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Abstract To guide future conservation actions and management decisions, it is crucial to assess the population status and identify the environmental or anthropogenic variables that affect species' abundance and persistence. The main goal of our study was to evaluate the population and conservation status of the three primate species inhabiting the Atlantic Forest of Misiones, Argentina: the brown howler monkey (*Alouatta guariba*), the black-and-gold howler monkey (*Alouatta caraya*), and the black-horned capuchin monkey [*Sapajus* (= *Cebus*) *nigritus*]. We conducted repeated surveys at 31 transects in the central-eastern portion of Misiones province where the three species co-occur, and used occupancy models to assess the effect of human accessibility on black-horned capuchins. In addition, we carried out interviews with local people to assess the status of all three species and the extent to which yellow fever outbreaks may have affected each of them. During the surveys we found no direct or indirect evidence of the presence of brown howlers or black-and-gold howlers in the study area, while we recorded 18 direct and indirect signs of presence of black-horned capuchins in a total of 12 sites. Based on interviews and comparisons with previous density estimates, we conclude that the abundance of both howler species has dropped drastically, possibly due to recent yellow fever outbreaks. Conservation action is thus urgent, especially for the endangered brown howler population. Although black-horned capuchins are not currently considered threatened, we found them to be sensitive to

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anthropogenic disturbance. In the next few decades, the predictable spread and increasing intensity of human activities in this region may cause a drastic decline of this capuchin population.

Keywords *Alouatta caraya* · *Alouatta guariba clamitans* · Occupancy · Population survey · *Sapajus nigritus*

Introduction

To guide future conservation actions and management decisions for primate species, it is important to assess the population status and understand which environmental or anthropogenic variables affect species' abundance and persistence. Individual species may show different degrees of susceptibility to different threats, such as hunting, habitat disturbance, and disease (Cowlishaw and Dunbar 2000; Nunn and Altizer 2006). Identifying the most important factors affecting a population is crucial for any conservation plan, to focus attention on managing these particular factors to ensure population persistence.

The Atlantic Forest of South America is among the most endangered tropical rain forests, with just 7–8 % of its original surface remaining as isolated forest fragments (Galindo-Leal and de Gusmão Câmara 2003). Argentina's northeastern province of Misiones currently hosts one of the largest continuous remnants of Atlantic Forest (Di Bitetti *et al*. 2003) (Fig. 1). Most Atlantic Forest primate species are endemic to this region (Rylands *et al*. 1996), and habitat destruction and fragmentation have brought several of these species to the verge of extinction in the last few decades (Brooks and Rylands 2003; Metzger 2009).

Three species of primates inhabit the Argentine portion of the Atlantic Forest: the brown howler monkey (*Alouatta guariba*), the black-and-gold howler monkey (*Alouatta caraya*), and the black-horned capuchin monkey [*Sapajus* (= *Cebus*) *nigritus*]. The brown howler is endemic to the Atlantic Forest, ranging from the Brazilian states of Bahia and Espirito Santo in the north to Rio Grande do Sul and the Argentine province of Misiones in the south (Cordeiro da Silva 1981; Kinzey 1982). The brown howler recently has been reclassified globally from Near Threatened to Least Concern by the IUCN (Mendes *et al*. 2008) because of its presence in most of the existing conservation units of the Atlantic Forest in Brazil. Nevertheless, the survival probability of this species over the long term is uncertain because its remaining habitat is highly fragmented. The southern brown howler (*Alouatta guariba clamitans*) has been classified for Argentina as Critically Endangered by the Argentine Society for the Study of Mammals (SAREM) (Agostini *et al*. 2012a). The province of Misiones has legally declared this species a Provincial Natural Monument (Provincial Law No. 3455). There are only a few records of its presence for the small Argentine portion of the brown howler's range (Crespo 1974, 1982; Di Bitetti 2003; Di Bitetti *et al*. 1994; Holzmann *et al*. 2015).

