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Original investigation

Local and continental determinants of giant anteater (*Myrmecophaga tridactyla*) abundance: Biome, human and jaguar roles in population regulation

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ABSTRACT

The giant anteater (*Myrmecophaga tridactyla*) is currently found in a wide variety of habitats from Honduras to Argentina. Across this wide range, researchers have postulated that anteater populations are negatively affected by several factors, including hunting, habitat loss and fragmentation, fire, vehicle collisions, and predation by jaguars. But no studies to date have evaluated the relative importance of these factors across sites, either at a regional or continental scale. We used camera traps to analyze variation in giant anteater abundance at two spatial scales. At a regional scale, we conducted camera trap surveys in the dry Chaco of Argentina and used occupancy models to explore the effect of protection status and human accessibility on giant anteaters' relative abundance. At a continental scale, we used data from 40 camera trap studies (representing 42 different locations) and Generalized Linear Models (GLM) to assess the potential relation of biome, human disturbance and the presence of jaguars on giant anteater camera trap records. In the Argentine Chaco, protection and human disturbance do not significantly affect the proportion of area used by the species. The average anteater records/100 camera days and the proportion of sites used are very high across the study area. At a continental scale, anteaters are more frequently recorded in dry forests than in moist forests. Locations with very high human disturbance have camera trap rates that are 5–10 times lower compared to intermediate or low disturbance locations. Finally, giant anteater capture frequency increases up to 70% where jaguars are absent. Dry biomes and intermediate levels of human disturbance may favor anteaters by providing greater habitat heterogeneity coupled with a lower jaguar abundance. This may explain the relatively high abundance of giant anteaters in the Argentine Chaco. However, growing human populations, the advancing agriculture-livestock frontier, and an expanding road network may in time eliminate giant anteaters from most of this region.

Introduction

The giant anteater (*Myrmecophaga tridactyla*; Linnaeus, 1758) is currently found in a wide variety of habitats from Honduras to northern Argentina (Miranda et al., 2014). Across much of its range, the giant anteater is threatened primarily by poaching, habitat loss and fragmentation, fire, and vehicle collisions (Cáceres et al., 2010; Lacerda et al., 2009; Noss et al., 2008; Merritt, 2008). Overall, the species is particularly threatened where human activities are relatively intense (Lacerda et al., 2009). Within Argentina its range has decreased by approximately 45% in the past 40 years, and the species persists only in sub-tropical forests in the north (Pérez Jimeno and Llarín Amaya, 2009; Superina et al., 2012). The species is categorized as Vulnerable both in Argentina and across its range (IUCN, 2014; Superina et al., 2012). However, very little

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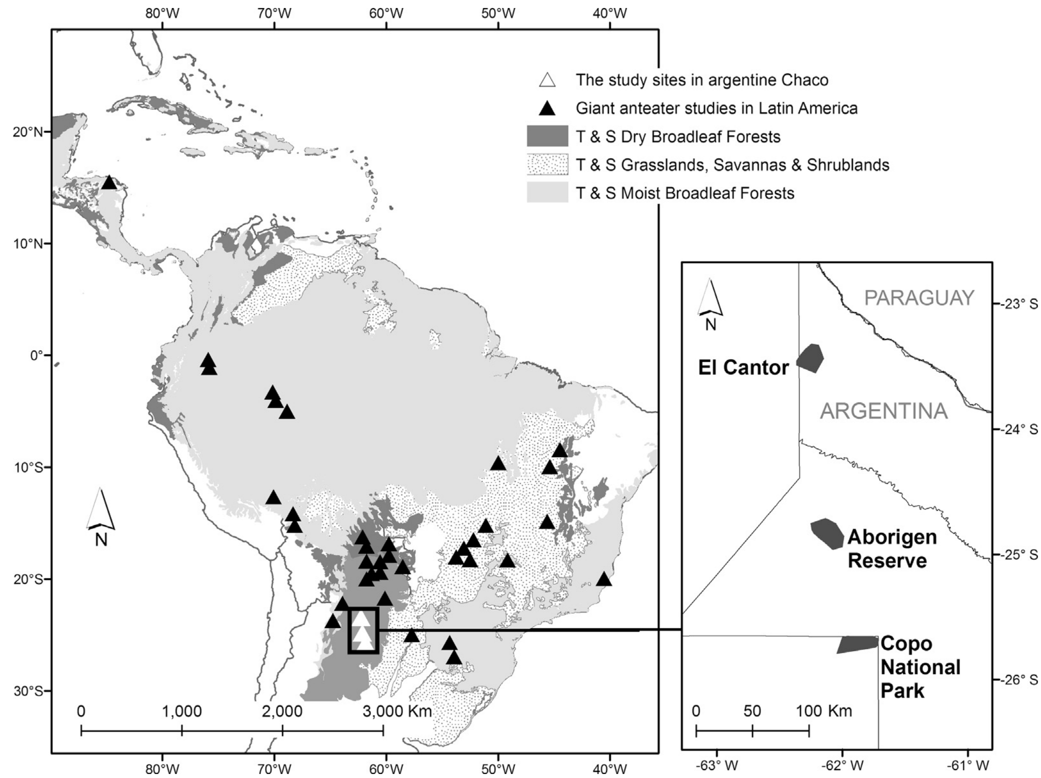

