Altered Activity Patterns and Reduced Abundance of Native Mammals in Sites with Feral Dogs in the High Andes

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Abstract

Negative impacts of some introduced carnivores like feral cats are well documented, widespread, and significant. Comparatively, effects of feral dogs (individuals that are not associated with people or human settlements) on native wildlife are poorly known, even though feral dogs occur worldwide. We assessed density of feral dogs and compared relative abundance, activity patterns and habitat use of 10 species of mammals in areas with and without feral dogs in Cayambe-Coca National Park in northern Ecuadorian Andes using line transect surveys, camera traps, and track and sign surveys. In areas where feral dogs were present, four native mammals were absent: mountain coati (*Nasuella olivacea*), mountain paca (*Cuniculus taczanowskii*), long-tailed weasel (*Mustela frenata*), and northern pudu (*Pudu mephistophiles*). Relative abundances of six species were lower compared to areas without feral dogs: puma (*Puma concolor*), Andean fox (*Lycalopex culpaeus*), Andean bear (*Tremarctos ornatus*), striped hog-nosed skunk (*Conepatus semistriatus*), mountain tapir (*Tapirus pinchaque*), and little red brocket deer (*Mazama rufina*). Three species significantly altered activity patterns where feral dogs were present (Andean bear, mountain tapir, and little red brocket deer). In contrast, none of the native mammal species exhibited shifts in habitat use in areas with feral dogs. Dogs used all habitat types according to availability. Our results point to feral dogs as a significant problem for the native mammal community of this Andean region, and highlight the need to consider feral dogs as a potential threat to wildlife in other regions where anthropogenic effects appear to be low but feral dogs are present, particularly natural areas that contain endangered and endemic species.

Keywords: Invasive species, large mammal, relative abundance, activity pattern, habitat use, Tropical Andes.

1. Introduction

Domestic dogs (*Canis lupus familiaris*) and cats (*Felis silvestris catus*) are the most widespread introduced carnivore species. Although the vast majority of cats and dogs are owned as pets, a large percentage of them range freely and many have become feral (i.e., individuals completely wild and independent of human sources of food; Campos et al. 2007; Hughes and Macdonald 2013; Vanak et al. 2014). Negative impacts of feral cats, including their role in species extirpations and extinctions, are well documented (Nogales et al. 2004; Medina et al. 2011). Comparatively, little is known about the global distribution, population size, and ecological impacts of feral dogs. Most information about impacts of dogs comes from populations of free-ranging, owned dogs restricted to urban and periurban areas (e.g., Macdonald and Thom 2001; Silva-Rodríguez et al. 2009; Young et al. 2011). However, feral dog populations have been reported worldwide, and in many localities where native predators have been extirpated or are absent, they function as apex predators (Allen et al. 2013; Vanak and Gompper 2009; Vanak et al. 2014).

Large predators have an important ecological role in structuring food webs and maintaining ecological processes that impact entire ecosystems (Estes et al. 2011; Terborgh et al. 2001). This structuring role occurs through lethal (e.g., predation) and non-lethal (e.g., fear) interactions (Lima 1998; Luttbeg and Kerby 2005; Paine 1966). Large predators alter density of prey by removing individuals, and the presence of predators also results in changes in behavior to reduce risk. Fear induced by predators may reduce fitness of prey by altering their activity patterns and habitat use, increasing vigilance time, reducing foraging time, and lowering mating success (Creel and Christianson 2008; Preisser et al. 2005). Although lethal and non-lethal impacts have been documented for numerous carnivores, until recently studies of introduced predators focused on lethal effects (Gerber et al. 2012; Hughes and Macdonald 2013; Silva-Rodríguez et al. 2010; Vanak et al. 2014).

Although the Ecuadorian Andes have long been occupied by people and threats to biodiversity such as habitat loss and fragmentation are widely recognized and well documented, threats posed by introduction of exotic animal species have been overlooked until recently (Hofstede et al. 2002; Sarmiento 2002; Olmedo and Montoya 2011). Free-ranging and feral dogs have become a problem for conservation, animal welfare, and public health in vast areas of the Ecuadorian highlands, as a result of human population growth, poor waste management practices, absence of responsible dog ownership, and low awareness of zoonotic disease issues (Olmedo and Montoya 2011). The current geographical distribution of feral dogs in the Ecuadorian Andes is unknown; but, free-ranging and feral dogs are believed to be widely distributed along the Ecuadorian Andes, including areas that otherwise would be considered pristine. Feral dogs are the largest mammalian predator in several protected areas (Olmedo and Montoya 2011). However, feral dogs differ from most native predators because they usually occur in relatively high population densities and form packs that can kill large prey (Vanak and Gompper 2009; Vanak et al. 2014).