Black-and-gold howlers typically inhabit forests of the Cerrado, Pantanal, and Chaco ecoregions (Rumiz 1990), occasionally spanning some ecotonal zones at the edge of the Atlantic Forest in Brazil (Aguiar *et al*. 2007; Gregorin 2006). A small population lives in the Atlantic Forest of northeastern Argentina at relatively low densities (Agostini *et al*. 2010a; Zunino *et al*. 2001). This species has been recently

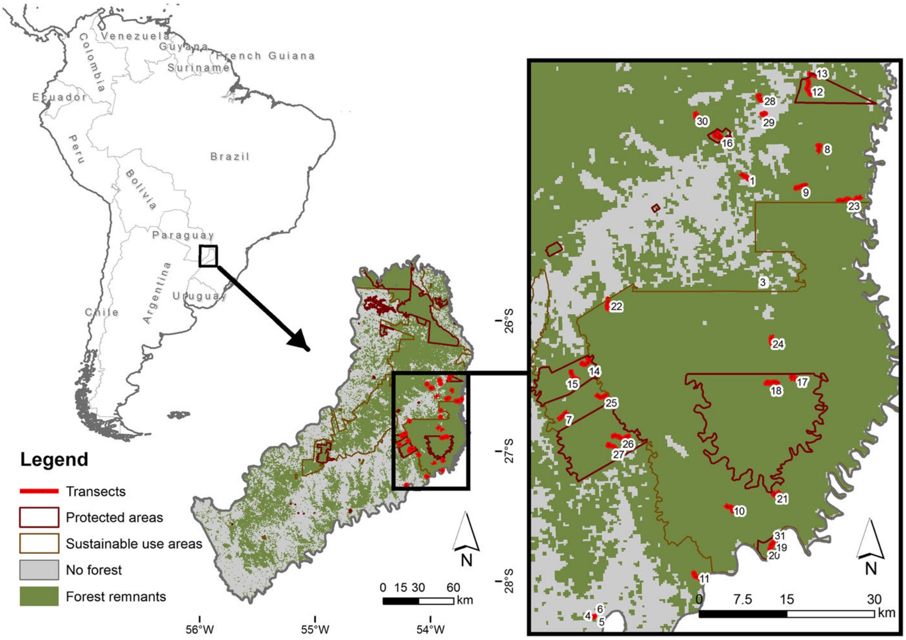

Fig. 1 Location of the study area in Argentina. The distribution of areas with different status (protected areas, sustainable use areas, and nonprotected areas, i.e., all forest remnants not included in the previous two categories) is illustrated for Misiones province. Within the zoom square, which corresponds to the study area, locations of transects (with their corresponding ID numbers) and status of areas where transects were placed are indicated.

reclassified from Least Concern to Vulnerable for Argentina because of the high degree of habitat loss and fragmentation it is suffering throughout its range in the northern portion of this country (Agostini *et al.* 2012a).

Black-horned capuchins are also endemic to the Atlantic Forest (Lynch Alfaro *et al.* 2012) and reach their southern boundary in Misiones. Although the Iguazú National Park of Argentina hosts a studied population (Janson *et al.* 2012), no information is available from other sites of Misiones. The species has been classified as Least Concern for Argentina (Agostini *et al.* 2012a); however, population estimates are based on extrapolations of one density estimate obtained at the Iguazú National Park field site (Di Bitetti 2001) and no assessment of its current distribution, abundance, and population status has been made for other portions of this country. It has been hypothesized that as a result of habitat destruction, the species may still be abundant in protected areas but declining outside the reserves (Di Bitetti 2003).

We conducted a 3-year (2005–2007) study of the behavioral ecology of a small population of brown howlers living in sympatry with the congeneric black-and-gold howlers in one protected area of Misiones, El Piñalito Provincial Park. This was one of the few studies conducted on two sympatric species of howlers (Aguiar 2010; Cortés-Ortiz *et al.* 2007). We found that the two *Alouatta* species lived at relatively low densities at El Piñalito (brown howlers: 10 ind/km^2; black-and-gold howlers: 15 ind/km^2; Agostini *et al.* 2010a); shared a high trophic, spatial, and temporal niche overlap; and could potentially compete for resources in sympatry (Agostini *et al.* 2010a,b, 2012b). We also reported direct evidence of hybridization between the two species occurring within the area of sympatry (Agostini *et al*. 2008). In 2008 and 2009, yellow fever outbreaks killed all members of our study groups and similarly decimated howler populations throughout Misiones and northeastern Corrientes province of Argentina (Holzmann *et al*. 2010). Because of the suspected high impact of this epidemic, there is a special concern about the current status of the brown howler, which is the rarest primate species in Argentina, found only in eastern Misiones.

The paucity of data about the current situation of the three monkey species in Misiones limits our understanding of the most important factors affecting their persistence. There may be differences in susceptibility to threats between howlers and capuchins. For example, it is well documented that howlers are much more susceptible to yellow fever than are capuchins (Kumm and Laemmert 1950). We thus hypothesized that howler populations declined and were affected by yellow fever to a greater extent than capuchins during the last outbreaks.

