carnivores in two national parks (Ratnayeke & van Manen 2012). The authors selected sloth bears because they were well-studied in comparison to other carnivore species, were widely distributed in areas of conservation interest where human densities and impact were low, and were known to co-occur with other species of interest. Based on these results, the authors suggested that sloth bears may be good indicators of the presence of other carnivores and that areas designated to protect sloth bears likely also protected less well-known and at-risk carnivore species.

Bear species in general may be effective conservation surrogates because most species are well-studied and relatively easy to detect, and require large areas and a variety of habitats. In particular, Andean bears (*Tremarctos ornatus*) frequently are cited as an umbrella, keystone, or flagship species for large-scale conservation projects. Andean bears co-occur with species of interest such as the mountain tapir (*Tapirus pinchaque*), the little spotted cat (*Leopardus tigrinus*), and the puma (*Puma concolor*) (Rodríguez et al. 2003). Andean bears can be easy to sample using feeding remains, scat surveys, or camera traps and are not highly sensitive to disturbance (Branton & Richardson 2011). They are also far-ranging, adapted to a wide range of environmental conditions (e.g. altitudinal), and use a variety of important Andean habitats including the cloud forest and páramo (high altitude grasslands and shrublands), the primary source of fresh water for many Andean cities (Peyton 1980; Cuesta et al. 2003; Buytaert et al. 2006).

Andean bears (*Tremarctos ornatus*) are the only extant species of bear in South America and are threatened throughout their range (Venezuela, Colombia, Ecuador, Peru, Bolivia) (Velez-Liendo & García-Rangel 2017). They are omnivores but mainly herbivorous, feeding on leaves and fruit, and opportunistically consuming animal protein. Because their digestive tract does not destroy seeds, they are thought to be seed dispersers, directly contributing to ecosystem health (García-Rangel 2012). Moreover, Andean bears also are important cultural symbols throughout the Andes, appearing in ancient artifacts and in extant myths and rituals (Paisley 2001). Despite their cultural significance they are endangered in Ecuador due to human-caused threats: habitat loss and fragmentation, illegal killing, and climate change (Tirira 2011; Velez-Liendo & García-Rangel 2017). Andean bears receive significant conservation attention from local and international governments, funding and conservation organizations, and the public (although public opinion can vary depending on the level of human-bear conflict).

Almost all threatened species occur on private lands yet private lands frequently are overlooked for conservation in protected areas (Knight 1999). Only 15% of the world's land is inside of protected areas, which likely will become less effective as environmental gradients shift due to climate change, and wildlife respond by shifting ranges and leaving protected areas (Gray et al. 2016; Iturralde-Pólit et al. 2017). Private lands may be critical for providing buffer zones and connecting otherwise isolated wildlife populations (Langholz et al. 2000). Furthermore, biodiversity in the tropics is being lost at an alarming rate (Schipper et al. 2008; Hoffmann et al. 2010; Ceballos et al. 2017). Habitat loss and fragmentation are principle causes of biodiversity loss; fragmented forests have low rates of biodiversity, fewer mammal species, and reduce the ability of wildlife to respond to environmental changes (Ahumada et al. 2011; Crooks et al. 2011). Private lands could also provide safe corridors for wildlife movement in fragmented landscapes. Despite their potential benefits, inclusion of private lands in the tropics for conservation strategies and research has been limited (Environmental Law Institute 2003).

Ecuador is considered a megadiverse country (Mittermeier et al. 1998) but much biodiversity occurs outside of protected areas on privately-owned lands (Falconi & Suárez 2010). Although the government of Ecuador has included private landowners in conservation incentives (e.g. conservation agreements, establishment of private reserves, tax breaks, etc.), the participation of rural landowners is constrained by a combination of factors, including land titling issues (e.g. lack of defined property boundaries) as well as lengthy and complicated enrollment processes (Falconi & Suárez 2010; Schloegel 2012).

Our objective was to test the idea that presence of Andean bears (number of observations) is an indicator of species richness of mammals on private lands and, as such, may act as a good conservation surrogate (Peyton 1999; Rodríguez et al. 2003; Clark 2004). Given their spatial and generalist ecology, we predicted that bears would be good indicators of mammalian species richness.

Methods

Study Area

The Nudo del Azuay region of Ecuador (2°32'S, 78°42'W) was adjacent to and overlapped by the southern boundary of Sangay National Park (see Chapter 1). In 1992, the park boundary was extended south encompassing privately owned lands. Park management was not enforced in the extension zone and there were no visible differences between park and privately-owned lands. Until recently, few landowners knew if or where the park boundary crossed their properties. The Nudo del Azuay region was a matrix of public and privately-owned lands, montane cloud forest and high montane evergreen forest (primary and secondary), grass páramo, scrublands, and pastures. Páramo is a grassland ecosystem with dominant plant species Poaceae (grass), Ericaceae (blueberry), and Asteraceae (daisy and sunflower family) (Luteyn 1992). In our study area, the predominant forest species are Myrsine dependens (Myrsinaceae), Weinmannia fagaroides (Cunnoniaceae), Hedyosmum cumbalense (Cloranthaceae) y Miconia crocea (Melastomataceae) (Salgado et al. 2007). An expanding agricultural and ranching frontier and rapid infrastructure development put the needs wildlife in direct competition with humans. Conservation efforts were conducted by individual landowners and a local NGO. The wildlife reported on these private lands, both through empirical and anecdotal evidence (Zug 2009; Jones 2010), are some of Ecuador's most threatened species, including the mountain tapir (Tapirus pinchaque), northern pudu (Pudu mephistophiles), and Andean bear (Tremarctos ornatus). Camera trap studies in our study area indicated that Andean bears on these private properties co-occur with other Andean mammals, at relatively low levels of conflict with landowners (Achig & Santillán 2009; Zug 2009; Jones 2010; Fundación Cordillera Tropical 2012).

Data Collection

We divided the study area into 1-km^2 grid cells across 100 km^2 of private lands in five different sub-watersheds within the Nudo del Azuay. We then went door-to-door, asking each landowner permission to use their property in the study. Only 16 landowners gave us access to their properties resulting in groupings of camera sites in western and northeastern portions of the study area. Both forest and shrubland vegetation in the study area was dense and terrain was steep so we selected sites as close as possible to the center of each grid cell on a human or wildlife trail.

We conducted a camera trap study from September 2012 to September 2014, at 80 different sites within 40 grid cells of bear habitat (see Chapter 1, Figure 1.2). Our camera-trap sites consisted of one Reconyx® PC800 (Holmen, WI, USA) rapid-fire digital camera per site. Camera start-up speed was 1/5 second and each was programmed to take 5 photos/trigger with no time delay between triggers. At night, the cameras used a semi-covert infra-red flash. When necessary we used an older model of camera trap, PC85 (Holmen, WI, USA) as replacement equipment. We placed each camera trap in a metal security box and bolted it to a tree to prevent equipment damage from bears. Because the study focused on bears, we mounted each camera at ~80 cm (~31 in) above ground level, facing up or down a wildlife trail.

We checked the camera traps every other month (~60 days) in groups based on site location and access points. We deployed camera traps for the duration of the project but collected all camera traps in December 2013 for maintenance, followed by redeployment in January 2014. We placed camera traps in two types of habitat: forest and shrubland. To map forest and shrubland habitats, we used program ArcMap® 10.2.2 (ESRI, Redlands, CA) to extract land cover class information from a 2010 multispectral sensor RapidEye image (the most current image available) with a spatial resolution of five meters (PROMAS, Universidad de Cuenca, Ing. Bastiaan Stoop). The area classified as forest in the satellite image includes two different forest types: montane cloud forest found between 1800 meters and 2800-2900 meters, and high montane evergreen forest found between 3400-3500 meters (Ståhl et al. 1997 in Salgado et al. 2007) (Sierra 1999) . We then ground-truthed this information in the field; forest habitat was determined by a relatively closed canopy where most vegetation was trees >2 meters tall. Shrubland was defined by brush-like vegetation, heavy groundcover with a relatively open canopy, almost no large trees, and distributed along the edge of forest habitat. We collected camera trap data during two rainy and two dry seasons, consecutively. Wet and dry season dates are based on rainfall data collected in the Nudo del Azuay in previous years (Fundación Cordillera Tropical 2010).

We reviewed camera trap photos to identify each species and recorded the date and time of each observation at each camera-trap site. We were unable to identify extremely small species, such as mice (*Rodentia*), so species weighing less than 2 oz. are excluded from the study. On occasion, it was difficult to distinguish little spotted cat (*Leopardus tigrinus*) from margay (*Leopardus wiedii*) because cats are similar in size and patterning (Breton & Sanderson 2011). We recorded melanistic examples of both species (6 total), which is not uncommon (local kichwa name: buru mishi) but also made species-level identification difficult. We consulted several small cat experts and are confident with the identifications we made. When we were uncertain we classified observations as *Leopardus spp.* (n=5).

To be able to compare our site to data from other studies, we calculated the capture rate (CR) per 100 trap days for each species (CR= observations / total trap days * 100). We calculated overall capture rate, capture rate in different habitat types (forested, shrubby), and seasonal capture rate (wet, dry).

Data Analysis

We used Andean bear presence (number of bear observations) as predictors of species richness (total number of species observed at each camera trap site) of mammal categories, defined by global and local conservation status. We followed Ratnayeke and van Manen (2012) who assessed sloth bears as conservation surrogates in protected areas in Sri Lanka. Our observational units were camera trap sites during each season (wet/dry). We used five categories of wildlife as response variables: (1) all species detected by our camera traps, (2) carnivore species, (3) globally at-risk species, (4) locally at-risk species, and (5) locally at-risk carnivores. At-risk species were those designated by the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (2017) and the Red Book of Mammals for Ecuador (*Libro Rojo de los mamíferos del Ecuador*) (Tirira 2011) as critically endangered, endangered, vulnerable, or near threatened. We did not have a globally at-risk carnivore species group because this group would only have two species, *L. tigrinus* and *L. wiedii*. We conducted a separate analysis for each category, controlling for both season (wet/dry) and habitat (forest/shrubland), and their interactions (8 models for each category). We included an off-set of active camera trap days to account for differences in active days between camera trap sites.

We used the statistical program RStudio (RStudio Team 2015). As is common with ecological data, our data set had a lot of zeros. We explored analysis methods that best handled this type of data, mainly quasi-Poison regression, zero-inflated negative binomial regression, and a negative binomial regression. After examining our residual plots, we eliminated the quasi-Poison regression. We decided not to use the zero-inflated negative binomial regression because the regular negative binomial model performed better using cross-validation and was less complex. In addition, because of the high dispersion parameter (4-7) for all tested models, the negative binomial regression was a better fit for the data set, reducing the pattern in the residuals (Richards 2008) (Appendix 2.1). We were satisfied that the requirements for a negative binomial regression were met and thus did not test for spatial autocorrelation. We used Akaike's information criterion for small sample size (AICc) to select the best model for each response variable. We then repeated these same steps to explore the effects of trail definition and species with highest capture rate on our results.

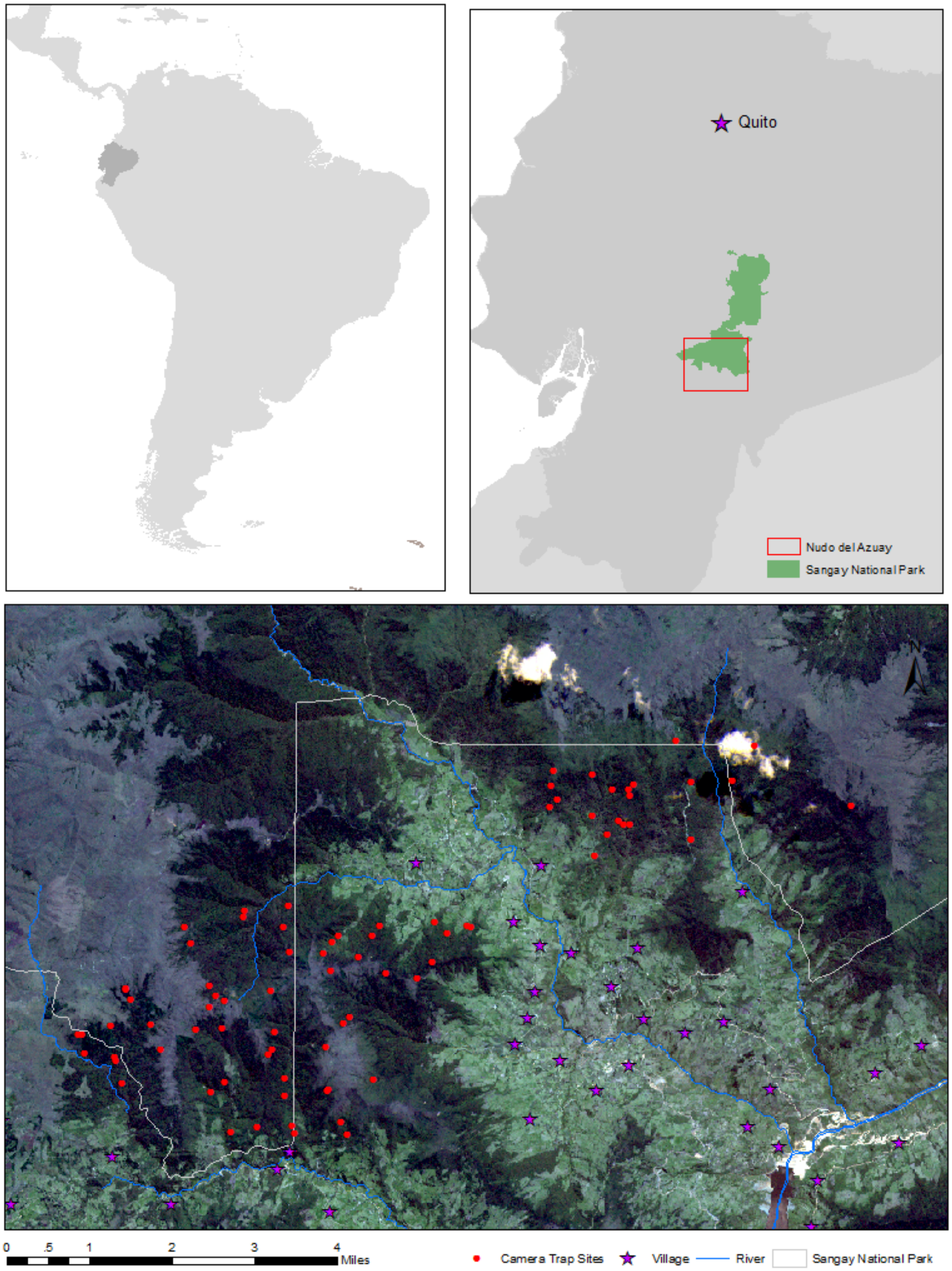

Figure 2. 1 Location of 2012-14 study area and camera trap sites in the Nudo del Azuay region, Ecuador.