Our objective was to identify potential effects of feral dogs on the abundance and behavior of native mammals of the high Andes in northern Ecuador. By focusing on feral dogs, rather than the more well studied free-ranging dogs, we address an important gap in understanding interactions between this pervasive introduced predator and wildlife. We carried

out our work in Cayambe-Coca National Park, the second largest protected area in the Ecuadorian Andes because this area is relatively free of other anthropogenic disturbance and has areas where dogs are present and absent that are ecologically similar in other respects. Of the 16 large mammal species (>1 kg) recorded in the study area, eight are endemic to the Tropical Andes (Tirira 2007). Seven species are categorized as endangered, vulnerable, or near threatened, and two species are data deficient in the IUCN Red List of Threatened Species (IUCN 2015). We predicted that abundance of native mammals in areas with feral dogs would be lower than in areas without feral dogs, and that native mammals would show differences in their diel activity patterns and habitat use between areas with and without feral dogs to avoid encountering them. An understanding of the interactions between feral dogs and the unique fauna of the Tropical Andes is crucial for design of conservation and management interventions for this region and will highlight potential challenges for conservation of biodiversity in other areas where feral dog populations have been established.

2. Methods

2.1. Study area

We conducted fieldwork in páramo highlands of Cayambe-Coca National Park (~4,000 km^2), which straddles the north-south oriented eastern cordillera of the northern Ecuadorian Andes. Páramo is a mosaic comprising high altitudinal grasslands (grass páramo) interspersed with patches of shrub páramo, cushion páramo, and Andean forests (Baquero et al. 2004). The ensemble of large mammal species (>1 kg) in páramo of Cayambe-Coca National Park is representative of the high altitude fauna of the Tropical Andes (Table 1), which is probably the least known group of large mammals in the Neotropics (Tirira 2007). Climate is highly aseasonal (average annual precipitation, approximately 2,500 mm with more than 250 rainy days; average monthly temperatures, 4 to 10 °C; Josse et al. 2011).

Our study area encompassed approximately 25 x 75 km in the core of the park (extending from 00°31'N to 00°28'S and 77°39'W to 78°06'W) with altitude ranging from 3,400 to 3,900 m. The study area was located on a plateau covered entirely by native páramo vegetation and divided by a deep gorge (Huataringo River). Soils, topography, and vegetation are similar north and south of the river (Baquero et al. 2004; Fundación Antisana 1998), and hunting is prohibited throughout the park. Law enforcement in the area is high because the main water supply for Quito, the capital city of Ecuador, comes from glacial lakes in the park. Park rangers of the Ecuadorian Ministry of the Environment and staff of the water utility company control human access to the area. Dogs are known to occur only south of the river providing the opportunity for a comparative design to examine relative abundance and behavior of native mammals in areas with and without dogs but similar in other respects. We consider these dogs to be feral because: 1) the closest human settlement to the study area is more than 50 km away, 2) dogs showed avoidance and aggression towards people, and 3) dogs were in good body condition compared to free-ranging dogs associated with human settlements. To verify that illegal hunting did not occur in the study area, we searched for signs of hunting (e.g., remains of ammunition, traps, etc.) while walking transects to collect data on dog abundance

and setting camera traps for mammals, and we looked for evidence of hunters in photographs from camera traps. We detected no evidence of hunting in the study area.

2.2. Survey methods for dogs and native mammals

From October 2010 to July 2011, we assessed abundance, habitat use, and activity patterns of native mammals and feral dogs in three randomly located sites in the area with dogs and in three sites in the area without dogs. Sites (each 100 km^2) were separated by a minimum of 10 km, and thus were spatially independent except for species with the largest home ranges (puma and Andean bear). Habitat was distributed similarly among the four types in sites with and without dogs [Mean percent of site $\pm$ SD, grassland: 54.5$\pm$7.5 (dog), 55.6$\pm$5.1 (no dog); shrub páramo: 18.5$\pm$4.4 (dog), 15.5$\pm$5.9 (no dog); cushion páramo: 4.3$\pm$2.2 (dog); 4.9$\pm$2.1 (no dog); Andean forest: 22.7$\pm$6.6 (dog), 24.0$\pm$2.7 (no dog); data from Ministerio del Ambiente, 2012]. Also, habitat at sample locations followed the same pattern. The proportion of cameras and transects in each habitat type was similar for areas with and without dogs (see below and Appendix A1). To verify our assumption about the presence or absence of dogs in the sites and evaluate dog density, we established six four-km transects in each of the six survey sites in grass páramo. Transects were surveyed between 06:00 – 10:00 hrs at weekly intervals for four weeks. We walked transects slowly (~1 km/h), and recorded dogs sighted, sighting (radial) distance, sighting angle, and location along the transect. When dogs were observed in groups, estimation of distance to the geometric center was difficult, so perpendicular distance to all individuals detected was recorded, and existence of the group was ignored (Buckland et al. 2010; Thomas et al. 2010).