To test this, we designed a survey with the main goal of evaluating the population and conservation status of the primate species of Misiones. Assuming that human accessibility correlates with the level of anthropogenic disturbance or protection of the area (Nielsen 2006; Peres and Lake 2003), we conducted repeated surveys at 31 transects and used occupancy models to evaluate whether there is a relationship between human accessibility and the status of monkey populations in the area. In addition, we conducted interviews with local people to assess the status of all three species and to what extent yellow fever outbreaks may have affected their populations.

Methods

Study Area

Sampling sites were spread across forest remnants of central-eastern Misiones, throughout San Pedro and Guaraní Departments, an area with an E–W altitudinal gradient ranging from the Araucaria montane forest (900 m asl) to lowland broadleaf forests (150 m asl). This area likely encompasses the whole range of brown howlers in Argentina (Fig. 1). San Pedro and Guaraní Departments cover a total of 680,834 ha, of which 41,747 ha are occupied by five strictly protected areas: El Piñalito Provincial Park (P. P.) = 3796 ha, Cruce Caballero P. P. = 600 ha, Esmeralda P. P. = 31,569 ha, Moconá P. P. = 999 ha, and Caa-Yarí P. P. = 4783 ha; and 253,000 ha constitute the Biosphere Reserve of Yabotí, an area of sustainable use, which contains the strictly protected Esmeralda P. P., Moconá P. P., and Caa-Yarí P. P., and the private reserves Papel Misionero (10,400 ha) and Guaraní Experimental Area (5300 ha).

Sampling Strategy

Based on satellite images from Google Earth and a GIS database of the study area, we selected and surveyed 31 transects using a stratified random sampling scheme. In particular, we distributed transects to represent four strata (highly accessible protected and nonprotected areas; scarcely accessible protected and nonprotected areas) and then randomly within each stratum, the only constraint being the existence of a trail (0–3 m wide) or path (>3–8 m) to facilitate census walking. Most importantly, we did not select sites according to previous knowledge of primate species presence. We set survey transects >1.2 km apart and considered them to be independent for howlers, based on the diameter of the maximum home range estimated for a howler group in Misiones (112 ha; Agostini *et al*. 2010b). Most sites were also independent for black-horned capuchins as they were >2 km apart, i.e., more than the diameter of the maximum home range estimated for a black-horned capuchin group in Iguazú—293 ha; Di Bitetti 2001); however two pairs of transects were closer to each other (distances of 1.2 and 1.4 km), so they might have been not completely independent for this species. Sites showed heterogeneity in their level of anthropogenic disturbance or protection, including strictly protected and relatively undisturbed areas, reserves with some degree of sustainable use of resources allowed, and highly disturbed nonprotected areas.

To evaluate whether human accessibility was related to the status of primate populations, we built an accessibility model for Misiones province using the Accessibility Modelling tool for ArcView 3.x developed by Farrow and Nelson (2001). We adapted the accessibility cost analysis developed by De Angelo *et al.* (2011) for our study. The accessibility cost was measured as the time it takes to access to each cell of the study area from the closest town or city, which depends on the speed of movement on different landscape features, e.g., presence and quality of roads, land use, etc. The accessibility cost model incorporated information on road quality (five categories ranging from main paved roads—90 km/h average speed—to trails—20 km/h average speed), rivers (10 km/h average speed), land use (native forest, pine plantations, navigable areas, intensive agriculture, extensive pastures, small farms, and urban areas—with average speeds from 4 to 60 km/h), slope (slopes >20% reduce the speed in a half), and barriers (international borders—2 km/h) (see more details in De Angelo *et al.* 2011). The accessibility model used in our study assigned a higher accessibility cost to protected areas not included in the original model of De Angelo *et al.* (2011), making cells within their boundaries less accessible than those outside their limits (two to four times less accessible than other cells according to their protection level following IUCN categories from III to I, respectively). This correction was made taking into account that, because of their protection status, monkeys within parks and reserves may be far less vulnerable to anthropogenic disturbance than outside those areas. The other parameters and cost values used in our model were those described by De Angelo *et al.* (2011), using the same cell size (330 × 330 m) and procedure.