Results

Our dataset represented 17,407 camera trap days (Year 1= 9,136; Year 2= 8,271). Our camera trap sites included forest (n=54) and shrubland (n=26) habitats during both wet (n=89) and dry (n=81) seasons. Many sites spanned both wet and dry seasons so the total number of sites x season (n=170) was higher than the total number of sites overall (n=80) (Figure 2.1). Occasionally, camera traps temporarily failed due to humidity and one failed permanently because of damage from a bear. We detected 15 species of mammals with our camera traps, including bears. Nine of these species are designated in an at-risk category by either the IUCN or Red Book (Table 2.1). Of the total number of species, nine are carnivores, six of which are designated at-risk. We detected bears or other mammals at 91% (73) of our camera trap sites but detected a bear and at least one other mammal at only 36% (29) of sites. We recorded a total of 124 bear observations at 46% (32) camera trap sites (mean=0.7, range 0-20) (Figure 2.2).

Species with the highest per 100 trap days capture rates were the little red brocket deer (*Mazama rufina*) (CR=0.95), mountain paca (*Cuniculus taczano*wskii) (CR=0.83), and Andean bear (CR=0.71) (Table 2.2, Figure 2.3). On a site by site basis, the wildlife categories varied in total species richness (SR), mean species richness, and range: all species (SR=14, range=0-6, $\bar{x}$=2.3), carnivore species (SR=8, range=0-5, $\bar{x}$=1.3), globally at-risk species (SR=5, range=0-3, $\bar{x}$=1.25), locally at-risk species (SR=9, range=0-6, $\bar{x}$=2), and locally at-risk carnivore species (SR=5, range=0-4, $\bar{x}$=1) (Figure 2.4, Figure 2.5). We found total species richness by habitat and season to be similar: shrubland (SR=11), forest (SR=14), dry (SR=13), wet (SR=14) but we did not observe any margay in shrubland habitat and bears only at 27% of shrubland trap sites with low a capture rate

(CR) when compared to forests (shrubland CR = 0.08; forest CR = 0.63). Based on landowner reports, we expected to see porcupine (*Coendou quichua*) and northern pudu (*Pudu mephistophiles*) in camera trap photos but we did not. Camera traps photo-captured birds, mammals weighing less than 2 oz. (rodents, unidentifiable mammals, etc.), humans, domestic dogs, and feral horses. These findings were not included in the analysis.

Table 2. 1 IUCN Red List status, Ecuadorian Red Book status, and wildlife categories used in analysis of mammal species detected by camera traps from 2012-14 in the Nudo del Azuay, Ecuador.

	Scientific Name	IUCN status (Ecuador)	All species	Carnivore species	Globally at-risk species	Locally at-risk species	Locally at-risk carnivore species
CARNIVORA (9)							
Ursidae							
Andean bear	*Tremarctos ornatus*	VU (EN)					
Canidae							
Andean fox	*Lycalopex culpaeus*	LC (VU)	●	●		●	●
Mephitidae							
Striped hog-nosed skunk	*Conepatus semistriatus*	LC (LC*)	●	●			
Mustelidae							
Long-tailed weasel	*Mustela frenata*	LC (LC*)	●	●			
Tayra	*Eira barbara*	LC (LC*)	●	●			
Felidae							
Margay	*Leopardus wiedii*	NT (VU)	●	●	●	●	●
Little spotted cat	*Leopardus tigrinus*	VU (VU)	●	●	●	●	●
Puma	*Puma concolor*	LC (VU)	●	●	●	●	●
Procyonidae							
Mountain coati ^	*Nasuella olivacea*	DD (VU)	●	●		●	●
ARTIODACTYLA (2)							
Cervidae							
Little red brocket deer	*Mazama rufina*	VU (VU)	●		●	●	
White-tailed deer	*Odocoileus virginianus*	LC (NT)	●			●	
PERISSODACTYLA (1)							
Tapiridae							
Mountain tapir ^	*Tapirus pinchaque*	EN (CR)	●		●	●	
DIDELPHIMORPHIA (1)							
Didelphidae							
Andean white-eared opossum	*Didelphis pernigra*	LC (LC*)	●				
LAGOMORPHA (1)							
Leporidae							
Brazilian cottontail	*Sylvilagus brasiliensis*	LC (LC*)	●				
RODENTIA (1)							
Cuniculidae							
Mountain paca ^	*Cuniculus taczanowskii*	NT (NT)	●		●	●	

IUCN = International Union for the Conservation of Nature, Red List of Threatened Species (www.iucnredlist.org)
Ecuador = Libro Rojo de los mamíferos del Ecuador (Tiria 2011)
Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near threatened (NT), Least concern (LC), Data deficient (DD)
* Listed as LC in 2001, not listed in 2011 (Tirira 2011)
^ Endemic species

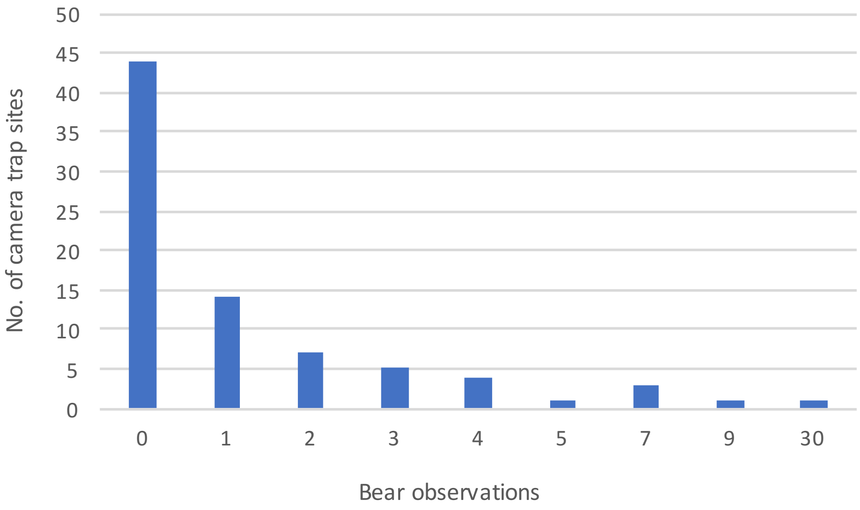

Figure 2. 2 Frequency of bear observations (n=124) at camera traps sites (n=80) from 2012-2014 camera trap study in the Nudo del Azuay, Ecuador.

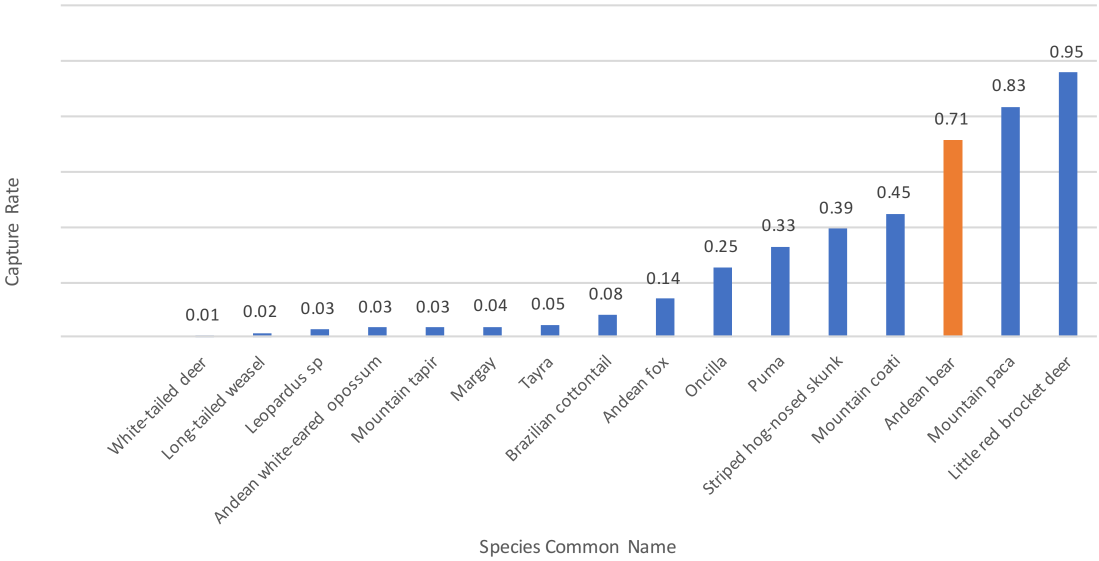

Figure 2. 3 Capture rates for mammal species (common name) observed during 2012-14 camera trap study in the Nudo del Azuay, Ecuador.

Table 2. 2 Mammal species capture rates by season, habitat, and overall from 2012-14 camera trap data from the Nudo del Azuay, Ecuador.

Mammal species	Wet	Dry	Forest	Shrubland	Total Capture rate	Total Captures
Andean bear	0.40	0.31	0.63	0.08	0.71	124
Andean fox	0.07	0.06	0.04	0.10	0.14	24
Andean white-eared opossum	0.02	0.01	0.01	0.02	0.03	6
Brazilian cottontail	0.04	0.04	0.07	0.01	0.08	14
Leopardus sp.	0.03	0.00	0.02	0.01	0.03	5
Little red brocket deer	0.61	0.34	0.61	0.34	0.95	166
Long-tailed weasel	0.01	0.01	0.01	0.01	0.02	3
Margay	0.03	0.01	0.04	0.00	0.04	7
Mountain coati	0.33	0.11	0.23	0.22	0.45	78
Mountain paca	0.59	0.25	0.29	0.55	0.83	145
Mountain tapir	0.02	0.01	0.02	0.02	0.03	6
Oncilla	0.17	0.09	0.15	0.10	0.25	44
Puma	0.26	0.07	0.29	0.03	0.33	57
Striped hog-nosed skunk	0.35	0.04	0.27	0.12	0.39	68
Tayra	0.01	0.03	0.05	0.00	0.05	8
White-tailed deer	0.01	0.00	0.01	0.00	0.01	1

*Capture rate = observations / total camera trap days * 100*

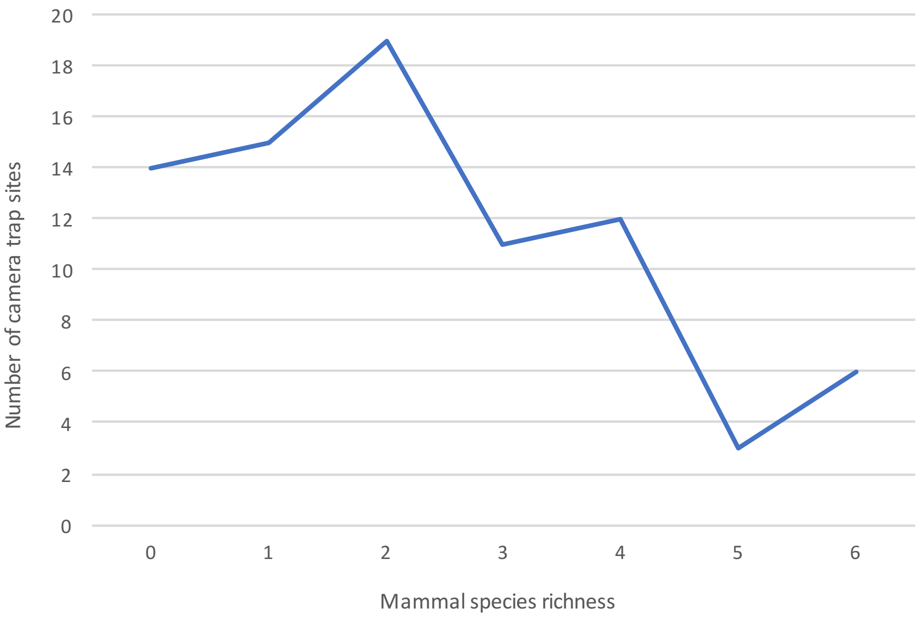

Figure 2. 4 Frequency of mammal species richness (excluding bears) at camera trap sites (n=80) from 2012-2014 camera traps study in the Nudo del Azuay, Ecuador.

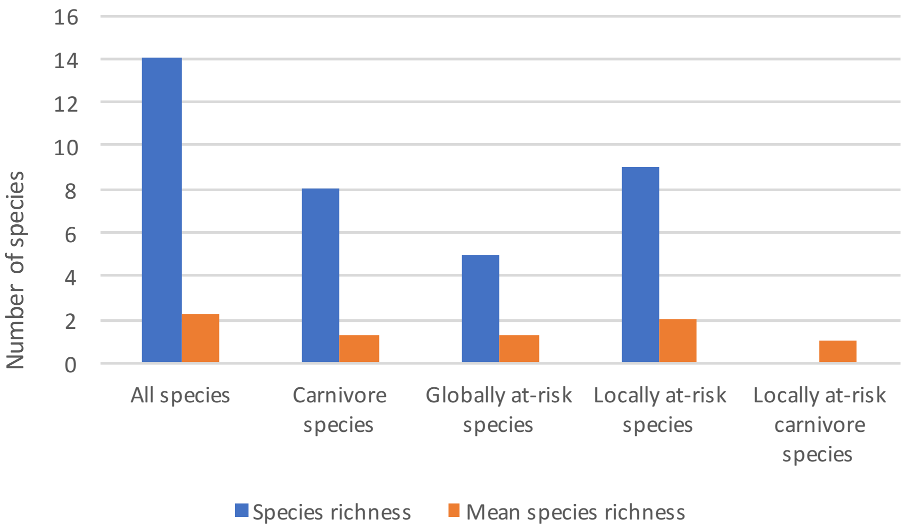

Figure 2. 5 Total species richness (number of species) and mean species richness of mammals at camera trap sites, organized by wildlife categories used in analysis of camera trap data collected in 2012-14 in the Nudo del Azuay, Ecuador.

Data Analysis

Model-averaged results from the negative binomial regressions (Table 2.3) and AICc model selection (Table 2.4) for all wildlife categories were relatively similar because all showed a positive association between bear presence in forested habitat and species richness.

All species: The AICc-optimal model included all five covariates: *bear*, *season*, *habitat*, *bear*season*, *bear*habitat* (AICc weight=57%). In the model-averaged results, *bear* and *habitat* alone showed a significant, negative association with species richness (PE=0.54, PE=0.62) but the interaction term *bear*habitat* showed a significant, positive association between bear presence in forested habitat and species richness (PE=1.99, CI=1.19-3.33). *Season* also showed a significant, negative association with species richness (PE=0.69).

Carnivore species: Model *bear*, *habitat*, *bear*habitat* (AICc weight=61%) was the AICc-optimal model. This model had a significant, negative association between *habitat* and species richness (PE=0.59). The interaction term *bear*habitat* showed a significant, positive association with species richness (PE=2.55, CI=1.13-5.74).

Globally at-risk species: The AICc-optimal model was *bear*, *habitat*, *bear*habitat* model (AICc weight=44%). *Season* and *habitat* had significant, negative associations with species richness (PE=0.67, PE=0.63) but the interaction term *bear*habitat* had a significant, positive association (PE=2.10, CI=1.10-4.01).

Locally at-risk species: The *bear*, *season*, *habitat*, *bear*season*, *bear*habitat* model (AICc weight=63%) was the AICc-optimal model. There was a significant, negative association between species richness and *bear* (PE=0.54), *season* (PE=0.69), and *habitat* (PE=0.61) but a significant, positive association between the interaction term *bear*habitat* and species richness (PE=1.98, CI=1.18-3.31).