All native mammal species > 1kg body mass and dogs were surveyed with camera traps and transect surveys for tracks and sign. Each of the six survey sites was subdivided in a grid with 25 cells each 4 km^2. Three camera traps (Bushnell Trail Sentry STD) were placed randomly in each cell at least 1 km apart for eight consecutive days, for a total of 600 trap-nights per site. Cameras were not on trails or roads. We conducted track and sign surveys at each site along five parallel transects (12 km each) that crossed all 25 4-km^2 cells. Because vegetation was open, we were able to walk transects without using pre-existing trails or cutting trails for transects. Tracks and other signs were counted within a 2-m strip centered on the transect. Characteristics of the soil (Cryandepts from volcanic ash; Fundación Antisana 1998) were similar in the six survey sites and on all transects. Thus, we assumed that differences in occurrence of tracks depended only on mammal abundance. Each transect was surveyed four times during a six-week period for tracks and signs (scats and diggings) of all species (Table 1). Each time we found a track or sign, we recorded the species and place along the transect where the track or sign was found. Independence of tracks was established based on the following (Carrillo et al. 2000): 1) tracks of an animal crossing the transect were considered as one sighting, 2) tracks of an animal walking parallel to the transect were considered as one sighting, and 3) groups of tracks of gregarious species (e.g., mountain coatis) were considered as one sighting. Scats also were identified easily for Andean foxes, mountain tapir, and Andean bears, and we considered all sightings of scats as independent observations. Mountain coatis were detected by their characteristic digging of numerous small holes (e.g., over an area of 3-5 m^2). Other species such as skunks that dig holes typically make only one or two small holes at a location. Each set of

coati diggings was considered an independent observation of coatis because diggings were far apart (mean distance between diggings, 2.3 +_ 0.39 km SD). Coatis are social and, thus, an observation represented a group rather than an individual.

2.3. Data analysis

Population densities of feral dogs were estimated independently for the six survey sites using transect data and DISTANCE 6.0 (Buckland et al. 2001; Thomas et al. 2010). The detection function was derived from data from all sites to improve estimation. Population densities were estimated by applying uniform and half-normal key functions, and cosine or simple polynomial adjustment terms as needed (Buckland et al. 2001; Thomas et al. 2010).

To evaluate abundance of native mammals in areas with and without dogs, we estimated a relative abundance index for each species at each sampling site based on photographic rates in camera traps (number of independent pictures/100 trap-nights; Kelly 2008; O'Brien et al. 2003) and, for track and sign data, we used an index based on encounter rates along transects (number of independent tracks or signs recorded for each species/10 km of sampling effort; Carrillo et al. 2000; Reyna-Hurtado and Tanner 2005). Relative abundance indices were used only for intraspecific comparisons because detectability with camera traps and animal signs varies among species. We compared relative abundance indices between areas with and without dogs using a one-factor analysis of variance with the three sites as replicates. Prior to ANOVA, data were tested for normality and homogeneity of variances with Shapiro-Wilk and Cochran's C tests respectively (Doncaster and Davey 2007).

We used nonparametric circular Mardia-Watson-Wheeler tests to evaluate whether diel activity patterns of native mammals differed between areas with and without feral dogs (Di Bitetti et al. 2009; Gerber et al. 2012). This analysis was restricted to species with ≥30 independent photographic events in areas with and without dogs. We considered the following photographic events as independent (O'Brien et al. 2003): 1) consecutive photos of individuals of the same species taken at least 30 minutes apart, 2) nonconsecutive photos of individuals of the same species, and 3) consecutive photos of different individuals of the same species where identification of individuals was possible. Data were pooled by hourly intervals across survey sites with dogs and across sites without dogs. Analyses were performed with Oriana 4.0 (Kovach Computing Services 2012).

If dogs affect habitat use of native mammals, we expected to see shifts in habitat use between areas with and without dogs, including reductions in the use of habitats most often used by dogs. For each species, data from camera traps (number of independent photographs) were stratified by the four vegetation types (grass páramo, shrub páramo, cushion páramo, and Andean forest) for areas with and without dogs and analyzed with X^2 goodness-of-fit tests to evaluate the hypothesis of no difference between proportions of habitat available and used. Habitat use by feral dogs also was evaluated. Also, 90% adjusted Wald confidence intervals ($\hat{w}$) for expected proportions of use were calculated for each habitat type (Agresti 2007). Where the observed proportion (p_{obs}) of use of any given habitat was greater than the expected interval ($p_{exp} \pm \hat{w}$), this habitat was identified as preferred habitat.

3. Results

3.1 Dog density

We recorded 156 observations of feral dogs, equivalent to 0.27 sightings/km, in 576 km of transects in the three sites that were expected to have dogs. In the other sites, we encountered dogs six times with a sampling effort of 587 km, a level of presence considered negligible for our study purposes. Average pack size was 9.8 ± 3.3 individuals (mean ± 95% CI). Dog density in the three dog sites was estimated as 0.89 individuals/km^2 (95% CI = 0.76-1.07), 1.16 ind./km^2 (1.11-1.32 CI), and 1.09 individuals/km^2 (0.99-1.24 CI).