Fig. 1. The 42 Neotropical locations considered in this study. For the three study locations in the Argentine Chaco, we included the minimum polygon convex (MPC) covered by the camera trap survey in each location. (T&S = tropical and subtropical).

information exists on the population status of the giant anteater across its range, or on what factors affect its distribution and abundance.

Large-bodied specialist-insectivores like *M. tridactyla* depend on resources that are energetically poor and, for that reason, they have a relatively low metabolism and require large areas for their survival (Mourão and Medri, 2007; Zimbres et al., 2013). Giant anteaters prefer environments presenting a mosaic of habitats, because they generally use forest patches for shelter and rest, and fire-managed grasslands and/or shrub savannas for foraging and daytime rest (Desbiez and Medri, 2010; Di Blanco et al., 2015; Mourão and Medri, 2007; Prada and Marinho-Filho, 2004; Shaw et al., 1987). Apparently they tolerate a certain degree of disturbance such as livestock and moderate fires (Shaw et al., 1987). However, they avoid areas with high levels of contact with humans, cattle and other domestic animals, and they seem to require well-conserved forest patches (Shaw et al., 1987; Vynne et al., 2011; Di Blanco et al., 2015). Their natural predators include the jaguar (*Panthera onca;* Linnaeus, 1758) and, occasionally, the puma (*Puma concolor*; Linnaeus, 1771) (De Oliveira, 2002; Silveira, 2004). Normally the giant anteater is not an important prey species for jaguars (Cavalcanti and Gese, 2010; Crawshaw and Quigley, 2002), except in some semi-arid environments, namely the Caatinga, the Paraguayan Chaco and the Cerrado (Astete et al., 2008; De Oliveira, 2002; Mc Bride et al., 2010; Rodrigues et al., 2008; Silveira, 2004).

Our study is the first attempt to assess the determinants of giant anteater abundance across its range. This study is also the first systematic field survey of giant anteaters in the Argentine Chaco, where its population status is unknown. The Gran Chaco is the second most extensive forest ecoregion in the Americas after the Amazon, and is the largest sub-tropical dry forest in the world (Morello and Adámoli, 1974; Morello et al., 2009). Currently several of the Chaco's mammal species are under threat from direct hunting and from deforestation (Altrichter, 2006; Gasparri and Grau, 2009; Quiroga et al., 2014). Compared to forests without hunting, the density of mammal species may decrease by as much as 80% under moderate hunting pressure, and as much as 93% where hunting is intense (Redford, 1992). In the Argentine semi-arid Chaco, over 95% of rural ranch residents consume wildlife, mostly mammals (Altrichter, 2006), resulting in the local extinction of some species (e.g., peccaries, Altrichter and Boaglio, 2004). On the other hand, the Argentine Chaco is one of the few areas where giant anteaters coexisted for a long time with their principal predators, jaguars, but where jaguars are virtually extinct today (Quiroga et al., 2014).