Locally at-risk carnivores: The AIC-optimal model was *bear*, *habitat*, *bear*habitat* (AICc weight=65%). There was a significant, negative association between *habitat* and species richness (PE=0.55) but a significant, positive association between the interaction term *bear*habitat* and species richness (PE=2.22, CI=1.04-4.75).

Further Analysis

Because we know Andean bears and other wildlife use trails that could potentially bias our data, we explored the effects of trail definition (poor, moderate, well) on our results. Results from a Fisher's Exact Test confirmed that trail definition and forest type were independent (p-value = 0.53). We used “trail definition” as our predictor variable instead of bear observations and conducted the same negative binomial regression and AICc model selection for the three wildlife categories with the highest species richness (all species, carnivore species, locally at-risk species). Trail definition was not a significant predictor of species richness for any of the three wildlife categories and the AICc-optimal model for species richness for all three wildlife categories was *bear*, *habitat*, and *bear*habitat* (AICc weight: *All species*=69%, *Carnivore species*=78%, *Locally at-risk species*=82%).

To explore the potential that capture rate was more important than species type (bear), we added Andean bear observations into the species richness calculation and removed little red brocket deer observations, the species with the highest capture rate (CR=0.95). We used little red brocket deer as our predictor variable and conducted a negative binomial regression and AICc model selection for the three wildlife categories with the highest species richness (all species, carnivore species, locally at-risk species). Little red brocket deer was not a significant predictor of species richness for *all species* and *locally at-risk species* categories but when combined with season, was a weak predictor of species richness in the *carnivore species* category. The AICc-optimal model for species richness for *All species* and *Locally at-risk species* categories was *season* (AICc weight: *All species* = 51%, *Locally at-risk species* = 41%). For the *Carnivore species* category, the AIC-optimal model was *deer*, *season*, *deer*season* (AICc weight: 52%).

Table 2. 3 Model-averaged results (exponentiated) of negative binomial regressions for each wildlife category. Results are based on the conditional average which includes only models that include the parameter of interest. Estimates <1 show a negative association with species richness; estimates >1 show a positive association with species richness.

Covariates	Model-averaged parameter estimate	95 % Lower	95% Upper
All species			
(Intercept)	0.02	0.01	0.03
bear*	0.54	0.30	0.95
season (wet)*	0.69	0.50	0.94
habitat (forest)**	0.62	0.45	0.86
bear x season (wet)	1.04	0.92	1.18
bear x habitat (forest)**	1.99	1.19	3.33
Carnivore species			
(Intercept)	0.01	0.01	0.01
bear	0.47	0.18	1.24
season (wet)	0.73	0.47	1.12
habitat (forest)*	0.59	0.38	0.93
bear x season (wet)	1.07	0.92	1.25
bear x habitat (forest)*	2.55	1.13	5.74
Globally at-risk species			
(Intercept)	0.01	0.01	0.02
bear	0.54	0.25	1.15
season (wet)*	0.67	0.47	0.96
habitat (forest)*	0.63	0.43	0.91
bear x season (wet)	1.04	0.91	1.20
bear x habitat (forest)*	2.10	1.10	4.01
Locally at-risk species			
(Intercept)	0.02	0.01	0.03
bear*	0.54	0.31	0.93
season (wet)*	0.69	0.51	0.94
habitat (forest)**	0.61	0.45	0.84
bear x season (wet)	1.04	0.92	1.16
bear x habitat (forest)**	1.98	1.18	3.31
Locally at-risk carnivore species			
(Intercept)	0.01	0.01	0.01
bear	0.54	0.23	1.28
season (wet)	0.73	0.47	1.14
habitat (forest)**	0.55	0.35	0.86
bear x season (wet)	1.08	0.94	1.23
bear x habitat (forest)*	2.22	1.04	4.75

**$p < 0.01$, *$p < 0.05$

Table 2. 4 AICc model selection results from negative binomial regressions of species richness of all wildlife categories (all species, carnivore species, globally at-risk species, locally at-risk species, locally at-risk carnivore species) used to determine relationship between number of Andean bear (*bear*) observations and covariates (*season*, *habitat*) and their interactions, at camera trap sites in the Nudo del Azuay, Ecuador, from 2012-14.

Model	AICc	∆AICc	AICc weight	Cumulative % AICc weight	K
All species					
bear, season, habitat, bear*season, bear*habitat	512.32	0.00	0.57	0.57	7
bear, habitat, bear*habitat	513.62	1.31	0.30	0.87	5
season	516.67	4.36	0.06	0.93	3
bear, season	518.68	6.36	0.02	0.96	4
habitat	519.04	6.72	0.02	0.98	3
bear, habitat	520.55	8.24	0.01	0.99	4
bear, season, bear*season	520.77	8.46	0.01	1.00	5
bear	522.14	9.82	0.00	1.00	3
Carnivore species					
bear, habitat, bear*habitat	380.62	0.00	0.61	0.61	5
bear, season, habitat, bear*season, bear*habitat	382.62	1.99	0.22	0.83	7
bear, habitat	386.11	5.49	0.04	0.87	4
bear	386.33	5.71	0.04	0.91	3
season	386.61	5.99	0.03	0.94	3
bear, season	386.68	6.06	0.03	0.97	4
habitat	387.30	6.68	0.02	0.99	3
bear, season, bear*season	388.77	8.15	0.01	1.00	5
Globally at-risk species					
bear, habitat, bear*habitat	504.47	0.00	0.44	0.44	5
bear, season, habitat, bear*season, bear*habitat	506.14	1.68	0.19	0.62	7
bear	507.28	2.82	0.11	0.73	3
bear, habitat	507.89	3.42	0.08	0.81	4
bear, season, bear*season	508.30	3.83	0.06	0.87	5
bear, season	508.39	3.92	0.06	0.94	4
season	509.48	5.02	0.04	0.97	3
habitat	509.89	5.42	0.03	1.00	3
Locally at-risk species					
bear, season, habitat, bear*season, bear*habitat	467.44	0.00	0.63	0.63	7
bear, habitat, bear*habitat	468.89	1.45	0.31	0.94	5
season	473.70	6.27	0.03	0.97	3
bear, season	475.37	7.93	0.01	0.98	4
habitat	476.07	8.63	0.01	0.99	3
bear, habitat	476.93	9.49	0.01	0.99	4
bear, season, bear*season	477.40	9.96	0.00	1.00	5
bear	478.99	11.55	0.00	1.00	3
Locally at-risk carnivore species					
bear, habitat, bear*habitat	330.38	0.00	0.65	0.65	5
bear, season, habitat, bear*season, bear*habitat	332.50	2.12	0.22	0.87	7
bear, habitat	335.06	4.68	0.06	0.93	4
bear	336.76	6.38	0.03	0.96	3
bear, season	337.41	7.03	0.02	0.98	4
habitat	339.34	8.96	0.01	0.99	3
bear, season, bear*season	339.49	9.11	0.01	0.99	5
season	339.57	9.19	0.01	1.00	3

Table 2. 5 Habitat preference, human-caused pressures, and major threats to wildlife species detected by camera traps from 2012-14 in Nudo del Azuay, Ecuador.

	Habitat prefernce	Hunting (sport, trophy)	Retalitory killing (threats, pest)	Susceptible to habitat disturbance	Disturbed by roads	Disturbed by human presence	Relative abundance when feral dogs are present^	*Major Threats*			
								Habitat Fragmentation	Habitat Loss	Isolated Populations	Other
Andean bear	forest páramo	yes	yes	yes	-	somewhat	lower	x	x	x	
Andean fox	forest páramo	yes	yes	no	yes	yes	lower	x	x		predation by dogs
Striped hog-nosed skunk	forest páramo	yes	-	no	-	-	lower				
Long-tailed weasel	forest	-	yes	no	-	no	absent	x			
Tayra	forest	yes	-	-	yes	-	-				
Margay	forest	yes	yes	-	yes	-	-	x			
Little spotted cat	forest	yes	yes	-	yes	-	-	x			
Puma	forest páramo	yes	yes	-	-	-	lower	x	x		decline of prey species
Mountain coati	forest páramo (rare)	-	-	yes	yes	-	absent		x		
Little red brocket deer	forest	yes	-	-	yes	-	lower	x	x		
White-tailed deer	páramo	yes	-	-	-	-	not disturbed		x		
Mountain tapir	forest páramo	yes	-	yes (very sensitive)	yes	yes	lower	x	x	x	
Andean white-eared opossum	forest páramo	-	-	-	-	-	not disturbed				
Brazilian cottontail	forest páramo	yes	-	no	-	-	-		x		
Mountain paca	forest páramo	yes	yes	prefers primary habitat	-	-	absent	x	x		

Dash (-) indicates no data in this category for this species.
Sources: IUCN Red List of Threatened Species (Version 2017-1), ^Zapata-Rios (2016), Tirira (2011), Tirira (2007)

Discussion

For all species categories, our models indicated that Andean bears alone were not a predictor of species richness. However, the interaction term of Andean bear presence and forested habitat was a strong, significant predictor of species richness and was predictive when the single variable term was also in model. Our results indicate that conservation on private lands with a mixture of broad habitat types (forested, shrubland, páramo) and human-use areas (pastures, crops) requires a more fine-scale approach to the use of Andean bears as conservation surrogates; bears may be a useful indicator of the presence of other mammals but only when forested habitat is also present. As such, in this case a single-species conservation approach might be more effective when combined with a broad category of habitat (Lambeck 1997; Simberloff 1999).

A notable characteristic of the forested habitat in the study area is that it was largely interconnected (*see* Chapter 1, Figure 1.2), with few completely isolated patches and proximal to large expanses of páramo. Bears use the páramo to move between forest patches (Peyton 1999) and eat terrestrial bromeliads (*Puya spp.*) found in grass páramo, the dominant type of páramo our study area (Troya et al. 2004). Previous studies indicate that Andean bears can persist in suboptimal habitat within fragmented and degraded forests if there is seasonal access to available food sources and páramo (Cuesta et al. 2003; Peralvo et al. 2005; Achig 2009; Molina et al. 2017). A finer scale analysis of habitat type, and a detailed study of connectivity could help conclusions about what type of forested habitat is important since Andean mammals may be sensitive to differences in forest type.

We detected 15 total species during our study. We photo-captured all the species we had seen in previous camera trap studies (Zug 2009; Jones 2010; Fundación Cordillera Tropical 2012) except the red-tailed squirrel (*Sciurus granatensis*). Notable but rare detections included mountain tapir (*Tapirus pinchaque*), white-tailed deer (*Odocoileus virginianus*). Of the carnivore species, the largest, Andean bears and pumas (*Puma concolor*), were among the most frequently photo-captured. The little spotted cat (*Leopardus tigrinus*), the striped hog-nosed skunk (*Conepatus semistriatus*), and the mountain coati (*Nasuella olivacea*) were also photo-captured frequently. Other carnivore species were photo-captures less. For example, on few occasions (n=8, CR=0.05) we photo-captured the tayra (*Eira barbara*) in forested habitat, 2,000 meters above its known range in Ecuador (n=8, CR=0.05)(Cuarón et al. 2016; Tirira 2017). Local landowners easily identified the tayra (*urku allku* in local Kichwa) from photos and reported a long history of conflicts related to crop raiding (corn). One landowner reported that he had not seen it in many years, but that it was once common. We hypothesize that the local population of this species was heavily hunted and its numbers severally reduced. However, our study may indicate that there is a slow recovery occurring, but that with continuing agriculture in the region, this species may never recover to previous levels.

The species we saw most frequently in camera trap photos, despite their low density, was the little red brocket deer (*Mazama rufina*) which is listed as vulnerable by the IUCN and in Ecuador (Tirira 2011; Lizcano & Alvarez 2016). This species is thought to have small territories and travel primarily in pairs. They favor the páramo-montane forest transitional area which is well represented in this region. Additional data collection and occupancy modeling could be used to estimate detection probability.

Notably, we saw a negative association with all measures of species richness when Andean bear was the sole predictor. We do not believe the bears themselves are causing this association but supports our results that indicate Andean bears as conservation surrogates on private lands require a more complicated strategy than a single-species approach. While most of the species we detected share broad conservation threats such as habitat loss and fragmentation, they differ in importance of fine scale threats (Table 2.5). Andean bears are known to live in marginal or low-quality habitat, experience varying levels of hunting and persecution, and while disturbed by human presence (see *Chapter 1*) can live relatively close to human settlements (Branton & Richardson 2011; Kunkel et al. 2013; Ibarra & Martin 2015). Sensitivity to disturbed habitat is a key concern for some species such as the mountain tapir, the mountain coati, and mountain paca, all endemic, locally at-risk species. The mountain tapir is extremely sensitive to habitat disturbances and human activity while Andean bears are more adaptable to both.

Understanding the level of human-caused mortality in focal areas might be key to determining how well Andean bears can serve as surrogates (Kunkel et al. 2013). Many species experience different levels of hunting (sport and trophy) and retaliatory killing due to threats to domestic animals, livestock, and crops. In our study area, it is well-known that it is illegal to kill Andean bears and that killing a bear may bring unwanted attention from community members and neighbors. For these reasons, they are probably hunted less than foxes, pacas, weasels, and other species that are seen as pests. Monitoring and controlling the hunting of Andean bears alone will not protect other, less charismatic species. Further, human presence and roads affect species differently. Andean bears are known to cross roads that other species may avoid. Most of the species we detected in this study are disturbed by roads which may further isolate populations. For these reasons, Andean bears alone may not be a suitable conservation surrogate for Andean mammals in human dominated landscapes.

However, this negative association between bears and species richness is probably not due to the presence of domestic dogs at our study area. Although landowners reported seeing dogs chase wildlife, we photo-captured domestic dogs on only eight occasions at only five camera trap sites. In habitat similar to our study area (Cayambe-Coca National Park, Ecuador), Zapata-Ríos and Branch (2016) found that the abundance of Andean mammal species varied with the presence of feral dogs (dogs not associated with humans), indicating species specific levels of sensitivity (Lenth et al. 2008). However, the species Zapata-Ríos and Branch found to be at the lowest abundance levels or absent (striped hog-nosed skunk, mountain coati, little red brocket deer, mountain paca) had the highest capture rates during our study.

Our analysis was limited by sample size. However, broad trends exist. An interesting finding by the category groupings include some effect of dry season on wildlife. Our study area has two distinct seasons, cool and wet from May-August (wet season), and dry and warm from October-January/February (dry season)(Fundación Cordillera Tropical 2008). In the *all species* category, dry season had a positive effect on species richness. Andean bears, like other bear species, show seasonal movement patterns which suggests a seasonal variation in food resources (Cuesta et al. 2003). Ten of the 15 species detected in our study are strict carnivores or omnivores. The increase in species richness during the dry season might be due to insects and prey species, such as rodents, becoming easier to detect during the dry seasons because of less conspicuous movement in dry vegetation and increased movement (insects) due to warmer temperatures. However, species specific behavior for many Andean mammals was unavailable.