3.2. Abundance of native mammals

Thirteen species of native mammals were recorded in the study area using camera traps, track and sign surveys, or both (Table 1). All species were found at the sites without dogs, but four of the smaller species were absent from areas with dogs. Of these four species, mountain paca and mountain coati were relatively abundant in areas without dogs (Figure 1). Long-tailed weasel and northern pudu were recorded in only a few occasions with camera traps ($n = 6$ and $n = 3$, respectively). Tapiti (*Sylvilagus brasiliensis*) was recorded infrequently with cameras. Although fecal pellets of this rabbit were encountered in dog and no dog sites, signs of individual rabbits could not be distinguished because pellets were broadcasted widely. Therefore, we did not include this species in our analysis. The remaining eight species had sufficient data to compare abundance in areas with and without dogs (minimum number of photographs for a species = 54 per area; minimum number of tracks or signs = 72). The data source (tracks/signs or photographs) that provided the most data for each species was used in the analysis (Figure 1). For six species, relative abundance was significantly higher in areas without dogs: puma ($F_{1, 4} = 28.05$, $p = 0.006$), Andean fox ($F_{1, 4} = 54.19$, $p = 0.002$), Andean bear ($F_{1, 4} = 26.38$, $p = 0.007$), striped hog-nosed skunk ($F_{1, 4} = 28.44$, $p = 0.006$), mountain tapir ($F_{1, 4} = 24.75$, $p = 0.008$), and little red brocket deer ($F_{1, 4} = 42.27$, $p = 0.003$). No significant differences in relative abundance occurred between areas with and without dogs for the Andean white-eared opossum (*Didelphis pernigra*, $F_{1, 4} = 5.28$, $p = 0.08$) and white-tailed deer (*Odocoileus virginianus*, $F_{1, 4} = 5.97$, $p = 0.07$; Figure 1). Data for all species met the required assumptions for analysis of variance (Shapiro-Wilk test for all species: $W \geq 0.95$, $p > 0.05$; Cochran's C test for all species: $C \geq 0.57$, $p > 0.05$).

3.3. Activity Patterns

We obtained more than 30 independent photographic events in dog and no dog areas for seven species of native mammals (Figure 2). Activity patterns of feral dogs were crepuscular with activity concentrated between 05:00 - 09:00 and 16:00 - 20:00 hrs. Three species of mammals showed significant differences in activity patterns between areas with and without dogs (Figure 2): Andean bear ($X^2 = 6.34$, d.f. = 2, $p < 0.05$), mountain tapir ($X^2 = 19.64$, d.f. = 2, $p < 0.001$), and little red brocket deer ($X^2 = 14.94$, d.f. = 2, $p < 0.001$). The Andean bear and little red brocket deer had a bimodal distribution of activity in the absence of dogs, and became

more diurnal when dogs were present. The mountain tapir exhibited activity throughout the day and night in areas with no dogs, and became mostly nocturnal in areas with dogs. The Andean fox tended to be more nocturnal in areas with dogs, but this difference was not statistically significant (X^2 = 4.08, d.f. = 2, p = 0.12). Three species did not change their activity patterns in areas where dogs were present: Andean white-eared opossum (X^2 = 2.76, d.f. = 2, p = 0.26), striped hog-nosed skunk (X^2 = 2.39, d.f. = 2, p = 0.28), and white-tailed deer (X^2 = 4.59, d.f. = 2, p = 0.11; Figure 2).

3.4 Habitat use

Feral dogs used habitat according to availability (X^2 = 6.16, d.f. = 3, p > 0.1), and none of the mammal species included in the analysis shifted their habitat use patterns with the presence of dogs. Four species used habitat according to availability in areas with and without dogs: Andean white-eared opossum, striped hog-nosed skunk, mountain tapir, and little red brocket deer (for all species, dogs: X^2 ≤ 7.01, d.f. = 3, p > 0.1; no dogs: X^2 ≤ 6.85, d.f. = 3, p > 0.1). Three species (Andean fox, Andean bear, and white-tailed deer) preferred grass páramo over other habitat types in areas with and without dogs (for all species, dogs: X^2 ≥ 29.8, d.f. = 3, p < 0.001; no dogs: X^2 ≥ 23.7, d.f. = 3, p < 0.001); Andean fox (dogs: p_{obs} = 0.69, $p_{exp} \pm \hat{w}$ = 0.47 ± 0.18; no dogs: p_{obs} = 0.75, $p_{exp} \pm \hat{w}$ = 0.52 ± 0.19); Andean bear (dogs: p_{obs} = 0.69, $p_{exp} \pm \hat{w}$ = 0.47 ± 0.12; no dogs: p_{obs} = 0.87, $p_{exp} \pm \hat{w}$ = 0.52 ± 0.23); and white-tailed deer (dogs: p_{obs} = 0.71, $p_{exp} \pm \hat{w}$ = 0.47 ± 0.18; no dogs: p_{obs} = 0.85, $p_{exp} \pm \hat{w}$ = 0.52 ± 0.19).