Data Collection

Between June and September 2010, I. Agostini and E. Pizzio spent a total of 46 days in the field, and surveyed the 31 selected transects for a total length of 151.3 km. We surveyed both protected and nonprotected areas within San Pedro and part of Guaraní Departments trying to cover fully the brown howler distribution and representing as far as possible the landscape heterogeneity. At each site, we walked together on a transect through a preexisting trail or path for an average length of 2.6 ± SD 0.8 km (range: 1.8–4.8). Surveys were repeated between one and three times (mean ± SD: 1.8 ± 0.8) per transect during the study period. We concentrated the survey effort only in the cold season (June–September 2010) to comply with the assumption of population closure of the patch occupancy single-season model and to avoid any potential seasonal variation in detectability due to changes in activity (MacKenzie *et al.* 2006). We walked each transect either in the morning [mean (± SD) start hour: 09:11 ± 00:53; end hour: 10:39 ± 00:43] or in the afternoon [mean (± SD) start hour: 14:47 ± 01:11; end hour: 16:00 ± 01:18], avoiding the midday hours when howlers are not usually active (Agostini *et al.* 2012b). We alternated morning and afternoon visits to the same site to control this possible source of heterogeneity. During each transect survey we walked slowly (*ca.* 1.5 km/h) to detect the presence of any primate species that could have been found in the study area. We detected presence either by direct observation (visual or unambiguous auditory contact) or by indirect evidence (remains of food eaten on the ground, e.g., pieces of bromeliad leaves consumed by black-horned capuchins that unambiguously indicate their presence; Brown and Zunino 1990).

During the same survey period, we conducted 55 semistructured interviews with local people (40% farmers, 14% loggers, 5% Guaraní indigenous inhabitants, and 41% park rangers) about the presence/absence of both species of howlers and black-horned capuchins, before and after the yellow fever outbreaks, in the region of interest. We used pictures of the three target species and pictures of monkey species not present in the region during the interviews to assess the reliability of the testimonies. The interviews were conducted in 33 areas distributed throughout our preestablished survey region, and included 7 protected areas and 26 nonprotected areas. The questions asked during interviews were: Have you seen/heard any of these monkey species in the area? If yes, can you tell which species it was? When was the last time you saw/heard each of these species? Where and how often have you seen/heard them? Have you found any dead monkeys during the yellow fever epidemic of 2008–2009? If yes, can you tell which species the corpse(s) belong(s) to? We asked these questions to determine for each primate species, locations where monkeys had always been absent, locations where monkeys had always been present, as well as sites where monkeys disappeared after the yellow fever outbreak.

Data Analysis

For capuchins, we pooled direct and indirect evidence of species presence collected during transect surveys. This could have led to a bias owing to differences in recording each type of evidence depending on transect width. However, the difference in the frequencies of direct and indirect evidence was not statistically significant for the two types of transects (trail vs. path) [$G = 1.14$, d.f. = 1, $P = 0.285$].

To evaluate if accessibility was related to the probability of presence of primate species in the landscape, we developed patch occupancy models that incorporated corrections for occupancy patterns based on presence–absence data when the probability of detection is <1 (MacKenzie *et al.* 2006). These models are used to explore the influence of different factors on the probability of occupancy and detectability of species. This method, when applied to single-species, single-season scenarios, entails the construction of a probability model in terms of occupancy and detectability based on a detection history built from data collected during repeated visits to sites. It then searches for the values of these parameters that make the observed data more likely (MacKenzie *et al.* 2006).

Human accessibility may affect both primate species occupancy and detectability. Animals may be relatively less prone to occupy or use a certain site when anthropogenic disturbance is high and, when they do, they may be more elusive and show avoidance behavior to minimize their exposure to risks associated with human activities, e.g., hunting. Because transect length varied across sites, we considered it as a further covariate for detectability: longer transects mean a greater survey effort, which may increase the probability of detecting a species when present at a site. Finally, the probability of detecting an individual may depend on the type of transect surveyed (path or trail), with more elusive individuals probably avoiding wide open transects compared to narrow trails. Thus, we evaluated the relationship between accessibility (whose values were based on the accessibility model described previously) and occupancy, and the relationship between accessibility, transect length, transect type, and detectability. We standardized the continuous covariates (accessibility and transect length) to Z values. We were able to develop these models only for black-horned capuchins (see Results). To reflect better the accessibility of each surveyed site, we estimated an average accessibility value for each transect taking into account a buffer area around it with a radius of 720 m, which is the radius of the average home range found for black-horned capuchins in Iguazú National Park (Di Bitetti 2001). We ran patch occupancy models using PRESENCE 3.1 (Hines 2006). We ranked models using the Akaike Information Criterion (AIC), and selected the models that better explained the observed data among those within 10% of the Akaike weight of the best model. We then examined the relative importance of individual factors using Akaike weights summed for all models in the set containing the covariate in question. Further, we assessed the goodness of fit of the most complex model using the MacKenzie and Bailey (2004) goodness-of-fit test run with 1000 bootstraps.