Species noticeably missing from the camera trap data include the northern pudu (*Pudu mephistophiles*) and the Andean porcupine (*Coendou quichua*). Landowners report seeing both species but we have not photo-captured either in five years of camera trap studies in this area. In the case of the northern pudu, landowners could be confusing the species identification with the little red brocket deer, a similarly sized species with relatively similar coloring. An alternative theory is that because northern pudus occur at very low densities throughout their range and are especially wary due to heavy hunting in the past (Barrio & Tirira 2008). Lack of Andean porcupines in our camera trap photos is more perplexing. Porcupines are not easily confused with other species and landowners report seeing quills on the ground and in puma scat. Little is known about the Andean porcupine (IUCN: data deficient) but they are thought to be a nocturnal, solitary species and uncommon throughout their range (Tirira 2007; Delgado 2016; Tirira 2017). Perhaps the arboreal nature of the porcupine meant they were not present on the ground near our camera traps (however, other species of porcupine are well represented in camera trap studies). We could also speculate that their numbers were too low to register in our camera traps.

In addition, the frequency and type of species photo-captured might be due to capture bias; we might have missed species that were present or over-captured species that were rarer due to their size, grouping behaviors, or use of trails (Tobler et al. 2008). Our camera traps were set at 80 cm above the ground for bears. Smaller species could have walked under the camera trap and missed detection. In addition, our trap placement was limited by landowner permission. We were not permitted to survey a heavily forested area in the center of the region. This area could have higher species richness by camera trap site and higher capture rates overall. Future studies would benefit from surveying these properties.

We recognize the potential bias in that our study area might be unique. This area has benefited from the intervention of a local NGO, has high-levels of emigration of men, and low levels of conflict. Fundación Cordillera Tropical has worked in this area for over a decade, supporting communities and landowners to conserve native forests. Their conservation outreach and education programs that targeted landowners and school-aged children may have resulted in a local population more likely to conserve wildlife. In addition, satellite photos of the Dudas subwatershed show the reforestation of some areas between 1977 and 2010. We hypothesize there is a correlation between this natural reforestation of remote areas and the high level of emigration of men to regional, national, and foreign cities, which is unique to this region (Wunder 2000; Instituto Ecuatoriano de Estadísticas y Censos (INEC) 2010). Landowners in our study area also had low-levels of conflict with wildlife, excluding extensive problems with pumas on a local alpaca ranch (see Chapter 3). We know hunting occurred in the study area and that locals from one watershed have an annual tradition of hunting in a neighboring watershed. This may disproportionately impact rare or targeted wildlife, such as the tapir and mountain paca. However, during and prior to the study period there no reports of retaliatory killing or sport hunting of bears in this region.

Future studies would benefit from including a wider variety of private lands, and comparing landowners who are dramatically different in their land use, conservation interests, and participation in conservation programs. Although our study area had a variety of types of landowners involved in different programs, we did not find enough variation between property types to determine how these differences in landowners could influence mammal presence (see *Analysis,* Chapter 1). Conservation programs that hope to use Andean bears as surrogates for conservation need to continue to test this idea under different circumstances. A comparison of private lands and protected areas simultaneously is important to gauge the usefulness of this approach. It might also be beneficial to explore techniques for different surrogate species. For example, a suite of Andean species facing similar threats or with similar life-history characteristics (e.g. carnivores) (Ibarra & Martin 2015) or two species that differ enough in life-history characteristics to maximize their potential as a conservation umbrella (e.g. bears and pumas) (Kunkel et al. 2013).

Global biodiversity is declining and deforestation and habitat fragmentation in the tropics are accelerating (Pimm et al. 2014; Kim et al. 2015; Ceballos et al. 2017). To address these crises, conservation planners need tools to measure biodiversity efficiently and respond quickly with comprehensive and effective conservation strategies. The use of conservation surrogates is one approach. This study highlights the importance private lands in wildlife conservation in the tropics, especially in the Ecuadorian Andes, where deforestation is advancing rapidly at an annual rate of 0.37% (47,000 ha) (MAE 2015 in Cuesta et al. 2017).The broader implications of our results are that successful conservation of Andean mammals in areas under human pressure also requires the conservation of forest. Successful conservation plans on private lands cannot ignore the pressures of habitat conversion and fragmentation by local landowners, nor can they ignore the reality of increasing human presence in wildlife habitat. Conservation managers need to include projects to slow or stop deforestation if they aim to conservation wildlife.

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Chapter 3: How camera trap data can help us understand puma-livestock conflict

Abstract

Pumas (*Puma concolor*) are the most widely distributed large terrestrial vertebrate in the western hemisphere. They are listed as least concern by the IUCN because of their geographic distribution but their population is decreasing due to habitat loss and fragmentation, depletion of prey species, and human-caused mortality. Across their entire distribution pumas depredate livestock which often results in retaliatory killing of pumas by livestock owners. Throughout a 2012-14 Andean bear (*Tremarctos ornatus*) focused camera trap study we observed pumas at our camera trap sites. During and shortly after our study period, a landowner in our study area experienced high levels of depredation of alpacas by pumas. We were able to use camera trap data to better understand these depredation events and discuss methods that might work best to mitigate conflict in this area. Our study area was in the Nudo del Azuay region of Ecuador, on 16 privately-owned properties where livestock owners had a long history of conflicts with pumas. From 2012-14 we placed camera traps on 40 km^2 of montane cloud forest for a total of 17,407 trap days. We observed pumas on 57 occasions at only 18% of trap sites. We estimate 5-6 pumas total present during our study period, including 1 adult female, 2 adult males, and 3 cubs. We observed what appeared to be a resident, breeding population of pumas. We recorded an increase in daytime puma observations at trap sites near pastures at times of intense depredations, potentially demonstrating a behavioral switch due to night corrals. We had high capture rates for the primary prey species of pumas in the Andes and the pumas did not appear to be injured, both frequent triggers of

depredation. It is likely that the problem animal encountered and took advantage of easy-to-hunt livestock. In our study area, non-lethal interventions such as constant monitoring of livestock during the day and corralling the animals at night may be able to deter pumas and prevent depredation opportunities. Our study demonstrates the utility of camera trap data as a tool to understand puma behavior during conflict events; it does not have conclusive results on puma ecology but lays the foundation for future research.

Introduction

Pumas (*Puma concolor*) have the largest geographic distribution of any native terrestrial mammal in the western hemisphere, extending across 28 countries and two continents, from Canada to the southern tip of Chile (Panthera 2017). Due to their wide distribution they are listed as least concern by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (Nielsen et al. 2015) but with a declining population and contracting range (Wolf & Ripple 2017). Pumas are an Appendix II species with controlled international trade to prevent them from becoming threatened with extinction (CITES 2011). In Ecuador, pumas are listed as vulnerable in the Ecuadorian Red Book of Mammals (Tirira 2011). The biggest threats to pumas throughout their range are habitat loss and fragmentation, depletion of prey species, and human-caused mortality.

Puma-livestock conflict is a major driver of pre-emptive and retaliatory killing. Livestock depredation by pumas was one of the principal causes for their eradication in North America by early European settlers (Ruth & Murphy 2010). In Latin America puma depredation is well-documented and studies show that pumas will not always attack livestock but in certain areas they can cause significant loss (Mazzolli et al. 2002; Polisar et al. 2003; Pacheco et al. 2004; Michalski et al. 2006). While attacks on people are rare, fear or a general dislike for pumas may also result in a shoot-on-sight strategy for the species (Inskip & Zimmermann 2009).

Pumas seem to favor smaller livestock, such as sheep and goats but are recorded killing smaller cows and cattle (Laundré & Hernández 2010). In Chile, Argentina, and Bolivia pumas prey on wild and domestic camelid species such as guanaco (*Lama* *guanicoe*), alpaca (*Vicugna pacos*), and vicuña (*Vicugna vicugna*) (Zacari & Pacheco 2005; Walker & Novaro 2010). A review of puma-livestock conflict shows a correlation between livestock loss and habitat type, which varies depending on the landscape (*Ibid.*). Night corrals work in some scenarios to protect livestock from pumas but a common response to problem animals is illegal and indiscriminant killing. High mortality rates due to retaliatory killing is a major threat to some puma populations in Latin America (Michalski et al. 2006).

In North America, puma (mountain lions, cougars, panthers) populations are well-studied (Logan & Sweanor 2001; Hornocker & Negri 2010) and conservation and management programs are well-established in many American states (for examples see The Cougar Fund and Panthera's Puma Program). They were largely extirpated from the eastern United States by the late 1800's and not long after populations in the West were severely reduced (Logan & Sweanor 2001). Except for a small isolated population in Florida, pumas are still absent east of the Mississippi and in the northern two-thirds of Canada. Populations in the western half of the US have recovered and long-term studies have provided most of what we know about puma behavior and ecology.

Despite these extensive efforts in North America, there is little published data on pumas in Latin America and even less in the northern Andes (Gallardo et al. 2009; Laundré & Hernández 2010). Genetic analysis identified six subspecies of pumas (*Puma concolor concolor* in northern South America) all six of which are represented in Latin America and correlate with geographical barriers (Culver et al. 2000; Laundré & Hernández 2010). Most of the published research on pumas in Latin America focuses on the southern Andes of Chile and Patagonia in Argentina, where their behavior and ecology are similar to North American pumas (Pacheco et al. 2004; Walker & Novaro 2010), and lowland forests where they co-occur with jaguars (*Panthera onca*) (Scognamillo et al. 2003; Novack et al. 2005; Kelly et al. 2008; Foster et al. 2013).

Jaguars are the largest and most charismatic felid in Latin America and have ranges that overlap with pumas (Pacheco et al. 2004).They have similar habitat needs, feeding behaviors, and face similar conflicts with humans over habitat destruction, prey depletion, and livestock depredation. Despite these similarities, in the tropics jaguars have attracted more public attention than pumas and thus more research and conservation efforts. Local people are sometimes even unaware that pumas are present in the area (Conforti & Cesar Cascelli de Azevedo 2003). Pumas are even noticeably missing from pre-Colombian artifacts while jaguars are important cultural symbols (Saunders 1994; Laundré & Hernández 2010). They are frequently compared to jaguars (Conforti & Cesar Cascelli de Azevedo 2003; De Angelo et al. 2011) but few studies have focused exclusively on pumas and fewer still in the northern Andes. Hernández-Guzmán et al. (2011) published the first puma-specific study in the páramo ecosystem and the first puma study in the highlands of Colombia. Much of what we know about highland populations is extrapolated from other habitats (Laundré & Hernández 2010).

Pumas are solitary cats, coming together only to breed and occasionally at the kill sites of large prey (Elbroch & Quigley 2017). They are primarily nocturnal but will switch activity periods based on prey availability. Males mark (scrape, urine) and defend large territories while females have smaller home ranges that typically overlap with other females (Logan & Sweanor 2010). North American range estimates (male: 150 km^2 to 700 km^2, female: 55 km^2 to 300 km^2) are considerably larger than for pumas in Latin

America where puma ranges differed by habitat and season (see Laundré and Hernández 2010 for full summary). Population density estimates between studies in North America are hard to compare because of lack of uniform calculation methods (Quigley & Hornocker 2010). Kelly et al. (2008) found that puma density estimates per 100 km^2 varied greatly between dense, lowland forests in Belize (6.80 ± 1.5), Bolivia (3.42 ± 1.3), and Argentina (0.67 ± 0.2). Dispersing pumas (males: 49-483 km on average) use contiguous or patchy, suitable habitat to move between less desirable areas (Logan & Sweanor 2010).

Pumas are habitat generalists and their historical distribution included every major habitat type in North America (Nowell & Jackson 1996). They are obligate carnivores that enact top down regulation of ecosystems (Ruth & Murphy 2010). Prey species are specific to habitat type but include both large and small mammals, an important dietary component for Latin American pumas (Laundré & Hernández 2010). A puma will come back to feed on a kill for several days, a behavior that makes them more susceptible to retaliatory killing after a livestock depredation.

Laundré and Hernández (2010) estimate that 40% of puma range in Latin America is already lost or threatened by human expansion, and that the remaining 60% is desert or faces future threats. In the Ecuadorian Andes, it is illegal to hunt, capture, sell, or transport live pumas or puma products. The population is thought to be declining due to habitat loss and fragmentation caused by development and the advancing agricultural frontier, intense hunting in cattle areas, and trade in parts (Tirira 2011). Pumas are the apex predator in the Andes but we could not find any published research focusing exclusively on pumas in this habitat in Ecuador. It is evident that more puma-focused research is needed to learn more about almost every aspect of puma ecology in the Andes.

During (2013) and shortly after (2014-15) our study period, a landowner in our study area experienced high levels of depredation of livestock by pumas. Camera traps have been used to study the behavior of a variety of species of carnivores, ranging from activity periods to physical health of individuals (Kays & Slauson 2008; Bridges & Noss 2011), and in conflict studies to confirm predator species and problem individuals (Karanth et al. 2014). Our goal was to use the data we collected on pumas during our Andean bear focused camera study to better understand these depredation events and discuss methods that might work best to mitigate conflict in this area.

Materials and Methods

Study Area

We conducted our research in the Nudo del Azuay (NdA) region of the eastern cordillera (mountain range), Cañar Province, Ecuador (2°33'S, 78°43'W) (Figure 3.1). The NdA has steep and rugged topography ranging from 1200-4500 meters above sea level (m.a.s.l.) (Fundación Cordillera Tropical 2008; Anderson 2010). Average annual temperatures range from 1ºC to 18ºC. Average precipitation ranged from 1,200 mm to 1,600 mm per year (Fundación Cordillera Tropical 2010) with two distinct seasons, wet and cool from May-August, and dry and warm from October-January/February (Fundación Cordillera Tropical 2008). Land cover included grass páramo (high altitude grasslands), high montane evergreen forest, montane cloud forest, scrublands, and pastures (see Chapter 1, Study Area for a more detailed description) (Sierra 1999).

An estimated 85% of the NdA was located within the southern portion of Sangay National Park (SNP), one of Ecuador's largest protected areas. This area was home to both mestizo and indigenous Kichwa groups who lived in small communities throughout the region. Land-use was primarily agriculture, small farms with several head of cattle, goats, sheep, chickens, and some crops (corn, potatoes). There was also one large alpaca ranch (1800 ha total). The entire study area was privately owned with some properties inside of the southern boundary of Sangay National Park.

The location of the alpaca depredations was within our study area in a wildlife reserve, a private ecological restoration and conservation initiative. The reserve covered 1800 hectares of montane forest, páramo, and lower altitude livestock pastures with elevation ranging from 2800-3700 meters above sea level.

The reserve was privately-owned and the landowner, who was considered a "conservation ally" in the region, lived off-site in a nearby city. The land was designed a wildlife reserve by the landowner who received no government support. On occasion, the reserve hosted groups of foreign students, educators, and researchers. In 2010, the landowner applied to have the reserve included in Ecuador's Socio Bosque program (a government conservation program for private lands) but the application was rejected because the land title did not include a georeferenced map of the holding (not uncommon in this region of Ecuador; Schloegel 2012).