4. Discussion

The threat that feral dogs pose to an entire community of large mammals has not been reported previously, though such impacts potentially are widespread given the global distribution of feral dogs. In our study area, relative abundance and behavior of herbivores, omnivores, and carnivores differ markedly between areas with and without dogs. Because our study was observational rather than experimental, the patterns we observed could be related to environmental factors other than presence of dogs. However, this appears unlikely. First, biophysical characteristics (e.g., vegetation, soils, topography, and rainfall) and protection from human disturbance, including hunting, are similar between areas with and without dogs in our study area (Baquero et al. 2004; Ministerio del Ambiente 2010). In addition, relative abundance and behavioral data were largely congruent for species that we analyzed. Species that shifted activity patterns and reduced overlap with activity patterns of dogs also had reduced abundance where dogs occurred. Density estimates of feral dogs in the study area (~1 individual/km^2) are lower than estimates for free-ranging dogs from other localities worldwide (e.g., 2.5–76.8 individuals/km^2; Campos et al. 2007; Lembo et al. 2008), but because feral dogs form packs, their impacts may be particularly large. The role of feral dogs as predators in natural ecosystems is unlikely to be equivalent to those of native predators in systems where native predators are mainly solitary and occur at low population densities, such as the high Andes.

Two species of conservation concern, the mountain paca and mountain coati, were not detected in areas with feral dogs. We cannot confirm that these species were extirpated by

dogs, but given that the study areas were in a large protected area with little other disturbance, we have no other plausible explanation. In addition, significantly lower relative abundance of six other species (puma, Andean fox, Andean bear, striped hog-nosed skunk, mountain tapir, and little red brocket deer) in areas with feral dogs suggests that robust populations of many native species may persist in the long-term only through control and eradication of this invasive species. In contrast, relative abundances of Andean white-eared opossums and white-tailed deer appear not to be affected by presence of dogs. The mostly arboreal and highly nocturnal behaviors of the opossum (Gardner 2007) may represent effective means for reducing interference and predation from dogs. Several studies carried out in North America concluded that feral dogs do not prey effectively on adult white-tailed deer (e.g., Causey and Cude 1980, Sweeney et al. 1971), but impacts of dogs on fawns of white-tailed deer are unknown. In contrast, lethal attacks of dogs on other smaller species of deer have been documented, including southern pudu (*Pudu pudu*, Silva-Rodríguez and Sieving 2012) and brown brocket deer (*Mazama gouazoubira*, Galetti and Sazima 2006).

With the exception of the Andean bear and mountain tapir, prior to this study little was known about diel activity patterns of mammals from the Tropical Andes (García-Rangel 2012; Lizcano and Cavelier 2000). For at least three native species (Andean bear, mountain tapir, and little red brocket deer), our results support temporal partitioning as a mechanism for decreasing encounters with feral dogs. Also, the Andean fox exhibited little activity during the period when dogs were active in early morning in areas with and without dogs, and nocturnal activity increased slightly in areas with dogs. Our results are congruent with data obtained in Madagascar, where the ring-tailed mongoose (*Galidia elegans*) changed activity patterns to avoid introduced species like free-ranging dogs and small Indian civets (*Viverricula indica*; Gerber et al. 2012). Such disruption of activity patterns can have significant adverse physiological and behavioral effects (Froy 2010; Karatsoreos et al. 2011; Reppert and Weaver 2002). Andean opossum, striped hog-nosed skunk, and white-tailed deer did not shift activity patterns where dogs occurred. This might be explained by physiological constraints that preclude shifts in activity patterns, prey naiveté, or existence of effective mechanisms of defense against feral dogs, as suggested by the lack of difference in relative abundance of the Andean white-eared opossum and white-tailed deer between areas with and without dogs (Ashby 1972; Kavanau and Ramos 1975; Sih et al. 2010).

In addition to temporal shifts in activity patterns, presence of dogs also can lead to changes in habitat use of native species (Silva-Rodríguez et al. 2010; Vanak and Gompper 2009). However, species in our study did not exhibit different patterns of habitat use in areas with and without dogs. Feral dogs used habitat types according to availability, probably making active avoidance of dogs through spatial shifts in habitat an ineffective strategy. This finding contrasts with other studies in Europe and Australia that have found that native species (e.g., wolves, *Canis lupus*; foxes, *Vulpes vulpes*; bandicoots, *Perameles nasuta*) alter habitat use to avoid competition and predation by dogs (Boitani et al. 1995; Carthey and Banks 2012; Krauze-Gryz et al. 2012; Mitchell and Banks 2005).

Given the breadth of species in our study area that exhibit changes in abundance and activity where dogs occur, several mechanisms are likely at play (Hughes and Macdonald 2013; Vanak et al. 2014). Shifts in activity patterns may have fitness consequences (e.g., linked to energetics of foraging) that impact abundance (Creel and Christianson 2008; Lima 1998;

Preisser et al. 2005). Also predation by dogs likely is an important source of mortality as dogs easily kill small prey such as mountain pacas, and packs of dogs can take offspring of large prey (e.g., tapirs) or even adults. Feral dogs in our study area also may affect native carnivores through depletion of their prey. Exploitative competition between dogs and native carnivores generally has not been considered important because free-ranging owned dogs, the subject of most studies, are fed by owners or scavenge on human waste as their primary source of food (Butler and du Toit 2002; Campos et al. 2007). In our study area, human sources of food are not available and feral dogs rely on native prey. This mechanism may be relatively more important than previously recognized for areas with feral dogs and low human population and, thus, deserves further attention.

