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Understanding species persistence for defining conservation actions: A management landscape for jaguars in the Atlantic Forest

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ABSTRACT

Habitat models constitute useful instruments for understanding species-habitat interactions and can constitute helpful conservation tools. The Upper Paraná Atlantic Forest (UPAF) of South America still holds the world's southernmost jaguar (*Panthera onca*) population. Our aims were: (i) to test several a priori hypotheses on the factors affecting jaguar persistence in this region, (ii) to map habitat suitability and identify areas with potentially conflicting habitat conditions, and (iii) to identify priority areas for management and improve the conservation initiatives for jaguars and the UPAF. Following an information-theoretic approach, we used presence records of jaguars and pseudo-absences in generalized linear models. We structured hypotheses into two groups which demand different management actions: land cover and human persecution. The best model of each group was used to develop a two-dimensional habitat model. Jaguar persistence was favoured by current and historical native forest cover, and hindered by human land uses. Protection favoured jaguar presence whereas human accessibility and high human population density had negative effects. The two-dimensional model suggests that <8% (20,670 km^2) of the landscape represents potential core areas for jaguars (good land-cover characteristics and low human persecution) and 11.8% (32,563 km^2) stands as potentially attractive sinks where good land-cover conditions conflict with high human persecution. Reduction of human persecution is urgently needed to increase the core areas for jaguars in this region, but improvement of land-cover conditions is important for sustaining the connectivity among jaguar populations that seem to be isolated in different areas of the UPAF.

1. Introduction

Understanding the relationship between landscape change and species persistence is a major issue of interest in applied ecology because of its direct relationship with biodiversity conservation (Tilman et al., 1994). Habitat models or species distribution models (SDMs) constitute useful instruments for predicting species distribution and understanding the species-habitat interactions, but also they can be used as conservation tools for delineating management actions (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000). However, implementation of SDMs in biological conservation is not always a simple task and often demands specific approaches for transforming these models into useful management tools (Guisan and Thuiller, 2005). Naves et al. (2003), for example, proposed an approach for mapping habitat suitability for large carnivores that involves two separate models: a natural model targeting habitat suitability regarding reproduction and a human impact model targeting habitat suitability concerning survival. This approach allows detection of not only the conventional categories where conditions for reproduction and survival are positively correlated (i.e., matrix, sink or poor habitat, and source or good habitat), but also otherwise undetectable areas with good conditions for reproduction though with low survival (attractive sinks), and areas with poor conditions for reproduction but with high survival (refuges). These areas have important management implications, mainly because attractive-sink areas may constitute ecological traps with large effects on populations' survival (Delibes et al., 2001).

The Upper Paraná Atlantic Forest (UPAF) of Argentina, Brazil and Paraguay, is the largest eco-region of the South American Atlantic Forest, and it constitutes one of the world's most endangered eco-regions (Mittermeier et al., 2005; Ribeiro et al., 2009). The main conservation initiative developed for the UPAF is the

Abbreviation: AICc, Akaike's Information criterion corrected for small samples; GLM, generalized linear model; UPAF, Upper Paraná Atlantic Forest eco-region.

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Biodiversity Vision (Di Bitetti et al., 2003), a tri-national conservation strategy designed to sustain a viable population of jaguars (*Panthera onca*), considering this species as an umbrella for the vast biodiversity that the UPAF hosts (Miller and Rabinowitz, 2002). However, only scarce information existed about jaguars in the UPAF when this conservation plan was developed, and one of Biodiversity Vision's aims was the study and monitoring of jaguars and the use of this information for validating this biodiversity conservation strategy (Di Bitetti et al., 2003). Additionally, jaguars are among the most threatened species in the Atlantic Forest and the UPAF hosts two Jaguar Conservation Units (JCUs) where jaguar experts encouraged research and conservation actions for this species (Sanderson et al., 2002b). Considering these demands of knowledge about jaguars in the UPAF, different research initiatives were developed that emphasized the urgent need of a deeper evaluation of the remaining habitat for jaguars in this region to delineate actions at an eco-regional scale (Cullen et al., 2005; De Angelo et al., 2011a,b; Paviolo et al., 2008).

In this study we compiled the previous information obtained about jaguars in the UPAF and used this information to: (i) test several a priori hypotheses on the factors influencing jaguar habitat suitability, (ii) map habitat suitability for jaguars and identify areas with potentially conflicting habitat conditions such as attractive sinks, and (iii) detect priority areas for implementing specific management actions and improving the conservation plans developed for jaguars and the UPAF.