In this study we evaluate variation in giant anteater abundance at two different spatial scales. At a regional scale, across three locations in the Argentine semi-arid Chaco, we use camera trap data and occupancy models to study the effects of different levels of protection and human disturbance on photo-capture rates, detectability and the proportion of the area used by giant anteaters. At a continental scale, we use data from 40 camera trap studies reporting the frequency of records of giant anteaters to compare their relative abundance across different biomes, different levels of human disturbance, and presence versus absence of their main predator, the jaguar.

Study area

The regional study was conducted in the Argentine semi-arid Chaco, where median annual temperature is 24 °C, but the climate is markedly seasonal with annual precipitation of 400–800 mm concentrated between December and April (Prohaska, 1959). The region is characterized by extensive plains (average altitude of 160 m above sea level) of dry forests dominated by red quebracho (*Schinopsis lorentzii*; Anacardiaceae), white quebracho (*Aspidosperma quebracho-blanco*; Apocynaceae), palo santo (*Bulnesia sarmientoi*; Zygophyllaceae), and mistol (*Ziziphus mistol*; Rhamnaceae). The dense shrub understory, from 1–10 m high, is dominated by *Capparis retusa* (Capparidaceae), *Acacia praecox* (Fabaceae), *Celtis pallida* (Ulmaceae), *Achatocarpus praecox* (Achatocarpaceae) and *Schinus polygamus* (Anacardiaceae) (Tálamo and Caziani, 2003). The area was colonized early in the 20th century by non-indigenous ranchers, who settled in isolated ranches, displacing the aboriginal people. The natural characteristics of the region support extensive cattle ranching combined with heavy hunting of wildlife (Baxendali and Buzai, 2009). We compared three locations, 100–260 km apart from each other (Fig. 1), across a gradient of conditions related to protection status of the area, human population density and degree of human disturbance.

Copo National Park (1180 km^2)

This site has the highest legal protection level, with four park rangers (1 park ranger/295 km^2) responsible for anti-poaching and other activities within the park. Livestock from neighboring ranch outposts enters the Park, but the livestock burden is relatively low in comparison to the other sites (Quiroga, 2013).

The Aborigen Reserve (2500 km^2)

Although it is categorized as an indigenous Reserve, no indigenous people reside inside its boundaries. It is sparsely populated (0.8 outposts/100 km^2), and has an intermediate livestock burden relative to the other two survey sites. The Reserve has no game rangers and no anti-poaching activities (Quiroga, 2013).

El Cantor (1966 km^2)

This site is not legally protected, and has neither game rangers nor anti-poaching activities. The local people hunt. The cattle stocking rate is the highest of the three sites and cattle have been established the longest here. The density of ranches is also the highest, at 1.3 outposts/100 km^2 (Quiroga, 2013).

For the continental study we compiled data from 42 Neotropical locations, from Honduras to northern Argentina (Fig. 1), covering three types of biome: tropical and subtropical moist broadleaf forests; tropical and subtropical dry broadleaf forests; tropical and subtropical grasslands-savannas and scrublands (Olson et al., 2001). We also characterized the level of human disturbance and assessed the presence or absence of jaguars for each site (Appendices A and C of Supplementary information).

Material and methods

Giant anteaters at a local scale: the Argentine Chaco

At the three Argentine locations, we collected camera trap data in the context of a larger study on jaguar, puma and their prey in the area (Quiroga et al., 2014). We undertook camera-trap surveys over three consecutive years (2008–2010), during a three-month period in the dry season each year. At each location we installed 24–35 camera-trap stations, separated by an average of 3000 m, along footpaths, abandoned roads or active unpaved roads. We used the camera-trap photographs to estimate the proportion of camera trap stations where the species was recorded, and to generate a relative abundance index based on the average anteater records per 100 camera trap days (considering records to be independent if they were separated by at least one hour). We used a Kruskal–Wallis test to compare this relative abundance index across sites, and a likelihood-ratio test to compare the proportion of camera trap stations per site where the species was recorded.