Interference competition, where direct aggression by dogs impacts native carnivores, has been reported as a serious threat to wildlife in numerous parts of the world (Lacerda et al. 2009; Silva-Rodríguez et al. 2010; Vanak and Gompper 2009) and likely is important in the Tropical Andes. During the course of our fieldwork, dogs were observed chasing native species (e.g., Andean foxes), and on several occasions killing small carnivores (e.g., striped hog-nosed skunks and mountain coatis) without predating on them. In all cases, dogs had the numerical advantage. This type of intraguild predation without consumption of subordinate species is common in carnivores (Donadio and Buskirk 2006; Palomares and Caro 1999). One additional mechanism that potentially could cause decline of native species in our study area is disease transmission. Spillover of pathogens resulting from close contact between dogs and native wildlife species is well documented (Murray et al. 1999; Smith et al. 2006). Diseases such as canine distemper and rabies, which have high mortality rates in domestic dogs and affect most wild carnivores, are common throughout the Andes (Ruiz and Chávez 2010; Young 1997).

Feral dogs are a significant problem in our study area not only because both native predators and prey may be affected by dogs, but also because many native mammal species are endemic to the Tropical Andes and already considered vulnerable to extinction. Currently, dogs are included as a threat in the assessment for the IUCN Red List of Threatened Species (IUCN 2015) for only four of the 13 species recorded in the study area (Andean fox, little red brocket deer, northern pudu, and white-tailed deer). Impacts of feral dogs on native species are poorly understood and likely hugely underestimated for the mammal community of the Tropical Andes and many other parts of the world. Moreover, because dogs are generalist species, their impacts may extend to other taxa such as ground-nesting birds and result in a broad range of secondary impacts that are undocumented (Aliaga-Rossel et al. 2012; Rosselli and Stiles 2012). Because of our findings, the Ministry of the Environment of Ecuador and other organizations are taking a very aggressive approach to managing and controlling feral dogs and their impacts in several protected areas of the Ecuadorian Andes. Actions include feral dog elimination, domestic dog vaccination and sterilization programs in buffer areas, as well as education and communication campaigns. Given the precarious state of mammals in the Tropical Andes and the potential for dogs to affect a large number of native species, similar strategies for reducing problems with dogs likely are needed urgently in other areas of the Andes as well as elsewhere feral dogs and wildlife interact.

Acknowledgements

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Table 1. Mammals with body mass > 1 kg known to occur in Cayambe-Coca National Park of Ecuador (Tirira 2007), species endemic to the Tropical Andes[1], status and trend in IUCN Red List of Threatened Species [2] and Ecuador's Red List[3], and survey method[4] used to register the species in this study.

Species	Endemic	IUCN Status and Trend (Status in Ecuador)	Survey Method
Andean porcupine (*Coendou quichua*)	E	DD, decreasing (VU)	Nd
Andean white-eared opossum (*Didelphis pernigra*)	E	LC, stable (LC)	C
Mountain paca (*Cuniculus taczanowskii*)	E	NT, decreasing (DD)	C
Tapití (*Sylvilagus brasiliensis*)	--	LC, unknown (LC)	C,S
Puma (*Puma concolor*)	--	LC, decreasing (VU)	C,T*
Andean fox (*Lycalopex culpaeus*)	--	LC, stable (VU)	C,T,S*
Andean bear (*Tremarctos ornatus*)	--	VU, decreasing (EN)	C*,S
Pampas cat (*Leopardus colocolo*)[5]	--	NT, decreasing (VU)	Nd
Colombian weasel (*Mustela felipei*)	E	VU, decreasing (DD)	Nd
Long-tailed weasel (*Mustela frenata*)	--	LC, stable (LC)	C
Striped hog-nosed skunk (*Conepatus semistriatus*)	--	LC, unknown (LC)	C
Mountain coati (*Nasuella olivacea*)	E	DD, unknown (VU)	C,D*
Mountain tapir (*Tapirus pinchaque*)	E	EN, decreasing (CR)	C,T*,S
Little red brocket deer (*Mazama rufina*)	E	VU, decreasing (VU)	C,T*
White-tailed deer (*Odocoileus virginianus*)	--	LC, stable (LC)	C*,T
Northern pudu (*Pudu mephistophiles*)	E	VU, decreasing (VU)	C

[1]Endemic to the tropical Andes: E
[2]Status in the IUCN (2015) Red List: Critically Endangered -- CR, Endangered – EN, Vulnerable – VU, Near Threatened – NT, Data Deficient – DD, Least Concern – LC
[3]Status for Ecuador taken from Tirari (2011)
[4]Survey method: Camera traps – C, Tracks – T, Scats – S, Digging – D, Not detected in this study – Nd. If a species was detected by multiple methods, the method that produced the most data (*) was used to estimate relative abundance.
[5]This species has been divided into three species by some authors, but more recent genetic analyses suggest that division at the species level is not warranted (IUCN 2015). Under the

