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Short communication

How are wetlands and biological interactions related to carnivore distributions at high altitude?

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A B S T R A C T

Determining the geographic range of species is a main objective in ecology and has implications for conservation. Key determinants of carnivore distribution in dry environments are competition and the availability of water. Here, we gathered and mapped the available information on carnivore habitat quality in the high Andes and Puna in the extreme north of Argentina. We investigated four carnivore species: the Andean cat (*Leopardus jacobita*), the Pampas cat (*Leopardus colocolo*), the cougar (*Puma concolor*) and the culpeo fox (*Lycalopex culpaeus*). We assessed the main determinants of their distribution, testing explicitly for the effects of seasonal and temporal wetlands and biological interactions. We used species distribution models, and created biophysical models using environmental and landscape variables. Then, by including the four species' biophysical models into the model of the focal species, we tested for the importance of biological interactions. Wetlands were most important for the culpeo fox, most likely because it uses aquatic birds as prey. The cougar was the least restricted species in this arid environment, perhaps due to its large home range. In general, environmental variables, distances to wetlands and the annual range of temperature defined species' distributions better than did biological interactions. Only the distribution of the Andean cat, a specialized species, was influenced by biological interactions with the Pampas cat.

Describing distribution patterns and explaining the mechanisms that control them are among the most important issues in ecology and biogeography, and have implications for conservation biology (Myers and Giller, 1988). Abiotic factors mainly determine distributions at continental and subcontinental scales, whereas biotic factors act at local or regional scales to cause changes in distributions (Hoffmann and Blows, 1994).

In mountainous regions, temperature largely varies with topography, even between very close localities. Studies on species distributions in mountainous regions must therefore consider climate and key landscape elements. In arid regions, water sources and their availability are crucial in determining carnivore distribution. Lions, for example, base their territories around water holes (Valeix et al., 2009). Intraguild competition plays a role in defining distributions; when resources are scarce, carnivores compete intensely (Creel, 2001).

In this study, we focus on four carnivore species: the Andean cat (*Leopardus jacobita*), which is endemic to this biogeographical region, the Pampas cat (*Leopardus colocolo*), the culpeo fox (*Lycalopex culpaeus*) and the cougar (*Puma concolor*), which are all more generally distributed carnivores. Climate factors and their role in determining these distributions are poorly understood, despite their practical interest and their theoretical importance in the creation of borders of distribution. Only a few studies have also accounted for competition, and these studies focused on the Andean and Pampas cat (Lucherini and Luengos Vidal, 2003), although the cougar may also be of special interest as it could predate on meso-carnivores (Donadio and Buskirk, 2006).

Species distribution modeling (SDM) is an important tool used to determine the distributions of species. SDM is especially useful when determining the distributions of species with low abundance, such as most carnivores, or species in areas that are difficult to access, such as the high Andes. SDM is also used to assess the

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factors that determine the fundamental niche of a species (Anderson et al., 2002a) or indicate the geographic potential for competition (Anderson et al., 2002b). Distribution of the Andean cat was modeled on a regional scale (Marino et al., 2011), but these authors suggest that future studies should include landscape variables at finer spatial scales.

In this study, we gather the available information on carnivore presence and map habitat quality in the high Andes and Puna of Northwestern Argentina. We identify the main drivers of the distributions, in particular testing for the influence of permanent and seasonal wetlands. We assess how interactions between these species may affect their distributions.

Because of the extremely dry climate, we expect that water availability will be a main driver in carnivore distribution, as observed in other arid regions (Valeix et al., 2009). In this environment of scarce resources, we expect competition between the culpeo and cougar (Pacheco et al., 2004) and between the Andean cat and Pampas cat (Lucherini and Luengos Vidal, 2003). Therefore, we expect that reduced habitat suitability for one species will increase the habitat suitability values for the other species.

The high Andes and Puna in the extreme northwest of Argentina are the highest parts of the country. The high Andes range up to 4200 msnm, whereas Puna is lower in altitude (3200–3700 msnm). The climate is severe, cold and dry with intense solar radiation and large daily and seasonal thermal variations. Mean annual temperatures vary from less than 0–4 °C in the high Andes and from 5 to 7 °C in Puna, with periods of night frost from March to October. Rainfall is scarce and largely seasonal (Bianchi and Yáñez, 1992), varying from less than 100–800 mm annually. Scattered small lagoons and bogs are the only water source available for wildlife. Our study area encompasses approximately 33,000 km^2 in the Jujuy province of Argentina (Fig. 1).