To evaluate the hypothesis that howler populations declined after the yellow fever outbreaks that occurred in the region in 2008–2009, we compared the encounter rate of groups (or individuals) of each *Alouatta* species in the present survey with the encounter rates obtained for the same species in a previous transect survey carried out in El Piñalito Provincial Park in 2005 (Agostini *et al.* 2010a), the only other encounter rate estimate of howlers in the region prior to the epidemic. To compare these two conditions, we evaluated the probability of obtaining a certain frequency of encounters assuming that the rate of group encounters is similar across areas and years and that the probability of encountering groups follows a Poisson distribution. A Poisson distribution is usually assumed for wild animal populations (Royle 2004). We tested this assumption. Based on the pattern of encounters with groups (on how many occasions we found 0, 1, 2, 3, etc. groups of howlers per transect surveyed) during the surveys conducted before the yellow fever epidemic at El Piñalito, we obtained an Index of Dispersion (variance/mean) of 0.79, which is close to 1, the value that would be expected for a Poisson distribution. Following Krebs (1989), we performed a chi-square test for the Index of Dispersion and then estimated 95% confidence intervals. Since our χ^2 value (=32.21) lay within the confidence interval, we accepted the null hypothesis of a random probability of howler group encounters, thus following a Poisson distribution. Finally, we calculated the expected frequencies for the comparison of encounter rates before and after the yellow fever outbreaks based on the frequency of group encounters obtained at El Piñalito in 2005.

For each primate species, we calculated the frequencies of sites in which the species was always absent, was always present, or was present but disappeared after the yellow fever outbreaks, in protected and nonprotected areas, according to the interviews. To determine whether interviewees indicated that there were differences in species status (presence–absence) between protected and nonprotected areas, we used the Fisher–Freeman–Halton exact test (Freeman and Halton 1951) for 2 × 3 contingency tables. To evaluate the hypothesis that the probability of disappearing after the yellow fever outbreaks was higher for howlers than for black-horned capuchins, we used the Fisher's exact test for 2 × 2 contingency tables. We used one-tailed statistical tests whenever predictions from our hypotheses were clearly directional, and indicated the relative *P*-values as "$P_{1\text{-tail}}$" in the results; otherwise we used two-tailed tests, with α set at 0.05. All statistical tests were performed with R (version 2.15.0, 2012-03-30, R Development Core Team 2012).

Ethical Note

All research reported in this article complied with the protocols approved by the Ethics Committee of SAREM, and adhered to the legal requirements of Argentina. All research protocols were reviewed and approved by the Ministry of Ecology and Natural Resources of Misiones Province.

Results

We found no direct or indirect signs of the presence of brown howlers or black-and-gold howlers in the study area. In contrast, we recorded 18 direct and indirect signs of presence of black-horned capuchins in 12 sites.

Because of the lack of encounters with howlers, we could run occupancy models only for black-horned capuchins. The naïve occupancy (Ψ), i.e., the observed proportion of sites occupied by black-horned capuchins, was 0.387. However, when including accessibility, transect length and type of transect as covariates for the detectability (p), the estimate obtained for Ψ increased to 0.819 (SE 0.116), and the estimates for p varied between 0.007 (SE 0.009) and 0.995 (SE 0.011). Including covariates that could affect occupancy (accessibility) and detectability (accessibility, transect length, and type of transect), we obtained 15 models in addition to the basic model [$\Psi(.)p(.)$] (which was the lowest ranked). Among these, we selected a confidence set of five candidate models (Table I). Three of these contained accessibility as a covariate for occupancy; four contained accessibility as a covariate also for detectability, three contained type of transect as a covariate for detectability, and all five models included transect length as a covariate for detectability. The top-ranking model included all of these covariates [AIC = 47.08 for Ψ (accessibility) p(accessibility, transect length, type of transect)]. Based on Akaike relative importance weights, we found that accessibility (64%) had a good support as an explanatory variable for occupancy, and accessibility (75%), transect length (95%), and type of transect (68%) had an even greater support as explanatory variables for detectability. Further, the best and most complicated model showed a very good fit [Ψ(accessibility) p(accessibility, transect length, type of transect): $\hat{c}$ = 1.001]; it adequately described the observed data (Table I).