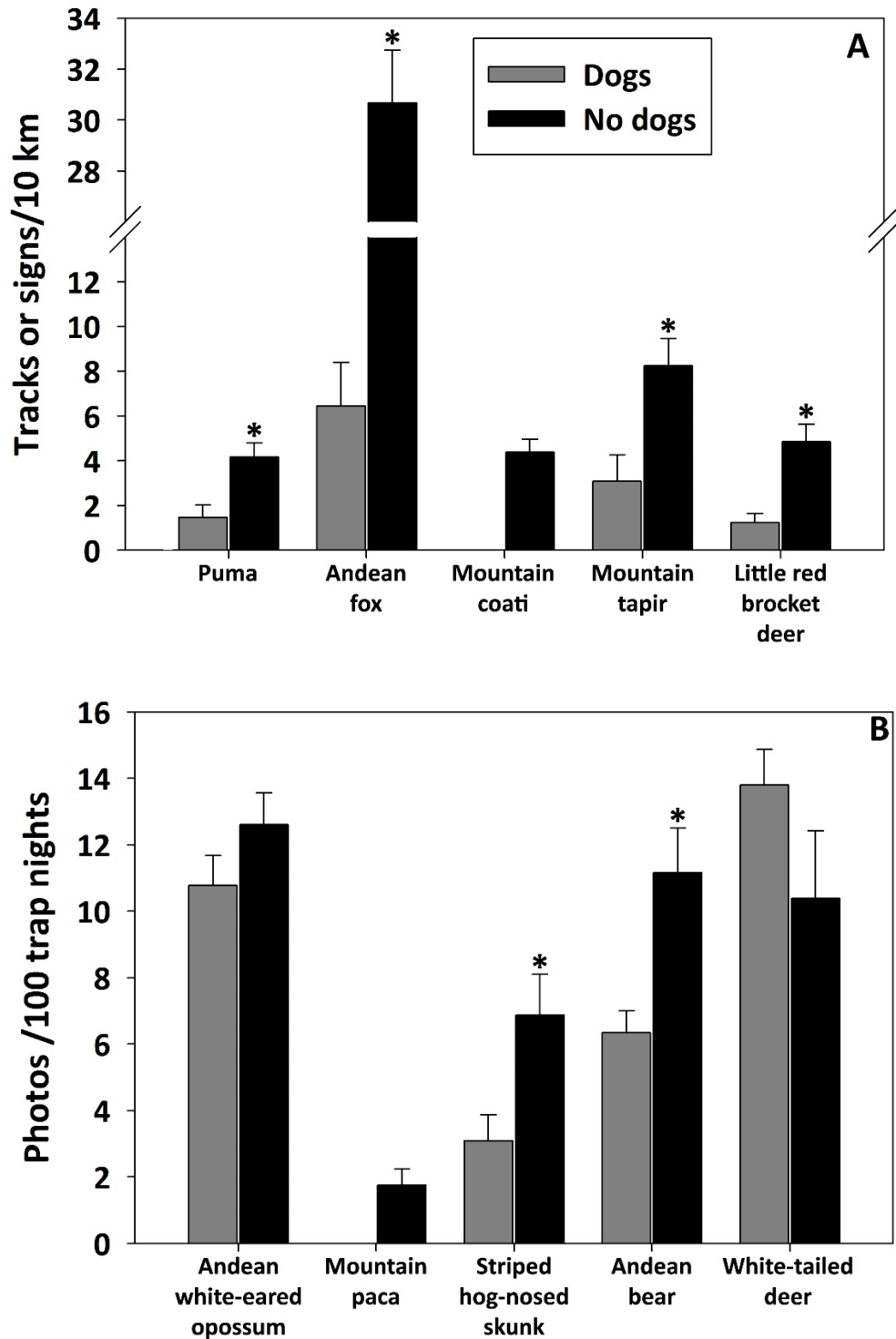three-species taxonomy, the species in Ecuador corresponds to *Leopardus pajeros* (Tirira 2007).