We used the presence records of the four species in our study area from 18 years (1990–2008) of field work of one of the authors (P.G.P), some of which were previously published (Perovic et al., 2003). We georeferenced all points with a GPS or *a posteriori* based on Google Earth©. A total of 39 presence records of the Andean cat, 67 of Pampas cat, 90 of the culpeo fox and 67 of the cougar were used for modeling.

We used the software MaxEnt for species distribution modeling. MaxEnt uses the maximum entropy principle that, when estimating an unknown probability distribution, considers the least biased solution to be the one that maximizes its entropy, subject to some constraints (Phillips et al., 2006).

To determine the ecological requirements of the four carnivores, we developed “biophysical models” using the 19 bioclimatic variables and three topographic variables: elevation, from which we derived slope and aspect (Worldclim database; Hijmans et al., 2005). We also included layers depicting the annual aridity index and the monthly and annual potential evapo-transpiration (www.csi.cgiar.org). To represent vegetation, we included mean annual Net Primary Production (NPP; http://glcf.umd.edu). We incorporated soil data (http://soilgrids.org/) and land cover types (globcover, http://ionia1.esrin.esa.int/). We developed layers of the Euclidian distances to permanent and seasonal wetlands. Wetlands were rasterized from the chards of the Argentinean National Geographic Institute (IGN; http://www.ign.gob.ar), where they are classified as permanent (wetlands that never completely dry) or seasonal (which completely dry periodically), and were updated by examining a series of 25 LandSat TM satellite images (from 2000 to 2001). All variables were obtained or created at a 30 arc-seconds resolution. We tested for correlations between the predictor variables using the Pearson coefficient (values of $r < 0.7$) and performed 100 replicates of the MaxEnt model, randomly selecting 75% of the presence points for training and leaving 25% for validation. For each pair of correlated variables, the one showing the lower contribution was deleted. We ran 100 replicates of the model again with the reduced set of variables. The Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot evaluated model performance.

For each species, we then developed an “interaction model” using as predictor variables the proper biophysical model as a surrogate for the biophysical variables, plus the biophysical models of the other three species. We performed 100 replicates. We used these “interaction models” to project the distributions on the study area, applying the fixed cumulative value 1 logistic threshold, which provided projections coinciding with known distributions of species. We divided the range of probabilities into absence (lower

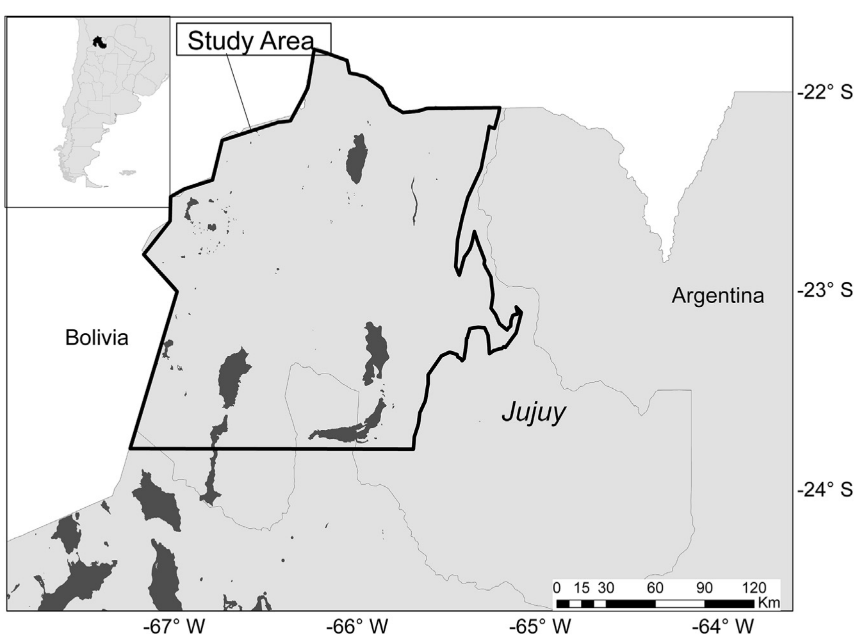

Fig. 1. Location of the study area in the high Andes of Jujuy province, Northwestern Argentina. Wetlands and salt pans are in black.