We used occupancy models (PRESENCE version 4.4; Hines, 2006) to reveal which factors affect the proportion of sites used (ψ), modeling the effects of these factors according to the species' detection probability (p) (MacKenzie et al., 2006). Depending on the detection probability, the models may suggest that additional individuals are present even though they were not photographed, and therefore actual occupancy is greater than observed occupancy (MacKenzie et al., 2002). In our analyses ψ should be interpreted as the proportion of sites used, because individual giant anteaters probably entered and left the survey area during the study period and because the camera stations are relatively close together (compared to likely ranging behavior) and probably were not independent for giant anteaters. We ranked models by their Akaike Information Criteria (AIC) weights. When one or more models had AIC weights > 10% of the highest ranked model, we used model averaging (Buckland et al., 1997; Burnham and Anderson, 2002; MacKenzie et al., 2006).

We evaluated the effects of four variables on ψ or p:

(1) The distance (in km) to the nearest active vehicle road (range 0–15 km; the value was 0 when the camera station was installed on the active road itself). We expected that ψ and p would vary positively with this distance, because of road kills as well as the hunting pressure concentrated along active roads. For this and the next variable we applied one-tailed statistical tests because our hypotheses were directional.
(2) The linear distance (in km, range 0.5–13.8) to the nearest ranch outpost (main building). We expected this distance to be positively related to ψ and p, because the combined disturbance effects of the ranch—human presence, cattle, goats, dogs, vegetation modification—decrease with distance from the ranch outpost.
(3) The type of path/road (active vehicle road, abandoned road, or footpath) where the camera-trap station was installed. We predicted this variable would affect p because we expected anteaters to use footpaths more than abandoned roads, and the latter more than active roads.
(4) The three camera-trap survey locations (Copo National Park, Aborigen Reserve, and El Cantor). We expected both ψ and p to be highest in Copo National Park, the best-protected location, intermediate in the Aborigen Reserve, and lowest in El Cantor where human pressures are the highest.

Giant anteaters at a continental scale: the Neotropics

Based on our experience and results in the Argentine Chaco where jaguars are absent, we sought to evaluate the relationship between giant anteater abundance and human disturbance across the Neotropics, considering jaguar presence/absence as well as biome at this continental scale. We compiled camera-trap data from 40 studies conducted in areas within the giant anteater's range, spanning 42 locations and eight countries (Fig. 1 and Appendix A of Supplementary information). We applied Generalized Linear Models (GLM) in R (R Development Core team, 2012) to assess the relation between giant anteater abundance (records/100 camera trap days) with the following three variables:

1) Degree of human disturbance: high, intermediate, or low. From the study description or by consulting the researchers directly, we assigned each site to one of these three categories, taking into consideration levels of hunting, cattle ranching, extractive activities like logging, human residents, and effective protection (Appendix C of Supplementary information). This was perhaps the most subjective and difficult-to-measure variable, because there are many anthropogenic factors that can affect giant anteaters. Therefore, the inclusion of this variable in the analysis is a first approach to assess the effect that human disturbance can have on the abundance of giant anteaters. We predicted

Table 1
Camera-trap survey effort and records of giant anteater at the three Argentine locations. a) % stations with giant anteater records; b) records/100 camera days ± SE.

Locations	Survey dates	No of stations	Trap-days	Mean distance separating cameras (km ± SD)	Camera minimum convex polygon (km^2)	a)	b)
El Cantor	1/Jul/2010–9/Sep/2010	35	2129	2.99 ± 0.32	363	54.3	3.4 ± 1.0
Aborigen Reserve	23/Jun/2008–7/Sep/2008	29	1937	3.04 ± 0.98	455	34.5	1.2 ± 0.4
Copo National Park	4/Sep/2009–19/Nov/2009	24	1204	2.85 ± 0.65	367	62.5	2.9 ± 0.6

that giant anteater abundance would be lowest where human disturbance was highest.