Figure 1. Relative abundance (grand mean for three sites + 95% CI) using A) number of tracks or signs on transects and B) number of photos/100 trap nights of 10 native species in areas with and without feral dogs in Cayambe-Coca National Park, Ecuadorian Andes. Asterisks indicate significant differences in abundance between areas with and without feral dogs ($p < 0.05$).
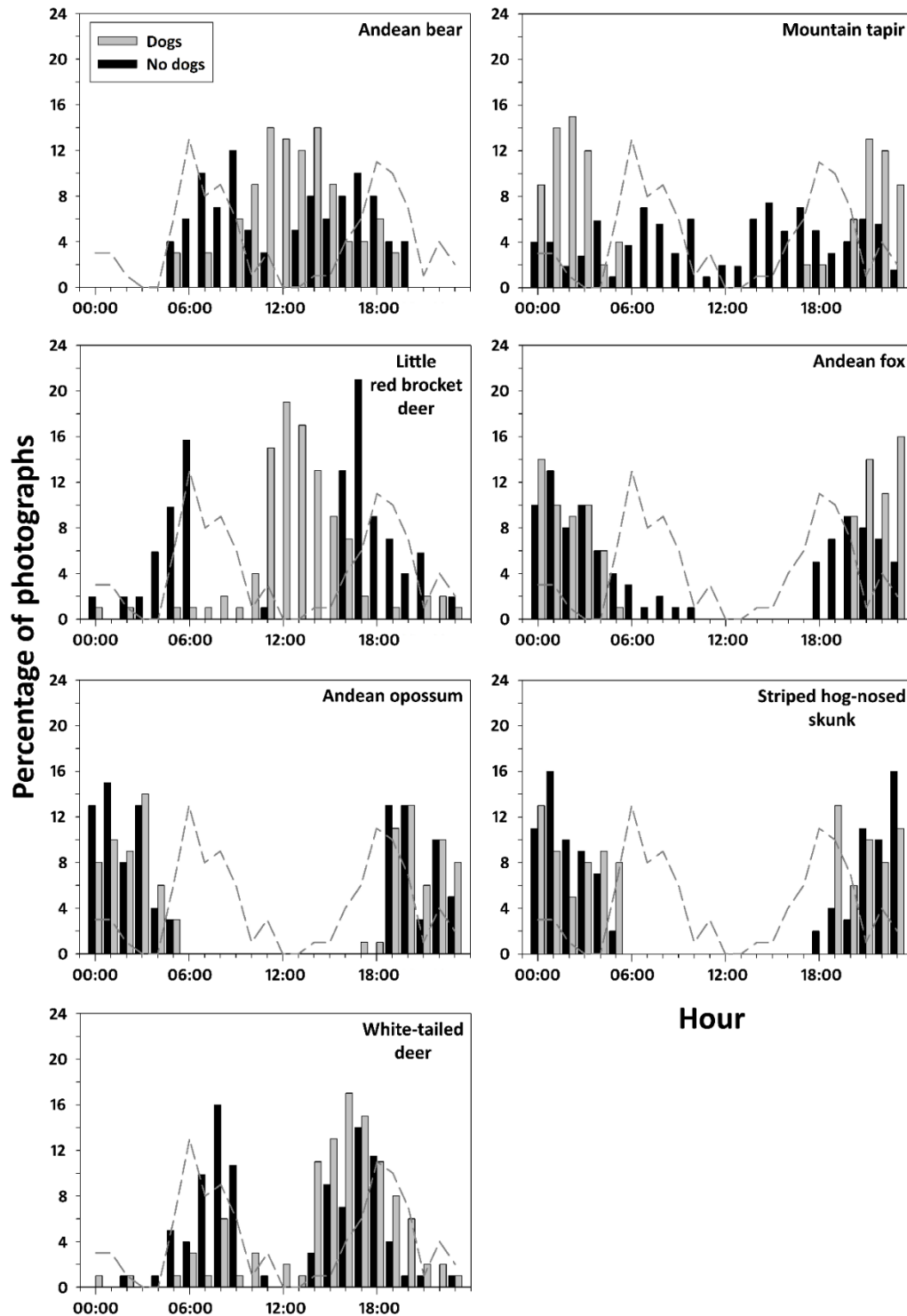
Figure 2. Activity patterns of seven native mammals in areas with and without feral dogs based on photographs taken during hourly intervals (percentage of total number of photographs) in Cayambe-Coca National Park, Ecuadorian Andes. The dashed line shows the activity pattern of feral dogs.

Supplementary information

Appendix A:

Table A1. Proportion of cameras and transects in each habitat type in areas with and without feral dogs. Data are means (± SD) for three sites.

Habitat	Cameras[1]		Transects[2]	
	Dogs present	Dogs absent	Dogs present	Dogs absent
Grass páramo	54.8±6.7	55.8±4.9	51.2±6.5	53.0±5.4
Shrub páramo	18.2±4.7	15.3+5.3	21.2+5.1	18.2+6.1
Cushion páramo	4.5±3.0	5.1±2.6	5.8±3.6	4.9±0.5
Andean forest	22.5±5.8	23.8±3.0	21.8±8.7	23.9±1.2

[1]Yates X^2_{15} = 14.8.0, p>0.4; [2]Yates X^2_{15} = 22.0, p>0.2;

Our information on habitat types was taken from a digital vegetation map obtained from the Ecuador's Ministerio del Ambiente (2012). A detailed description of the methods for construction of this map is available with the map from the Ministerio del Ambiente. We present a brief summary of these methods here. This map was based on classification of Landsat 7 ETM+ and Spot 5 HRG images taken 14 days apart. Images were orthorectified to remove relief displacement. An unsupervised classification of vegetation types was conducted using a traditional maximum likelihood. Training areas then were defined through fieldwork, and a supervised classification was performed. The final hybrid classification combined the maximum likelihood classification with visual edits based on aerial photographs, expert knowledge, and contextual information. For the area of the map used for our study, this process included acquisition, orthorectification, and interpretation of 38 black and white aerial photos (1:7000).