2. Material and methods

2.1. Study area

The UPAF is a subtropical and semi-deciduous forest (annual precipitation range: 1000–2200 mm; mean temperature range: 16–22 °C), and it constitutes a highly degraded and fragmented region, where less than 8% of the forest remains (Di Bitetti et al., 2003). The history and dynamics of human settlement, land-use change, and fragmentation processes are heterogeneous along the UPAF (De Angelo, 2009; Izquierdo et al., 2008; Jacobsen, 2003). In the Brazilian UPAF, most of the forest was replaced around the middle of the last century (Ribeiro et al., 2009), while the Paraguayan UPAF has a more recent but accelerated process of forest destruction (Huang et al., 2007). The Argentinean UPAF has a long history of human settlement and forest exploitation but with much lower rates of forest replacement (Izquierdo et al., 2008).

We selected an area of 276,843 km^2 at the border shared by Brazil, Paraguay and Argentina, which includes most of the remnants of the UPAF (Fig. 1). This area encloses all the area surveyed by De Angelo et al. (2011b) in their monitoring of jaguar presence and is the same area used by De Angelo et al. (2011a) in their habitat suitability analysis for pumas and jaguars using a presence-only technique.

2.2. Species data

We utilized the presence records of jaguars collected by participatory monitoring between 2002 and 2008 (De Angelo et al., 2011b). We obtained records from different sources (tracks, scats, camera traps, radio-tracked animals, etc.), that were carefully selected and accurately identified for avoiding false positives. Jaguar tracks were identified using a discriminant model developed for recognizing jaguar tracks (De Angelo et al., 2010), and scats were identified through specific molecular markers developed for differentiating jaguar and puma (*Puma concolor*) faecal samples (Haag et al., 2009).

In total we obtained 974 jaguar records (De Angelo et al., 2011b). To reduce potential pseudo-replication biases caused by the unsystematic data collection, we superimposed a grid of 144-km^2 cells (the size estimated for a female jaguar home range; D. Sana, unpublished data; A. Paviolo, unpublished data; Cullen et al., 2005; Paviolo, 2010) and randomly selected one observation if more than one record occurred in a cell (Kanagaraj et al., 2011). This resulted in a total of 106 presence records to be used in our analysis. To test if our results were influenced by this particular selection of records, we created 10 further subsets of 106 records following the same procedure. This allowed us to explore whether the selected presence records were representative and whether models constructed with alternative sets of presence records agreed (see below Sections 2.3 and 2.4).

To obtain a binomial response variable we followed the approach developed by Engler et al. (2004), and we generated randomly the same number of pseudo-absences as presences (Liu et al., 2005). To this end, we followed several rules to ensure that pseudo-absences were located inside surveyed areas but not in areas that were known to be suitable areas for jaguars (Appendix A and Fig. A1). We also generated 10 further sets of pseudo-absences for model validation (see below Section 2.4).

2.3. Biological hypotheses and environmental variables

SDMs that predict average habitat suitability based on a single function may overlook areas where habitat conditions related to key factors with different management requirements are conflicting (Kanagaraj et al., 2011; Naves et al., 2003; Nielsen et al., 2006). For example, it is well known that deaths of large carnivors are mainly caused by humans, but nutritional condition determines reproductive rate (Naves et al., 2003; Woodroffe and Ginsberg, 1998). If key factors that determine reproduction and survival are not positively correlated, a single function SDM will overlook attractive sinks (good conditions for reproduction but low survival) and refuges (poor conditions for reproduction but with high survival). Thus, using a model based on two SDMs that describe habitat suitability from the perspective of different key factors that affect either survival or reproduction, allows for a more subtle and management relevant assessment of habitat suitability.

Indeed, we can identify such two management–relevant key factors for the jaguar in the UPAF. First, landscape conditions related with land cover and physical environment are important determinants of jaguar habitat suitability at a regional scale (e.g. forest cover, presence of water, or different human land uses; see Table 1). The main management actions associated with these conditions are related to policies of forest restoration and territorial or land-use planning (e.g. defining which human land uses will be promoted in certain regions, designing corridors, protecting river basins) (e.g. in Fernández et al., 2006; Muntifering et al., 2006; Wikramanayake et al., 2004). Second, the presence or absence of this species is also determined by direct human persecution of jaguars and their prey (see Table 2). The most important management actions needed to improve habitat conditions in relation with these threats are different from those mentioned before: the priority actions would be protection, law enforcement, and actions for reducing jaguar mortality (e.g. for reducing poaching activity and other sources of jaguar mortality as road kills) (e.g. in Nielsen et al., 2004; Woodroffe and Ginsberg, 1998). By analyzing habitat suitability with respect to these two dimensions we can identify critical areas that need to be prioritized for the different management actions. We therefore tested several a priori hypotheses on factors that determine jaguar habitat suitability regarding the two main key factors: land-cover and physical environment [L], and human persecution [H] (Tables 1 and 2 respectively). We then