As the highest ranked five models had all fairly similar AIC values (ΔAIC range: 0–1.77), we performed model averaging using Akaike weights to weight the parameter

Table I Summary of model selection procedure for occupancy estimates of black-horned capuchins (*Sapajus nigritus*) in central-eastern Misiones

Model	K	ΔAIC	w	$\hat{c}$
Ψ(ACC) p(ACC, TL, TT)	6	0.00	0.31	1.001
Ψ(ACC) p(TL, TT)	5	0.90	0.20	—
Ψ(.) p(ACC, TL, TT)	5	1.19	0.17	—
Ψ(.) p(ACC, TL)	4	1.59	0.14	—
Ψ(ACC) p(ACC, TL)	5	1.77	0.13	—
Ψ(.) p(.)	2	16.27	<0.01	—

The upper shaded part of the table shows the confidence set of five candidate highest-ranked models selected on the basis of the Akaike's Information Criterion (AIC) weights (within 10% of the highest). The basic model (without covariates), which is also the lowest ranked, is reported below for comparison

Ψ = occupancy probability; p = detection probability; ACC = accessibility cost considering protected areas as less accessible than nonprotected areas; TL = transect length; TT = transect type; K = number of parameters; ΔAIC = relative difference in AIC values from the model with the smallest AIC value; w = AIC model weight; $\hat{c}$ = estimated overdispersion parameter

estimates and variability, i.e., standard errors, from each model and combine them. The logit link parameter values obtained from the averaged model indicated that, as the cost of access increased, i.e., human accessibility decreases, the probability of capuchins occupying a site increased (β = 1.734), as did the probability of detection if present (β = 0.864), supporting our predictions. Further, as predicted, longer transects increased the probability of detecting capuchins (β = 2.346), while contrary to our predictions, wide paths increased the probability of detecting this primate species (β = 1.546). Although the AIC selection of high-ranking models showed the importance of all covariates, the one-sided 90% confidence intervals for averaged model estimates indicated that only transect length had a statistically significant effect (range: 0.856–∞). The larger confidence intervals that included zero found for the other covariates for occupancy and detectability were probably the result of the small sample size relative to the high number of covariates included in the models.

After extrapolating the averaged model (with accessibility as a covariate for occupancy, and accessibility, transect length and transect type as covariates for detectability) to all forest patches in Misiones province, we obtained a map of probability of occurrence for black-horned capuchins throughout their entire distribution in Argentina (Fig. 2). This map showed that, overall, the probability of occupancy for black-horned capuchins is relatively high (0.85–1.00) in the northern and central-eastern portions of Misiones, while this species is scarcely present in the southern portion of the province.

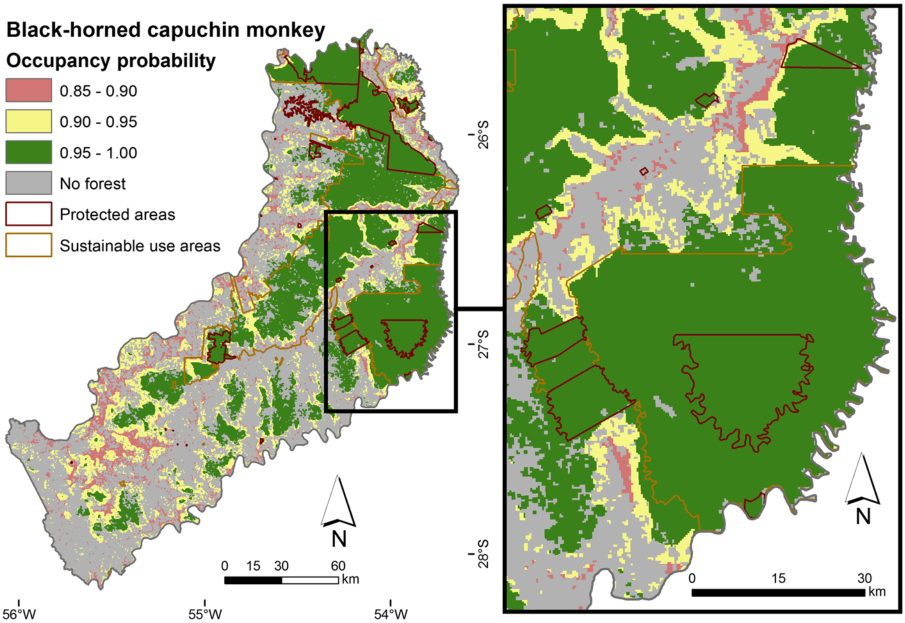

Fig. 2 Map of occupancy for black-horned capuchins in Misiones, Argentina, based on model averaging calculated from five AIC high-ranked models. The zoom square includes the area covered by the transect survey carried out between June and September 2010.