2) Presence or absence of jaguars in the photo records. Most locations lack jaguar density data or occupancy estimation. No correlation exists between the frequency of camera trap records and jaguar population density (Maffei et al., 2012), therefore we decided to use the presence or absence of jaguars instead of a relative abundance measure as a response variable. We evaluated this variable when the presence of jaguars was assessed in the same camera trap study estimating giant anteater abundance. We predicted that giant anteaters would be more abundant where jaguars were absent.
3) Biome: tropical and subtropical moist broadleaf forest; tropical and subtropical dry broadleaf forest and tropical and subtropical grasslands, savannas and shrublands (Olson et al., 2001). We predicted that giant anteaters would be more abundant in dry forests than in moist ones.

We considered locations separated by at least 45 km to be independent, based on the maximum recorded home range size and displacement of wild giant anteaters (Rodrigues et al., 2008). But we also used the Moran's I spatial autocorrelation analysis (Gittleman and Kot, 1990) to test for lack of independence among sites. Ten locations lacked jaguar data, but we were unable to confirm that jaguars are absent there. Therefore, we first ran the models with all 42 sites but excluding the jaguar presence variable. We modeled the data as a negative binomial function, using a logarithmic link due to the over-dispersion of the data, and a polynomial relation introduced in the GLM models as an offset term to control for the uneven camera trap survey effort across locations.

Of the 32 locations which included jaguar presence data, we excluded the single remaining location in the "grasslands-savannas" biome, and we ran the subsequent models with only the remaining 31 locations and two biomes. In this analysis we evaluated the effect of jaguars and the interaction between biome and jaguar presence, predicting that jaguar presence would affect giant anteater abundance more strongly in dry biomes, where the species more commonly preys on giant anteaters (Astete et al., 2008; Mc Bride et al., 2010; Rodrigues et al., 2008). For this subset of data we again ran the Moran's I spatial autocorrelation analysis.

In both analyses using GLM we estimated the AIC parameters for all models and ranked the models according to their AIC values. We followed the same criteria used for occupancy models to conduct model averaging (Buckland et al., 1997; Burnham and Anderson, 2002).

Results

Giant anteaters in the Argentine Chaco

We found no statistically significant differences in giant anteater camera trap records among Argentine locations: neither the capture rate (records/100 camera trap days/station) ($H = 4.5$; $p = 0.08$) nor the proportion of camera trap stations where the giant anteater was recorded ($G = 2.5$, $p = 0.29$) varied significantly among the three surveyed locations (Table 1).

Table 2
Estimated parameter values in the model averaging of the four highest-ranked occupancy models, their standard errors and 95% confidence intervals, at the Argentinean scale.

	Estimate	Std. error	CI 95% Lower	CI 95% Upper
Site use (ψ)				
(Intercept)	0.39	0.28	−0.15	0.93
Distance to ranch	−0.01	0.09	−0.16	0.14
Distance to road	0.07	0.14	−0.15	0.29
Detectability (p)				
Intercept	−1.69	0.31	−2.30	−1.07
Location Copo	0.66	0.39	−0.11	1.42
Location El Cantor	1.09	0.36	0.38	1.79

The best-ranked model was the one that included "location" as a covariate that affected detectability (p). Three other models had an AIC weight > 10% of the AIC weight of the top model. These models include an effect of distance to ranches and distance to roads on ψ (Appendix B1 of Supplementary information). The averaging of these four models indicates that none of the variables affected the proportion of sites used (ψ) by giant anteaters (zero fell within the 95% confidence interval for each), and only the variable "location" affected the detectability of giant anteaters (p) (Table 2). According to the top-ranked model [ψ(.); p(location)], the detection probability for the species ranged (lower and upper 95% confidence intervals) from 8 to 24% in the Aborigen Reserve, 17–36% in Copo National Park, and 26–44% in El Cantor. With no overlap in the confidence intervals observed for the Aborigen Reserve and El Cantor, we consider these two sites to differ significantly. All the other variables include zero in the 95% confidence interval, with respect to both p and ψ, thus their influence is not considered to be significant. According to the highest-ranked model, the proportion of the study area utilized by giant anteater varied (95% confidence intervals) from 46 to 72% at the three locations (compared to a naïve occupancy of 50%).