The vast majority of the reserve (1500 ha) was unoccupied by people and livestock. The landowner used 300 ha to operate an alpaca ranch and managed 600 to 800 alpacas in total on a variety of different pastures. The ranch produced high-quality alpaca wool for export and live animals for local sale. The alpaca pastures were typically located at lower altitudes (~3000 m), near the houses of the landowner and the *alpaqueros* (alpaca ranch hands). The alpaqueros lived permanently on the ranch and the landowner made weekly visits. The alpacas were separated into different pastures depending on wool quality and color, age, and sex. Pastures varied in proximity to the houses and forest edge. The landowner provided alpaca husbandry training on his property to local and foreign students.

In the mid-2000s, repeated puma attacks on alpacas prompted the landowner to install night corrals in the pastures. The corrals were made of a 2-meter tall chain-link fence with 3 rows of barbed wire at the top and the bottom either staked to the ground or in a trench. At dusk the alpacas were put into the corrals and at dawn they were released to graze in pastures with varying levels of supervision by the alpaqueros.

Camera Trapping

Our camera trap study was designed to collect data on Andean bears (see *Chapter 1*). One of the benefits of camera trapping is the ability to also collect data on non-target species, such as pumas and their prey. Pumas and Andean bears are relatively similar in size so camera traps mounted on trees at average shoulder height of an adult male Andean bear (~80 cm above ground level) captured pumas as well as bears. When possible we selected sites with bear sign to maximize our Andean bear capture rate.

We selected trap sites by first dividing the study area into 1-km^2 grid cells across 100 km^2 of private lands. We eliminated sites with more than 80% páramo (36%)

because the movement of the grassy vegetation caused the cameras to trigger and quickly fill the memory card and drain the batteries. Then we went door-to-door to ask landowner permission to use their property in the study. Sixteen landowners gave us access to their properties resulting in groupings of camera sites in western and northeastern portions of the study area (40 total grid cells). Vegetation in the study area was dense and terrain was steep so we selected sites as close as possible to the center of each grid cell on a human or wildlife trail with bear sign present. This site selection method was developed to optimally sample dense forests in the study area.

We used one Reconyx® PC800 (Holmen, WI, USA) rapid-fire, digital camera trap per site. This model used infra-red technology to trigger the camera when an animal passed in front and had a semi-covert infra-red flash with a range of up to 70 feet for black and white nighttime photos. Daytime photos were in color. As replacement equipment, we used an older model of camera trap, PC85 (Reconyx® PC85, Holmen, WI, USA) when necessary (6 camera traps). This model had the same specifications and was programmed with the same settings as the PC800. We set the camera traps on high sensitivity to take 5 photos per trigger, rapid fire, with no time delay between triggers. Camera start-up speed was 1/5 second. Camera traps also collected data on date and time of observation, temperature (C°), and moon phase. We placed each camera trap inside a metal housing to protect it from bears and facing up or down a trail. We checked the camera traps every other month (~60 days) in groups based on site location and access points. When each camera trap site was first set-up, we used field datasheets to record a GPS point, altitude, and groundcover type.

We deployed camera traps from September 2012 – September 2014 and surveyed 80 sites total within our 40 1-km^2 grid cells. We moved a camera trap to a new location inside the same grid cell when we determined that no bears were present at a location based on lack of photos and lack of bear sign. We collected the camera traps for maintenance in December 2013 and redeployed them in January 2014.

Data Analysis

We uploaded our camera trap photos of pumas to the program MapView Professional™ (Reconyx LLP, Holmen, WI, USA) and organized them by camera trap site. We used MapView to tag photos with details about behavior (scraping, marking, resting), physical condition (pregnant, healthy, unhealthy, hurt), sex (m/f), presence of cubs (yes/no), and multiple individuals in the photo (pair-adult, pair-unknown ages, mother with cubs, cub, cubs-2, cubs-3). We then exported this data along with temperature and moon phase for each observation and created a covariate database. We used field datasheets to determine groundcover type at each camera trap site. We used the program ArcMap® 10.2.2 (ESRI, Redlands, CA) to extract information about land cover and covariates (distances to pastures, habitat type [forest, shrubby, páramo], river, road, or areas of high human use, or villages) from a 2010 multispectral sensor RapidEye image (the most current image available) with a spatial resolution of five meters (PROMAS, Universidad de Cuenca, Ing. Bastiaan Stoop); and about the physical features of our study area (slope, aspect, and elevation) from a 5 x 5 m digital elevation model (DEM) (U.S. Geological Survey (USGS) et al. 2014). We added these covariates about each trap site to our database. We reformatted the database to use the observational unit "site-season" (n=143) instead of camera trap sites (n=80) to explore a seasonal effect (wet/dry) on puma observations. We used this database to analyze our camera trap data using several methods: basic descriptive statistics, behavioral observations to look for patterns in temporal and spatial movements, and regression analysis.

For the regression analysis, we created models to determine the influence of covariate groups (distances to macrosite features, areas of human influence) on puma observations. We explored our data using a zero-inflated negative binomial regression to account for the high number of zeros in the dataset. We did not have any significant results from this analysis because our dataset had too many zeros. We than reformatted the data to reflect observations per site (n=80). We tried a zero-inflated Poisson regression accounting for overdispersion and it still did not perform well due to the number of zeros in the dataset. We then converted the covariates most useful in determining how pumas were using the different habitats in our landscape (distances to páramo, forested habitat, shrubby habitat, pastures) into categorical variables and used 2 x 2 tables to conduct hypothesis testing using both Pearson's Chi-square test and Fisher's Exact Test when count data were too low (on 4 of 5 occasions). The null hypothesis was that puma observations were independent of distance to our covariate of interest. Our alternative hypothesis was they were not independent ($p < 0.05$) (Table 3.1). We failed to reject the null for all variables.

Conversations about livestock depredation

During Study Year 1 (2012-13) we were notified by our field team that several alpacas had been killed by a puma in the reserve. Shortly after, the alpaca ranch owner contacted us and asked to see the camera trap photos of pumas around the pastures to help decide how to respond to the problem. We shared our data and continued talking with the landowner as this and a future conflict (2014-15) unfolded. From 2013-2017 we talked with the landowner in person and by email. We complied notes and photos from depredation events that occurred in 2013 and 2015 in the reserve and compared them to what we had learned from our camera trap photos about puma behavior in the area.

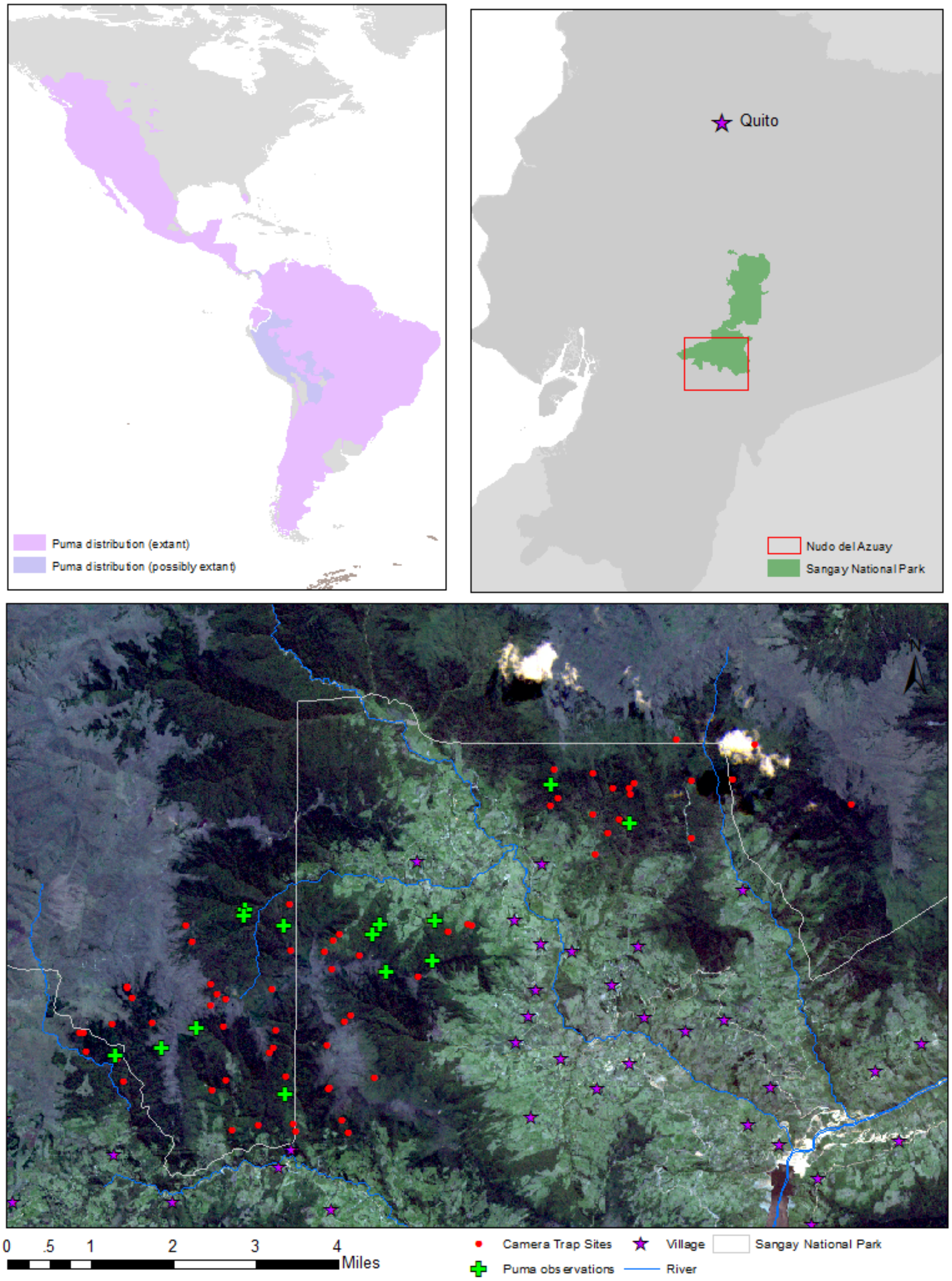

Figure 3. 1 Global distribution of *Puma concolor* (IUCN 2015), the study site in the Nudo del Azuay region of Ecuador, and camera trap locations with puma observations from 2012-14.

Results

Camera trap data and analysis

We had a total of 17,407 camera trap nights. We observed pumas on 57 occasions at 18% (14) of trap sites from 2900-3400 m on eight different properties (Figure 3.1). We examined camera trap sites with and without visits from pumas and detected no obvious difference in distances to pastures, habitat type (forest, shrubby, páramo), river, road, or areas of high human use, or villages. Based on the size of the study area (40 km^2), the close proximity of most of the traps (~1-2 km apart), and characteristics of individuals we saw in the photos we estimate that during the study period we saw five to six different pumas: one or two males (one in 2013, and possibly a different male in 2014) and one female with three cubs. Thirteen (93%) trap sites with puma observations were on well-defined trails. Fifty percent (29) of observations were at two camera trap sites (C13-1, E11-1) (Figure 3.2, Figure 3.3).

Overall puma capture rate was 0.33 per 100 trap days with noticeable differences in capture rate between wet (0.26) and dry (0.07) seasons and forest (0.29) and shrubland (0.03) habitats. Capture rates of two well-known prey species of pumas in the Andes were the highest of all species detected by camera traps during our study period (little red brocket deer: CR=0.95, mountain paca: CR=0.83) (see Chapter 2, Figure. 2.1 for capture rates of all species detected by camera traps). Detection of pumas and these two prey species overlapped at most camera traps sites but at different time periods, resulting in no obvious pattern. The pumas in our study area were active both day and night, with peak activity periods at sunrise (5:00-7:00 am) and sunset (6:00-8:00 pm) (Figure 3.4).

Monthly puma activity increased from May-June, coinciding in 2013 with an increase in conflict events on the alpaca ranch (Figure 3.5).

We observed pairs and family groups of pumas: two adults together on two occasions (E14-1, May 2013 and B14-2, June 2013), a mother and three cubs on one occasion (G11-2, March 2014), a group of pumas that included one large puma, one possibly smaller female or sub-adult puma, and two small cubs (D11-2, May 2014), and two adult pumas with one cub (D11-2, June 2014) (Appendix 3.2). On several occasions photos showed pumas marking the trail with urine or sniffing where another puma had lain down. We have one photo of a female puma apparently pregnant, with a very large belly (B14-2, August 22, 2013), approximately 80 days after we saw a pair together at the same trap site in June (puma gestation time is ~ 90 days). We also have a photo of a very unhealthy-looking (very thin) puma (G11-2, December 23, 2013).

Depredation events

From March to June 2013 a puma in the reserve killed nine alpacas in two different pastures. The puma killed the alpacas during the day (alpacas were in a corral at night) and then dragged the carcass into the nearby forest to eat it. As was standard practice, the alpaqueros buried the carcasses when they found them. On several occasions, they returned to the burial site and found scratching on the ground where the puma had tried to disinter the carcass. The landowner and the alpaqueros believed it was the same puma each time because the animal repeated the same depredation pattern: a daytime kill followed by consumption of the carcass in the forest. In June 2013, the landowner decided to try to capture and relocate the puma. The landowner borrowed a large cage from a local zoo and assembled it in a pasture. A few days later, the alpaqueros returned from a lunch break and noticed the alpacas were nervous and all looking in the same direction. They counted the herd and found one missing. The missing alpaca had been killed and the carcass dragged into the nearby forest where the puma fed on it. As was the plan, the alpaqueros used a rope to drag the carcass into the cage. They set the cage to close when the puma stepped on a pressure plate and put a camera trap on a tree near-by to document the capture. Around 9 PM the same night, camera trap photos showed a male puma circling the trap and within 3 minutes, he entered the cage and the door closed. The next day the landowner called authorities at the Ministry of Environment to alert them of the captured puma, sought authorization for a relocation, which was granted, and invited them to accompany the release. The following day the landowner drove the puma 100 km to a protected forest, "crossing the eastern cordillera toward the Amazon" and released it at night on the edge of páramo and forest in a "very steep and very wild" area without any human settlements. After the relocation, alpaca depredations ceased until October 2014 (15 months).

In October 2014, the landowner reported more depredation of alpacas by pumas. The landowner was keeping alpacas in a remote pasture (~3200 m) where they were close to forest, not using night corrals, and unwatched for days at a time. The landowner knew it was risky but had never had problems with pumas there. Over three consecutive nights, the puma killed several alpacas. In response, the landowner removed the alpacas from this pasture but did not remove the horses. The alpaquero later reported that a puma returned and tried to attack the adult horses who were able to defend themselves. After the alpacas were removed from this distant pasture, the puma then went to one of the lower pastures where it got into a night corral through a gap between the fence and the ground. The puma killed 15 weanlings (young alpaca calves) in a single night. The next day the landowner and the alpaquero skinned and removed the carcasses but could not complete the task before sunset. They put the remaining carcasses back into the night corral until morning. The next morning, the landowner found that the puma had returned and gotten into the corral again. The landowner followed the trail where the puma had dragged the carcass into the woods. Approaching the forest edge he could hear the puma eating. When he returned later he found the alpaca carcass 8 m into the forest. The landowner again borrowed a cage from a local zoo and tried to capture the puma to relocate it. When the attacks started, the landowner and the alpaqueros increased the security of the night corrals. In response, the puma switched to hunting and killing during the day; it was even seen in pastures during daylight hours with another puma. By January 2014, the puma had killed 44 alpacas, 8-10 of which were pregnant females, and had not yet been captured. The stress of the depredations caused another 3-4 alpacas to abort, inflicting further damage to the alpaca herd.