Based on the encounter rates recorded at El Piñalito Provincial Park in 2005, the expected Poisson probability of zero encounters with howlers of any species over the 151.3 km covered in this survey would be <0.01. Interviews showed that local people's knowledge about primate species status was far lower for nonprotected areas ("unknown": 37–42% of the areas, depending on species) compared to protected areas (0%; Fig. 3). According to the interviews, the species status (always present, always absent, or disappeared after the yellow fever outbreaks) was not significantly dependent on the site's protection status for any of the primate species (Fisher–Freeman–Halton's exact test: brown howler, d.f. = 2, P = 0.834; black-and-gold howler, d.f. = 2, P = 0.152; black-horned capuchin, d.f. = 2, P = 0.668; Fig. 3). Given that we did not find any difference according to the area's protection status, we pooled the frequencies across all areas and evaluated if howlers (*Alouatta* spp.) were more susceptible to the yellow fever outbreaks than capuchins. According to the interviews, the probability of disappearing after the epidemic outbreaks was significantly higher for howlers than for capuchins (Fisher's exact test: d.f. =1, $P_{1\text{-tail}}$ = 0.028). Moreover, interviewed people reported to have found dead corpses of brown howlers in three different locations and dead black-and-gold howlers in six locations, but no dead black-horned capuchins during the 2008–2009 yellow fever epidemic.

Discussion

Our study provides an update on the status and main threats of the three primate species of the province of Misiones, Argentina. The survey provides the first description of

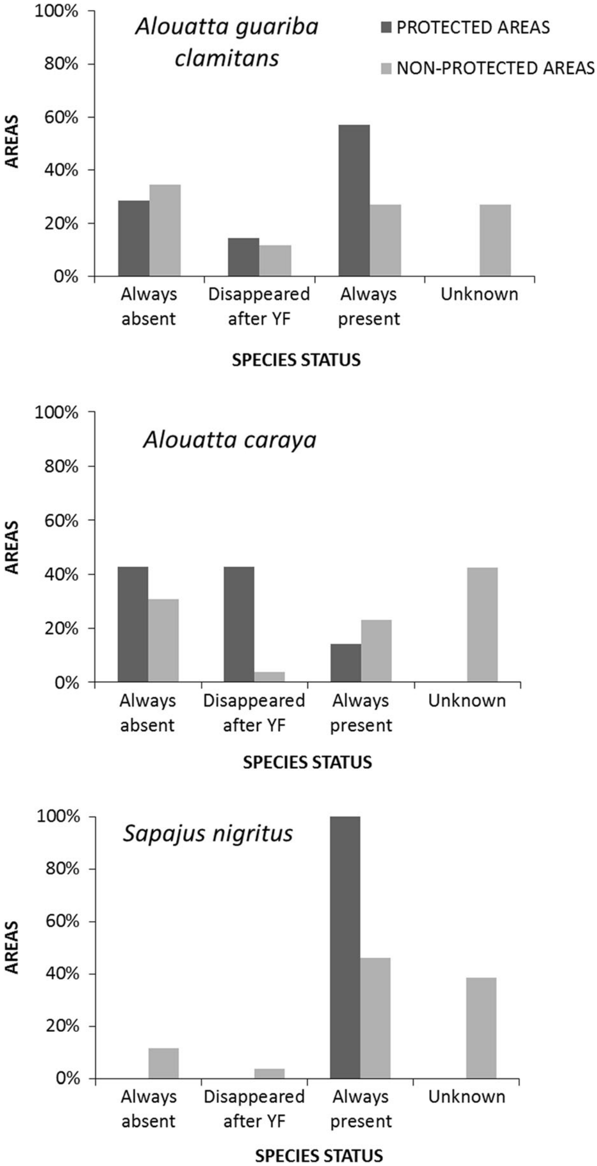

Fig. 3 Percentage of areas where interviewees classified each primate species as "always absent," "always present," "disappeared after the YF (yellow fever outbreaks)," or "unknown" status in protected ($N = 7$) and nonprotected areas ($N = 26$) between June and September 2010. The Yabotí Biosphere Reserve is included among nonprotected areas.

occupancy patterns of black-horned capuchins outside the protected areas in Misiones (Fig. 2), and results suggest that this species is indeed relatively susceptible to high degrees of anthropogenic disturbance. The inclusion of human accessibility as a covariate for both occupancy and detectability in the top ranked model and in the averaged model suggests that capuchins have a lower probability of occupying areas with high anthropogenic disturbance, and when they are present they tend to be elusive in more disturbed sites, e.g., forests located very close to roads or human settlements, compared to less disturbed ones, e.g., strictly protected areas. Although the extrapolation of our model to build the occupancy map demands cautiousness in interpreting patterns of unsampled areas of Misiones, we argue that higher probabilities of occupancy for capuchins in northern and central Misiones could be due, at least partially, to the higher degree of forest coverage, i.e., larger forest remnants, and protection compared to the southern portion of the province.