Giant anteaters at a continental scale: the Neotropics

Across the 42 locations the model averaging of the two highest ranked models suggests that the frequency of giant anteater records is higher in dry broadleaf forests and grasslands than in moist broadleaf forests, and three to four times higher at low and intermediate human disturbance locations than at high disturbance locations. However, Moran's I for this data set indicates spatial autocorrelation for the abundance of giant anteater (observed value: 0.11; expected value: −0.02; sd: 0.04; p value: 0.002), and the model results are therefore unreliable due to lack of independence of the study locations. When we include the variable "jaguar presence", the data set is reduced to 31 locations, but with no spatial autocorrelation (Moran's I analysis = observed value: 0.04; expected value: −0.03; sd: 0.06; p value: 0.20). Our analysis therefore focuses on this subset of data.

The best-ranked model was the one that included jaguar presence, biome and human disturbance as predictive variables (Appendix B2 of Supplementary information). The model

Table 3
Estimated parameter values in the model averaging of GLM, their standard errors and 95% confidence intervals (considering 31 locations at the continental scale).

	Estimate	Std. error	CI 95% Lower	CI 95% Upper
(Intercept)	0.8986	0.6651	−0.443	2.240
Jaguar presence	−1.1976	0.523	−2.268	−0.128
Biome moist	−1.648	0.6145	−2.901	−0.395
Intermediate disturbance	1.7798	0.6137	0.518	3.042
Low disturbance	2.5864	0.6718	1.205	3.968
Biome moist: jaguar presence	0.2935	1.2133	−2.176	2.763

averaging indicates a strong relation between biome and giant anteater records, with nearly 80% higher abundance in dry forests as compared to moist forests (Table 3). The model also shows a negative relation with jaguar presence: giant anteater records are up to 70% higher at locations where jaguars are absent. Finally, giant anteater abundance at locations with intermediate and low disturbance is 6–13 times greater than those at high human disturbance locations (excluding sites where giant anteaters were not recorded at all). The interaction between biome and jaguar presence, though present in the second-ranked model, was not important (the 95% confidence interval included zero) (Table 3).

Discussion

In the semi-arid Chaco in Argentina, across the three locations surveyed, neither the legal protection status nor the degree of human disturbance significantly affects giant anteater abundance. Although anteaters may be accidentally killed by dogs during hunting outings, local residents agree that anteaters are rarely hunted intentionally and that their meat does not taste good (Altrichter, 2006; Quiroga, personal observation). Although the species' detectability varied among the three locations, we found no effect of any other variable either on p or ψ. Studies from the Paraguayan and Bolivian Chaco, Brazilian Pantanal and Cerrado report that hunting, fire and vehicle collisions are the principal threats to the species (Cáceres et al., 2010; Ferreira da Cunha et al., 2010; Merritt, 2008; Silveira et al., 1999; Tarifa, 2009), with strong giant anteater declines near human settlements (Lacerda et al., 2009). However, we found only a weak tendency for giant anteaters to avoid ranch outposts and active roads, and these factors did not strongly affect their abundance. Perhaps the differences between our three locations, in degree of human disturbance, were not as important for the giant anteater as for other species which are indeed affected in the Argentine Chaco (Altrichter, 2006).

At the continental scale, the species is more frequently recorded in dry forests (and possibly in grasslands-savannas) than in moist forests. Dry biomes may provide more food for anteaters, accessible at ground level, compared to humid biomes where prey species and biomass may be concentrated in the canopy. The giant anteater generally benefits from habitat heterogeneity (Desbiez and Medri, 2010; Prada and Marinho-Filho, 2004; Vynne et al., 2011), and the vegetation structure of dry biomes may favor giant anteaters by providing greater habitat heterogeneity as compared to more humid biomes (Cardoso Da Silva and Bates, 2002). Some studies even report giant anteater preference for areas with intermediate levels of disturbance, because of the greater habitat heterogeneity that results (Shaw et al., 1987). The same environmental patterns of the Argentine Chaco are replicated in parts of the Paraguayan Chaco and Bolivian Chiquitano dry forest, coinciding with the relatively high photo-capture rates for giant anteaters there (Arispe et al., 2006; McBride, 2004).