The landowner continued his attempts to capture the puma with new cages, placing one cage in each pasture. In February 2015, a dead puma was found further down valley and since then, the landowner has not had any more depredation of his alpacas (almost 2 years at the time of writing this document). The alpaqueros continue to see pumas in the high altitudes of the reserve but have not had any problems.

A note on verification of puma kills

The landowner and the alpaqueros were confident that pumas were responsible for the alpaca depredations for several reasons: the alpacas had wounds consistent with felid depredations (open or skinned neck with bite marks or lacerations, entrails eaten, noticeable lack of blood left in carcass) (Hoogesteijn & Hoogesteijn 2014) (Appendix 3.3), puma tracks were seen around the carcasses, and several puma were sighted near pastures. In addition, Andean bears are the only other predator in this habitat large enough to kill an animal the size of an alpaca. Bears kill differently from cats, taking the animal down from the back, not by the neck in the front. Our team did not confirm the first alpaca depredation in 2013 or 2014, which we acknowledge as a critical step in the verification process (*Ibid*). A carcass in a pasture can attract and be fed on by a predator making true cause of death difficult to discern. We were confident, however, that a puma was the cause of the subsequent depredations based on the information above, photos of the carcasses, and conversations with the landowner who had prior experience with puma attacks.

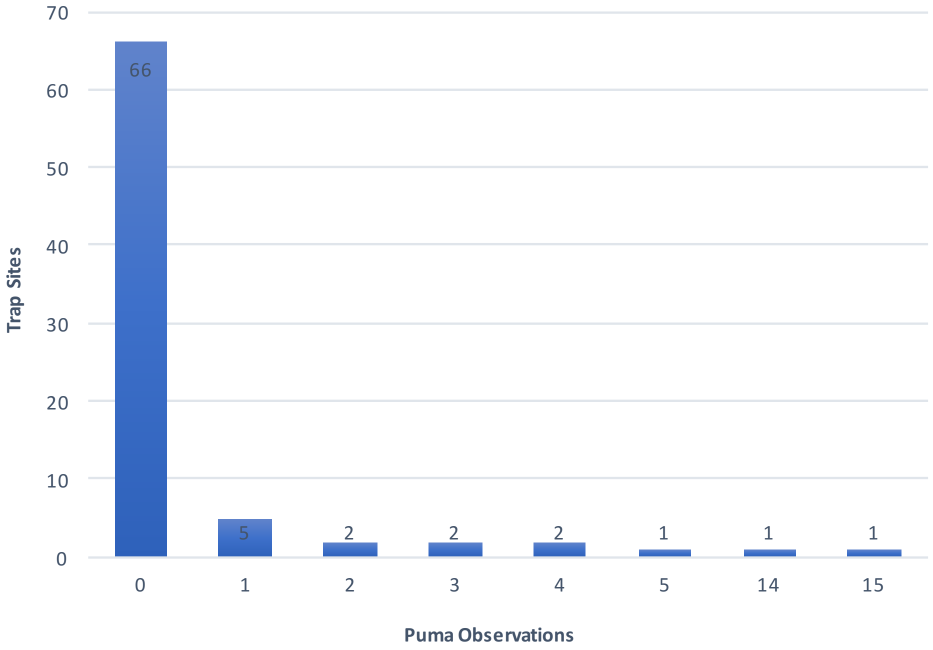

Figure 3. 2 Total puma observations by camera trap sites (n=80) in the Nudo del Azuay from 2012-14. Sixty-six trap sites had zero puma observations.

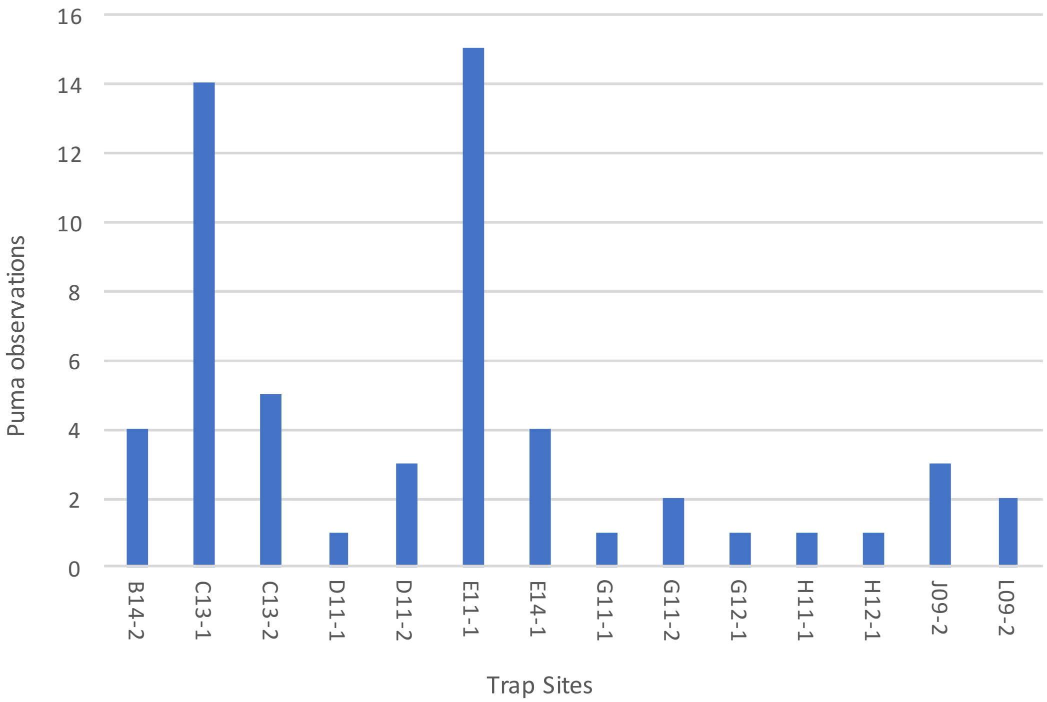

Figure 3. 3 Puma observations by trap site from 2012-14 in the Nudo del Azuay, Ecuador.

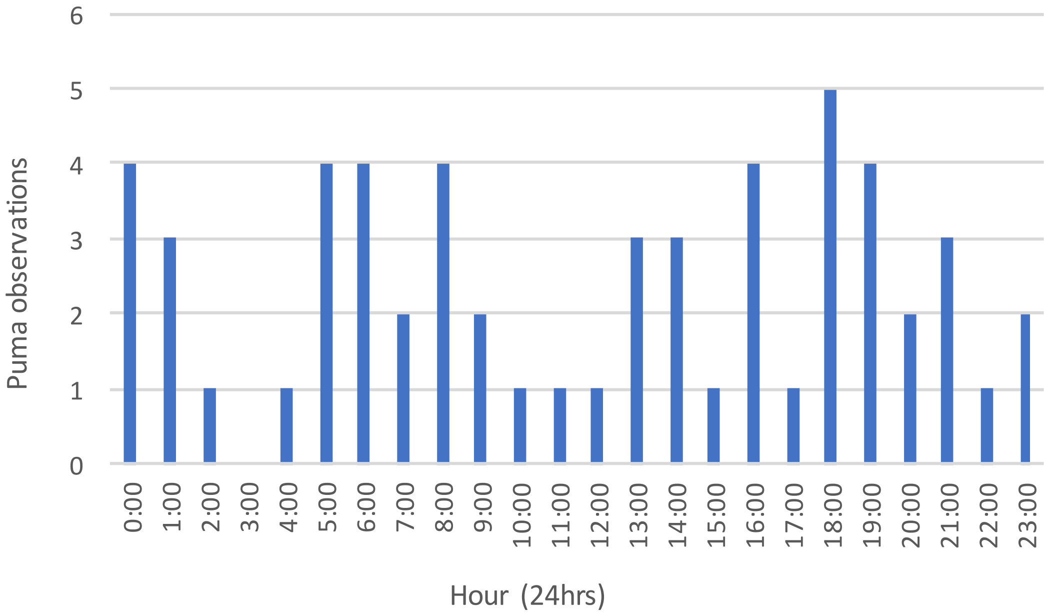

Figure 3. 4 Frequency distribution of puma observations (24-hours) by camera traps in the Nudo del Azuay from 2012-14 (n=57).

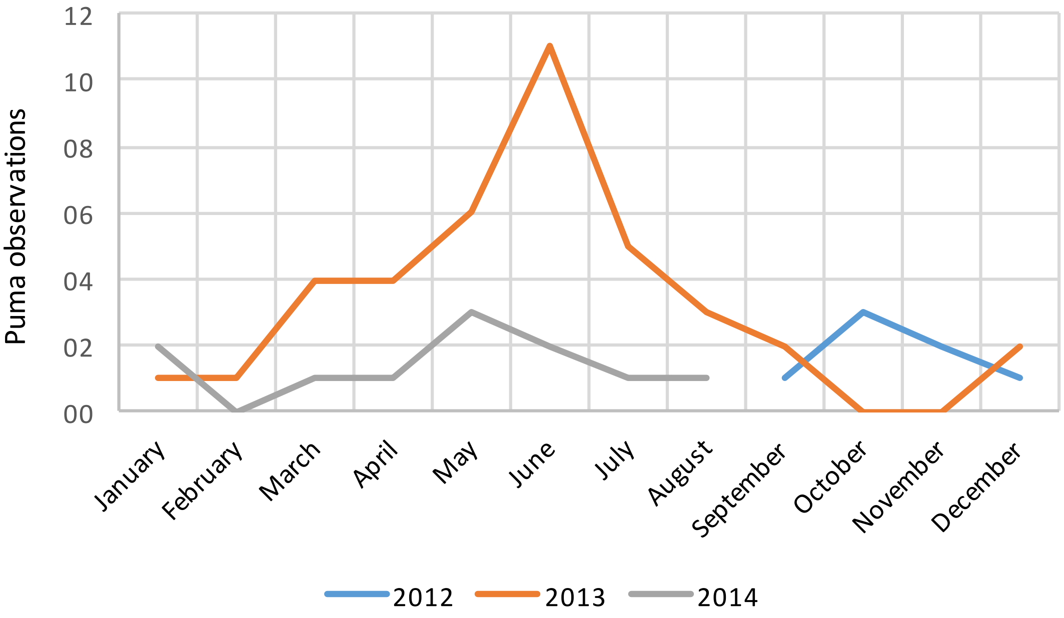

Figure 3. 5 Frequency distribution (n= 57) of puma observations by month for 2012, 2013, 2014 in the Nudo del Azuay, Ecuador.

Table 3. 1 Results of Chi-square test of puma observations from 2012-14 camera trap study in the Nudo del Azuay, Ecuador. We failed to reject the null for all variables ($p < 0.05$).

			Pearson's Chi-square		Fisher's Exact Test		
		p-value	X^2	df	θ	2.5 % CI	97.5 % CI
	habitat*	1			0.80	0.16	3.19
Distance to:	paramo	0.16	1.9845	1			
	forest with trees	0.73			1.91	0.36	19.33
	shrubby forest	0.43			0.58	0.12	3.88
	pasture	0.10			0.17	0.00	1.26

*forested or shrubby

Discussion

Pumas are common in the Nudo del Azuay and attack and kill domestic animals including alpacas, llamas, sheep, and young horses. Using our camera trap data, we were able to make observations about puma movement, behavior, health, and prey species. We determined that it was likely that the depredations occurred because of easy-to-kill livestock rather than an injured puma unable to hunt wild prey, a lack of prey species, or a resident population of pumas that will always attack and kill livestock. Below we explain how we came to these conclusions, how landowners might prevent future puma depredations, and make management recommendations.

For the depredation event in 2013, our camera trap data supports the theory of a problem animal that encountered and began hunting alpacas. First, we do not believe that the puma responsible for the depredations in 2013 was sick or injured, often a trigger for animals that start to hunt livestock (Hoogesteijn & Hoogesteijn 2014). The pumas we saw in camera trap photos appeared healthy (except on one occasion) and in fact the male puma that was captured and relocated was in good condition. It is unlikely that the male in the photos was different from the male that was relocated, although we were not able to find any distinguishing marks in camera trap photos to compare to the trapped puma. Male pumas have territories they defend and will fight-off other males when trying to mate with a female (Logan & Sweanor 2010). Given this information, it is not likely that two males were in the same area during these depredation events.

Second, depletion of prey species is another cause for pumas to switch to livestock (Hoogesteijn & Hoogesteijn 2014). Our photos showed that prey species were present, especially little red brocket deer and mountain paca. Further support for a substantial prey base is the presence of a female puma with cubs observed on several occasions. Females need to kill deer-sized prey every four days to feed older cubs (Ackerman 1982; Logan & Sweanor 2010). If the prey base in the area was depleted, the female would have either left the area or the cubs would have died. We saw cubs in camera trap photos until June 2014. Another alternative was that the female would could have also started killing livestock but both pumas involved in the depredation events were male.

Finally, it is more likely that the alpacas were easy to catch so a puma would not need to develop specialized behavior. Alpacas lack the natural anti-predator defenses of their ancestors and when they are near forested areas are probably seen as easy prey (Linnell et al. 1999). Furthermore, camera trap photos continued to show a resident population of pumas the entire time there were no depredations. This supports the theories that individuals within a species might kill livestock at a disproportionate rate or that the problem puma was a dispersing male that encountered alpacas (*Ibid.*).

These events show how difficult it can be to protect livestock from pumas. Pumas are thought to be mostly nocturnal but are known to adjust their activity period based on prey availability (Nowell & Jackson 1996; Foster et al. 2013). Indeed, the landowner in our study area reported that the puma switched to killing alpacas during the day in the open pasture after the night corrals had been secured. Our camera trap photos show pumas active both day and night and an increase in monthly puma activity coinciding in 2013 with an increase in alpaca depredation.

These changes in behavior reflect how adaptable pumas can be and that night corrals alone might not be sufficient to protect livestock. Landowners will need to protect their livestock during daylight hours as well but these options can be costly and frequently beyond the means of many rural landowners.

Once an individual puma successfully hunts livestock, it is unlikely to stop and the targeted removal of the problem animal could be necessary. Indeed, this appeared to be the outcome of both events: in 2013, the problem puma was fairly easily captured and relocated and depredation stopped for nearly 15 months; and in 2015 after the likely problem puma was found dead, depredations stopped for at least two years.

It is notable that the conservation-minded reserve owner accepted puma depredation as part of his operating costs, and invested time and expense to live trap the problem animal. He estimated that based on five categories of costs (value of alpacas killed, initial corral construction, periodic movement of night corrals, mortality and lowered production resulting from night corral use, and additional labor costs associated with the night corrals) he was spending $12,800/year to protect the alpaca herd from night depredation, representing 42% of total production costs. For typical livestock owners in rural Ecuador, this expense greatly exceeds their annual income.