The forests of Misiones are being cleared to make room for agricultural activities, both by large companies that replace native trees with pine monocultures and small farmers for subsistence agricultural practices and cattle ranching (Izquierdo *et al.* 2008). The resulting proximity to human settlements increases the chances for opportunistic and adaptable primates such as capuchins to enter farms to raid crop such as corn, bringing them into close contact with farmers that may react negatively to their presence. Also, by providing increased access to hunters, progressive forest fragmentation can dramatically enhance the susceptibility of primates to hunting pressure (Fragaszy *et al.* 2004). In Misiones, capuchins are known to raid corn crops (Massoia *et al.* 2006) and have been frequently reported to damage young pine plantations (Agostini *pers. obs.*) as they do in nearby Brazilian plantations (Mikich and Liebsch 2014). This eventually leads small farmers to shoot individuals that approach their lands (Massoia *et al.* 2006). Further, although it is not among the most widely consumed prey, black-horned capuchins may be hunted by native Guaraní populations for their meat (Di Bitetti 2003), and infants are captured to be kept as pets among indigenous communities (Massoia *et al.* 2006; C. Maciel *pers. comm.*). While flexible habitat preferences and feeding ecology have helped black-horned capuchins maintain their presence through a large portion of Misiones, all of these factors suggest that forest destruction and agricultural encroachment represent a serious threat for the species. It is likely that the predictable spread and increasing intensity of human activities in this region will negatively affect the conservation status of black-horned capuchins in Misiones in the next few decades, and their population may become fragmented and restricted to the protected areas.

Although occupancy models were run only for black-horned capuchins, the data obtained through interviews helped to highlight the critical situation of both howler species in Misiones. The difference in levels of local acquaintance with the species between protected and nonprotected areas suggests that park rangers, who are responsible for patrolling parks and reserves and were the most frequently interviewed people within protected areas, have a much deeper knowledge of landscape and wildlife compared to other local inhabitants outside protected areas. Farmers, who were the most frequently interviewed people outside the protected areas, may not pay particular attention to the species inhabiting the forest portion of their land unless they represent a pest for their crop or a predator for their cattle. Guaraní people and loggers are probably an exception because their living habits may bring them in closer contact with wildlife, but they constituted only a small part of the interviewees.

Results of the interviews indicate a greater susceptibility of howlers to yellow fever compared to black-horned capuchins. It is known that *Cebus* and *Sapajus* spp. are easily infected by the yellow fever virus but show low fatality rates and generally acquire immunity (Kumm and Laemmert 1950; Strode 1951). During the outbreaks that occurred in 2008–2009 in Misiones, no suspected deaths attributable to yellow fever were recorded for *Sapajus nigritus*, and one group of this species was observed during the first days of the epizootic alert when a thorough search was conducted at El Piñalito Provincial Park in January 2008 (Holzmann *et al*. 2010).

In contrast, *Alouatta* spp. are highly susceptible to yellow fever and when infected with minimum doses of the virus they rapidly develop clinical symptoms of the disease and die (Strode 1951). During the 2008–2009 yellow fever outbreaks, 59 howlers of both species were found dead in Misiones and a minimum of 83 casualties were estimated for the province (Holzmann *et al*. 2010). People interviewed during our surveys indicated that both howler species disappeared after the yellow fever outbreaks in 18% of the areas where they have been recorded previously. We found no direct or indirect evidence of howlers during our surveys. Although this could be partly explained by the cryptic nature of howlers, the chances of obtaining no record over the distance surveyed was extremely low on the basis of pre–yellow fever encounter rates for El Piñalito. This suggests that, assuming that the density of howlers before the yellow fever epidemic was fairly homogeneous across their distribution range and thus comparable between El Piñalito and other surveyed areas, the abundance of both *Alouatta* populations has heavily dropped after the outbreaks.

Given its initial small size, we consider the remnant brown howler population now to be seriously endangered and at risk of disappearing from Misiones in the next few decades due to the increasing habitat loss and recurrent yellow fever outbreaks. To establish conservation priorities for this species and its habitat in Argentina, assessments of the current brown howler monkey status, the main threats faced by this species, and potential management alternatives are being tackled with the objective of developing a species conservation strategy in the near future (Agostini *et al*. 2014).

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