Although a high level of disturbance correlates negatively with giant anteater records, giant anteaters may also withstand and even prefer some degree of habitat fragmentation, because this habitat heterogeneity may be associated with a higher availability of food sources. For instance, leaf cutter ants (*Atta* spp.) are relatively scarce in undisturbed Atlantic and Amazonian moist forests, but increase in abundance with disturbance (Dohm et al., 2011; Farji-Brener, 2001; Jaffe and Vilela, 1989; Urbas et al., 2007; Vasconcelos and Malcolm Cherrett, 1995). However, disturbance reduces abundance of another key prey category, termites, in the same forests (Martius et al., 1996; Vasconcellos et al., 2010), and the potential net benefit/cost to giant anteaters remains unknown.

Another important factor with a strong influence on giant anteater abundance across its distribution is the presence of jaguars. In some areas the giant anteater is one of the jaguar's principal prey species, particularly in habitats such as the Caatinga, the Paraguayan Chaco and Cerrado in Brasil (Astete et al., 2008; De Oliveira, 2002; Mc Bride et al., 2010; Silveira, 2004). Researchers have hypothesized that high giant anteater abundance at some locations in the Caatinga may result from low jaguar density (Rodrigues et al., 2008). The relatively high photo capture rates of anteaters in the Argentine Chaco—some of the highest rates recorded anywhere, when compared to other Neotropical sites (Appendix A of Supplementary information)—may result in part from the absence or very low abundance of jaguars. At the three locations surveyed, the level of human disturbance has not greatly affected anteaters but has produced the ecological extinction of jaguars (Quiroga et al., 2014). The convergence of these two factors—a moderate level of disturbance with the decline of its principal predator—may have favored giant anteater populations (or at least not negatively affected them). Similarly, across the species' distribution, capture rates only decline where human disturbance is high, perhaps because at intermediate disturbance levels, the two effects—negative effect from the disturbance versus positive effect from jaguar decline—cancel each other out. These results suggest again that top predators exert an important top-down regulation of populations of the other species in the ecosystem (Ripple et al., 2014). Although only correlational, this result is particularly important because few (if any) previous studies provide empirical evidence of a relationship between the presence of jaguars and the population status of their prey.

Although a certain level of disturbance may not affect or may even favor giant anteaters, the benefit in regions like the Argentine Chaco or the Brazilian Cerrado may be transitory. Colleagues working in the southern reaches of the Argentine Chaco report very high human-induced mortality of giant anteaters (Ignacio Jiménez Perez, personal communication). Higher human population density and the advancing agriculture-livestock frontier in these areas imply a higher density of ranch outposts and roads, a higher abundance of dogs, and an increase in hunting, compared with the locations we surveyed farther to the north, where hunting of giant anteaters is still very rare. The same factors that have extirpated jaguars in much of the region may in time eliminate giant anteaters as well, if current trends continue (Lacerda et al., 2009; Vynne et al., 2011; Zimbres et al., 2013). The giant anteaters that we surveyed in Argentina represent one of the largest populations in the American Gran Chaco, thanks to a set of fortuitous factors that make the region an optimal refuge for the species. Although relatively well-conserved dry forests remain, the region faces a strongly advancing agriculture-livestock frontier from the south, east, and west, threatening in particular those wildlife species with large territorial requirements (Altrichter and Boaglio, 2004; Quiroga et al., 2014). Without the creation and effective management of sufficiently large strictly-protected areas, the giant anteaters in the Argentine Chaco will surely decline as they have elsewhere in the country.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2016.03.002.

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