Puma behavior in camera trap photos

In addition to helping us to understand alpaca depredation, the photos revealed noteworthy puma behavior. On several occasions, we observed pumas marking the trail with urine or scraping. It is common for males to mark their territory this way, alerting other pumas in the area of their presence. We observed two adult pumas together in May and June of 2013, indicating a breeding pair. Adult pumas typically do not socialize unless at time of plentiful food or to breed (Elbroch & Quigley 2017). Cubs leave the den around 6 weeks old and have black spots which begin to fade at five months, eventually fading completely (Logan & Sweanor 2010). These details are consistent with what we observed in our camera trap photos. Repeated sightings of this family group also indicate that this area forms some part of the female's home range. Based on this information we conclude that there is a breeding population of pumas in the study area which includes the territory of at least one male and the home range of one female. The presence of cubs means that sometime in 2015, these three cubs dispersed looking for a territory of their own. Livestock without protection could mean an easy meal for young pumas.

Also, on two occasions we photo-captured an adult puma with a female and cubs. This could have been the father of the cubs or an unrelated male. Male pumas maximize fitness by killing the cubs of other males thus causing the female to go into estrus. But occasionally, female pumas with cubs are seen with males who are not the father. The theory behind this behavior is that these interactions will reinforce male-female pair bonds and confuse paternity, thus protecting her cubs and herself from the male (Logan & Sweanor 2010).

Management Recommendations

Based on what we learned from our camera trap data and the puma-livestock conflicts, we make the following management recommendations.

1. *Prevent puma-livestock conflicts instead of responding to depredations.* The events in this case study demonstrate how difficult it is for livestock owners to find solutions to conflicts with pumas. Research shows that extirpation of the problem species from an

area can result in an increase in depredation as dispersing individuals who are inexperienced hunters occupy the newly vacant territories and target easy prey (e.g. livestock). Unsuccessful attempts to kill predators can also create problem animals by only injuring, not killing, individuals that then become "cattle killers" (Ruth & Murphy 2010). Using husbandry techniques such as fencing to prevent livestock from accessing the forest, maintaining short birthing seasons, and protecting birthing and young livestock in fenced and guarded areas has proven to be more successful (Palmeira et al. 2008; Hoogesteijn & Hoogesteijn 2014). In our study area, well-secured night corrals and daytime protection of livestock could reduce depredation.

2. *Outside support for landowners to prevent conflicts and resolve problems.* Landowners in this region do not necessarily have support when pumas and other predators attack their livestock. In the case of landowner in the reserve, the local authorities did not provide support to monitor, trap, or relocate the problem animal. Instead, the landowner assumed the responsibility to capture and relocate the animal on his own after he was given permission to do so. His interest in a non-lethal solution to problem wildlife is an exception. In many cases, livestock owners respond lethally to depredations rather than incurring the cost and effort of capturing and relocating a problem animal. A lethal outcome is a far more common solution than a non-lethal one. Landowners, local authorities, and conservation allies could develop a participatory plan for immediate response to wildlife conflicts (Treves et al 2006). Successful participatory planning encourages participants to think of opportunities and responses that might not have been considered in isolation, and collaboration is expected to lead to improved conservation

outcomes (*ibid*.). Improved communication between landowners, authorities, and conservation allies would allow landowners to communicate threats to local partners, and to seek information and support.

3. *Focused research on pumas in the Ecuadorian Andes.* Puma management and conservation efforts in Ecuador and throughout the Andes would greatly benefit from puma-focused research. Pumas can be difficult to study because they use large areas, occur at low densities compared to other vertebrates, and it can be difficult to consistently monitor all individuals in the entire population (Pacheco et al. 2004). Although we were able to get collect some data on pumas in our study area, our sample size was too small to collect meaningful data on puma ecology. We make the following recommendations for future studies:

- Research area size: Male territories can overlap several female home ranges (females are not territorial) but in North America, male pumas have had ranges from 150 km^2 to 700 km^2, or typically 1 ½ to 3 times the size of the home range of a female puma (Logan & Sweanor 2010). Studies in Latin America indicate range size is significantly smaller but if the ratio is at all similar, our study area of 40 km^2 could have been a small section of a male's territory and the home range of one female. We observed at least one male puma and one female puma. Future studies in the Andes need to significantly expand the study area to increase sample size.
- Prey species and habitat use: The pumas in our study area were photo-captured more in the wet season and in forested habitat (vs. shrubby). Southern pumas

were observed to have larger home range in the wet season for both males (male, 90 km^2) and females (60 km^2) (Laundré & Hernández 2010; Núñez-Pérez 2011). This pattern also matches most species we observed in camera traps. Puma-prey interactions are complicated and greatly influenced by environment and humans (Ruth & Murphy 2010) making the interpretation of these results difficult without more data on prey species.

- Puma-focused studies: Our small sample size could also be because our study is inherently biased toward Andean bears. We selected camera trap sites with bear sign; pumas and Andean bears might be avoiding each other through spatial segregation although there is not yet decisive evidence to support this claim (Springer et al. 2017). North American black bears (*Ursus americanus*) are known to scavenge puma prey when there is dietary overlap (e.g. *Odocoileus virginianus*) (Ruth & Murphy 2010). Andean bears will scavenge carcasses (García-Rangel 2012) but in Latin America, the only large predator in competition with pumas is the jaguar (Laundré & Hernández 2010). These two big cats overlap in dietary preferences (large and medium mammals) and ranges but the jaguar is not present in the Andean ecosystem. During our study period, we found bears and pumas to be active at the same time of day (daylight hours) and at the same trap sites within a few days of each other. On only one occasions did we see a bear and a puma at the same site within 24 hours of each other. There were several sites where we observed pumas but no bears (n=4) and many sites where we observed bears and no pumas (n=18). This is not evidence that the two species are or are not avoiding each other because trail use, human activity, and food availability play key roles in the movement of both species. Future puma studies should focus only on pumas to remove potential bias.

Puma-livestock conflict in the Nudo del Azuay will continue and will likely increase as the agricultural frontier advances into puma habitat. The cost of non-lethal interventions is beyond the budgets of many rural landowners. As such, landowners without outside support will handle problem animals according to their value system and ability to tolerate loss. If local authorities want to protect wildlife, they will need to develop interventions and support landowners in non-lethal mitigation of conflicts with pumas.

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Conclusion

The goal of this research and dissertation was to examine the role of private lands in wildlife conservation in the Ecuadorian Andes. In Chapter 1, our results indicated that Andean bears were slightly disturbed by human activities but that habitat and access to annual changes in resources might be more important when planning for bear conservation on private lands. In Chapter 2, we interpreted depredation events through our camera trap data and laid the foundation for future research on pumas. In Chapter 3, we determined Andean bears can be strong conservation surrogates for Andean mammals but only if forested habitat is also conserved. Collectively, our results demonstrate that private lands play an important role in the conservation of wildlife in the Ecuadorian Andes. In areas with low levels of conflict and human-caused mortality, private lands can support populations of the two largest carnivores in the ecosystem, Andean bears and pumas. Conservation planning must include habitat protection and find alternatives to deforestation. Landowners who experience conflicts with wildlife, especially large predators, need support from local authorities to prevent private lands from becoming mortality sinks. Conservation planning for wildlife on private lands must be multifaceted, prioritizing wildlife, habitat, and landowners.

Appendices

Appendix 1. 1 Reinterpretation of land cover classes based on a 2010 RapidEye Image of the Nudo del Azuay region (PROMAS, Universidad de Cuenca, Ing. Bastiaan Stoop).

Original Layer Name	**Reinterpretation**	**Comments**
Burned areas *Quemas*		
Cultivated lands *Tierras cultivadas*	Rural areas with high levels of human use	• occur near towns, agriculture, and pastures
Culture site *Rasgos Culturales*		
Eroded land (natural), plowed or eroded *Tierras eriales, Arenales (arado o erosionada)*	Eroded Land	• occur near cultivated land and pastures; associated with human activity
Eroded land (natural), rocky outcrops *Tierras eriales, Afloramientos rocosos*	Rocky Outcrops	• occur near cultivated land and pastures; associated with human activity
Land with forest, trees *Tierras con bosques Arbóreos*	High-quality habitat for bears	
Land with forest, shrubs *Tierras con bosques Arbustivos*	Shrubby forest	• occur around the edge of high-quality forest
Land with natural forest in the process of degradation *Tierras con bosque naturales en proceso degradativo*	Low-quality habitat for bears	• typically occurred far from high-quality habitat
Land with pastures in good condition *Tierras con pastos cultivados en buenas condiciones* Land with pastures in the process of degradation *Tierras con pastos cultivados, proceso degradativo*	Pastures	• combined pasture categories, the difference was in soil type which was not relevant to our study
Páramo *Tierras de páramo*	Páramo	
Water *Cuerpos del agua*	Rivers (2nd & 3rd order)	• does not include small streams, small lakes, or seasonal water sources

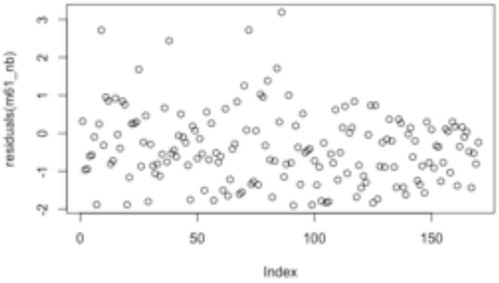
Appendix 1. 2 Details of landowner characteristics by covariate type for negative binomial analysis of 2012-14 camera trap data from the Nudo del Azuay, Ecuador.

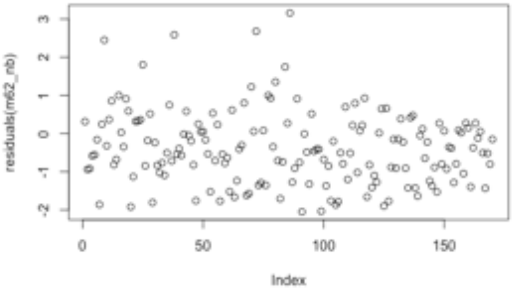
Active participation in conservation on own property	Property size	Owner lives on/off property
yes = 5 (31%) no = 11 (69%)	0-50 ha = 4 (25%) 50-150 ha = 8 (50%) >150ha = 4 (25%)	on = 9 (56%) off = 7 (44%)

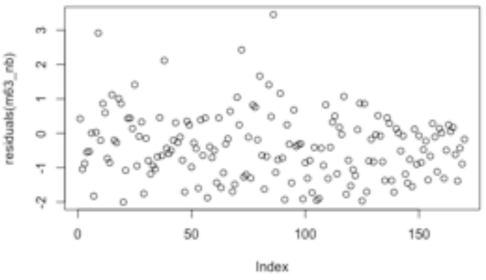
Appendix 1. 3 Bear 5/F (also identified in 2008 and 2009) with cub in 2014 at site E11 in Nudo del Azuay, Ecuador.

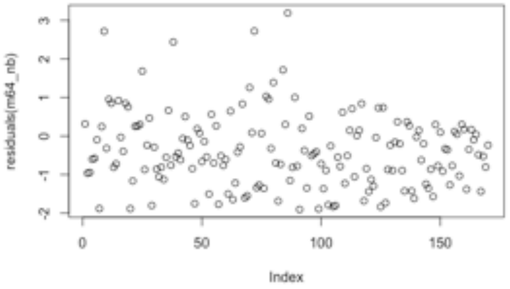
Appendix 2. 1 Negative binomial regression residuals for all wildlife categories used in the analysis of 2012-14 camera trap data from the Nudo del Azuay, Ecuador.

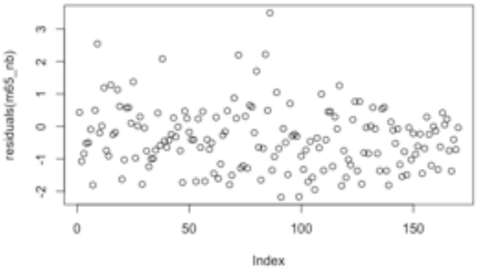
All species

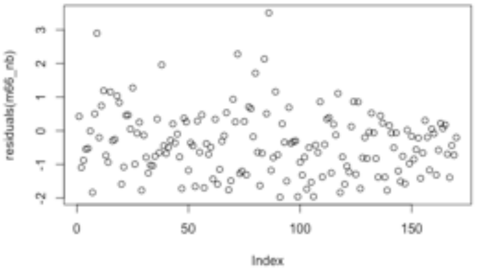


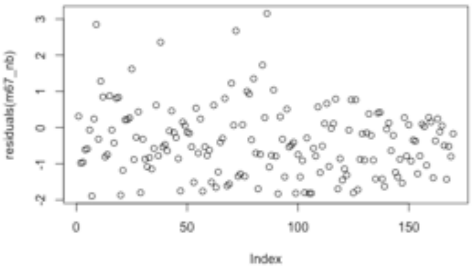


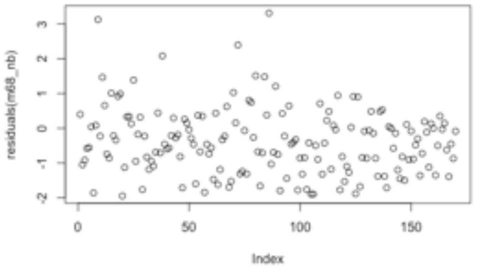




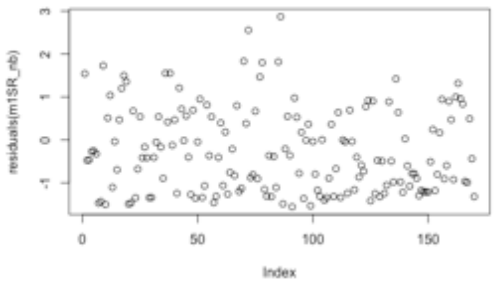


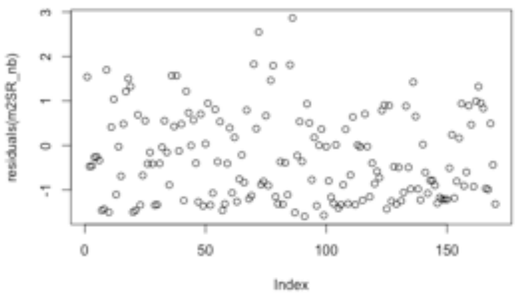


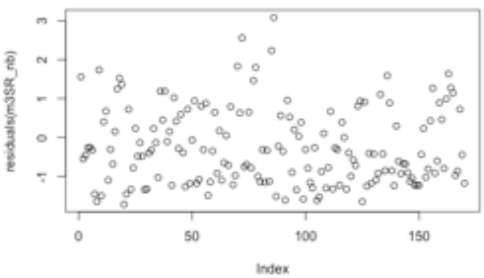


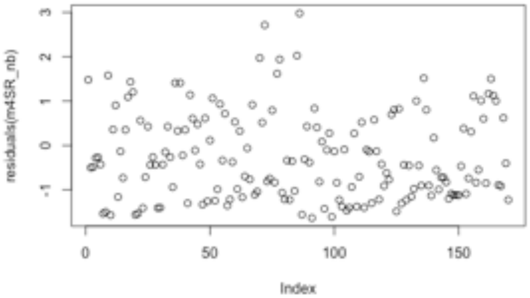


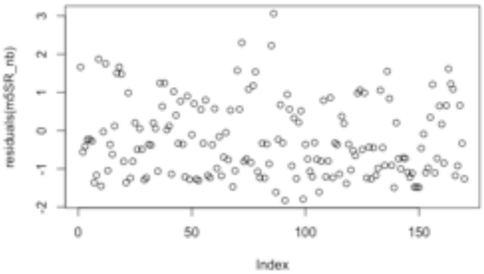
Carnivore species

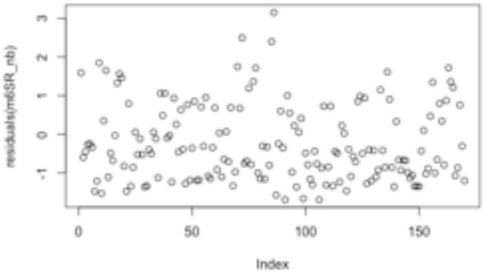


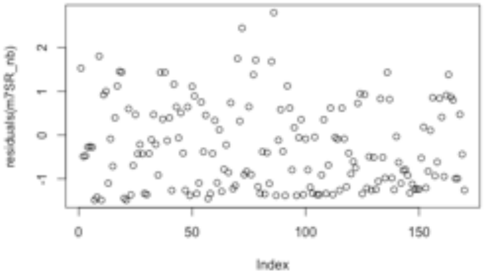


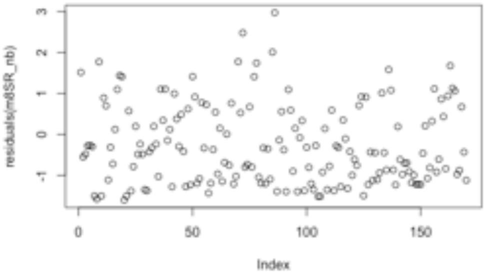




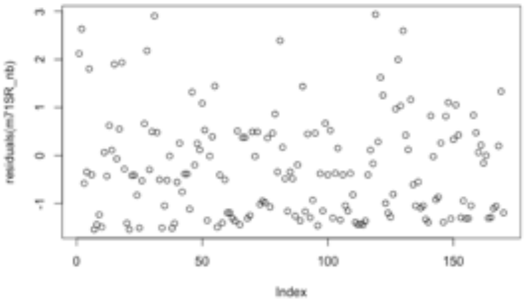


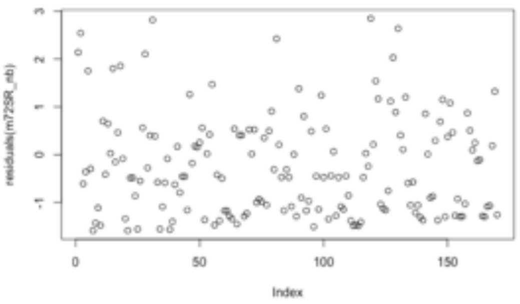


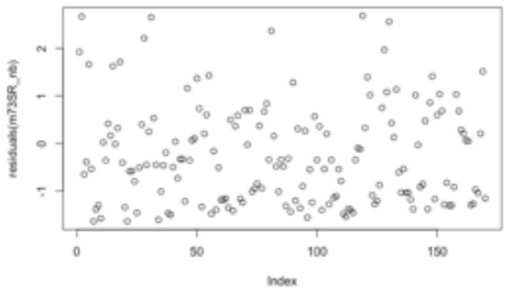


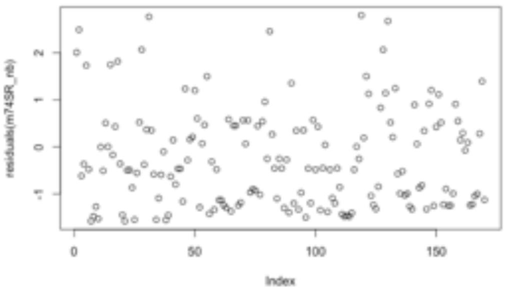


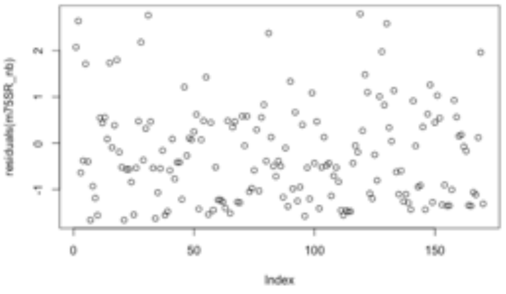
Globally at-risk species

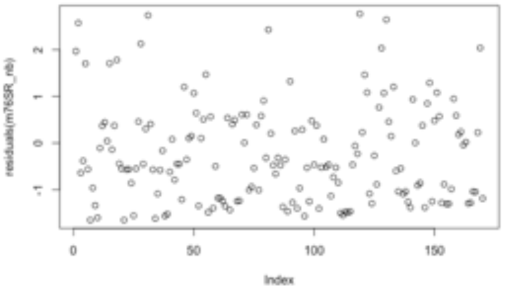


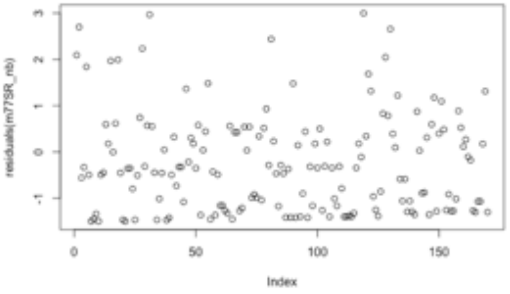


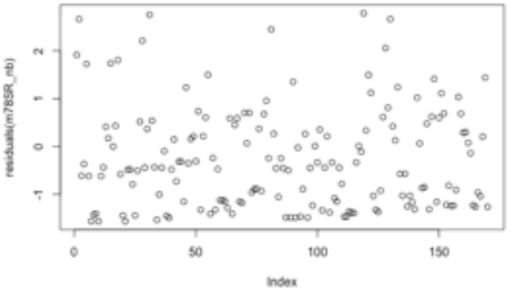




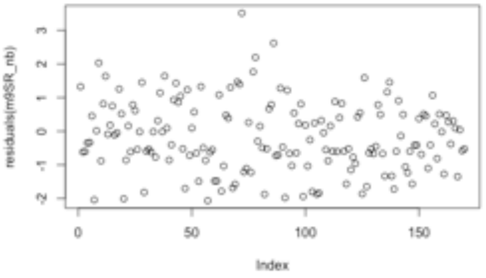


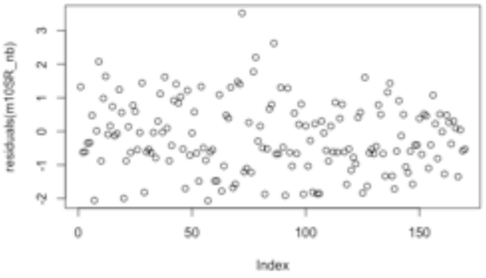


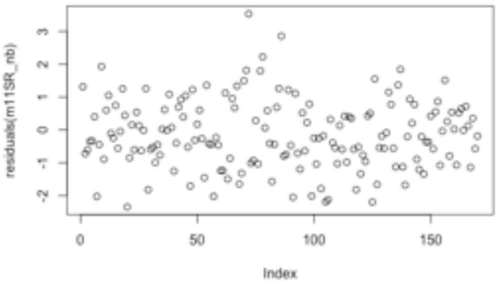


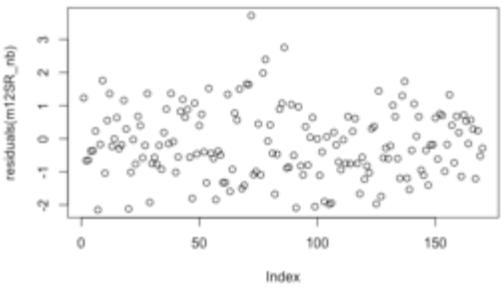


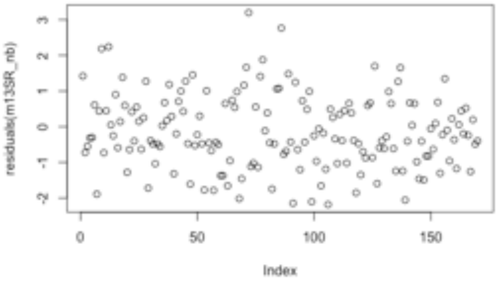
Locally at-risk species

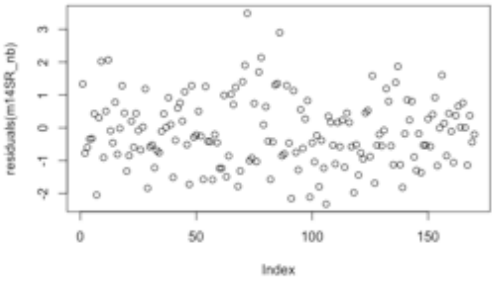


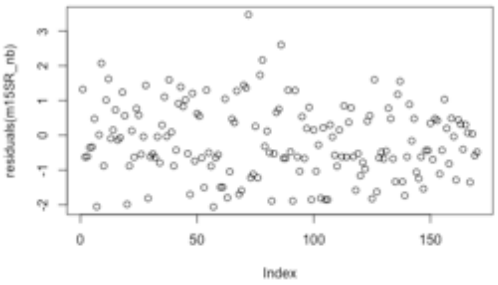


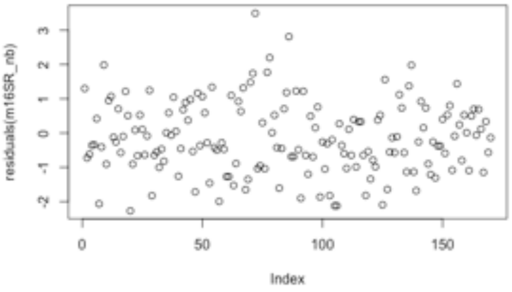




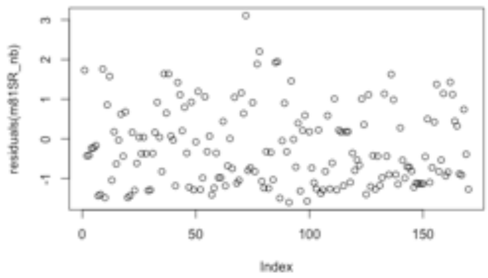


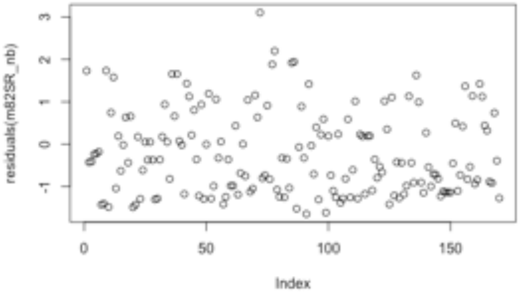


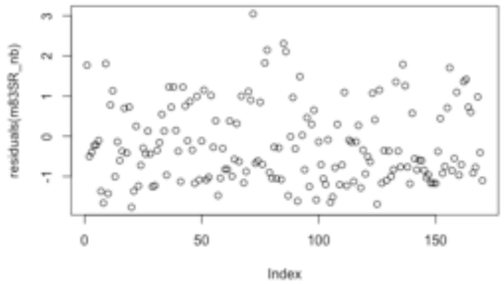


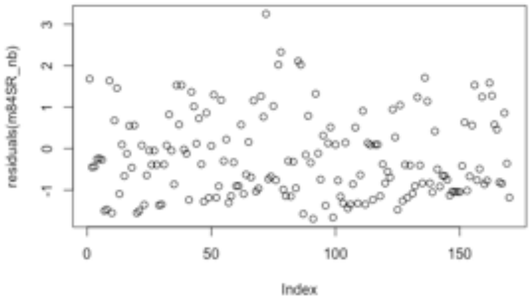


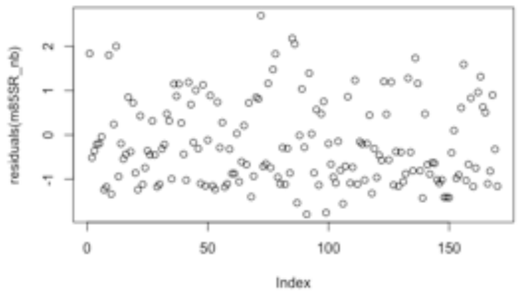
Locally at-risk carnivore species

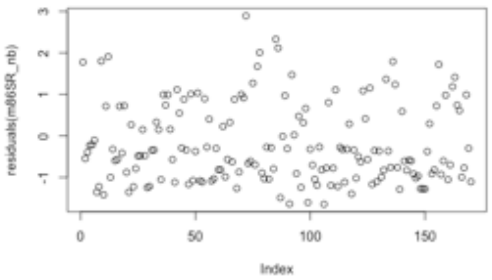


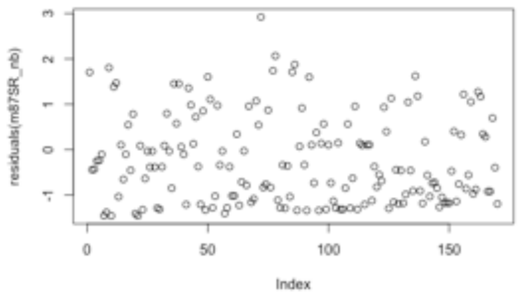


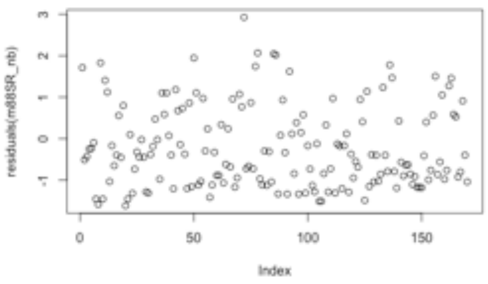












Appendix 3. 1 Two different pumas photo-captured in 2013 in the Nudo del Azuay, Ecuador, at the same camera trap station (E11-1) within ~24 hours of each other. The photos series from both observations clearly showed the differences in individual size and color.

Appendix 3. 2 Three examples of pumas traveling together at different trap sites during the 2012-14 camera trap study in the Nudo del Azuay, Ecuador: (1) two pumas on a trail at site B14-2 on June 6, 2013 @ 7:23 PM, (2) two pumas and a cub (seen later in photo 5/5) together at site D11-2 on June 15, 2014 at 8:21 PM, and (3) four pumas (two larger and two cubs) at site D11-2 on May 14, 2014 at 6:46 PM.

(1)

(2)

(3)

Appendix 3. 3 Alpaca carcass after puma depredation in December 2014 in the Nudo del Azuay, Ecuador. Pumas kill prey by holding the animal by the throat to cut off oxygen.